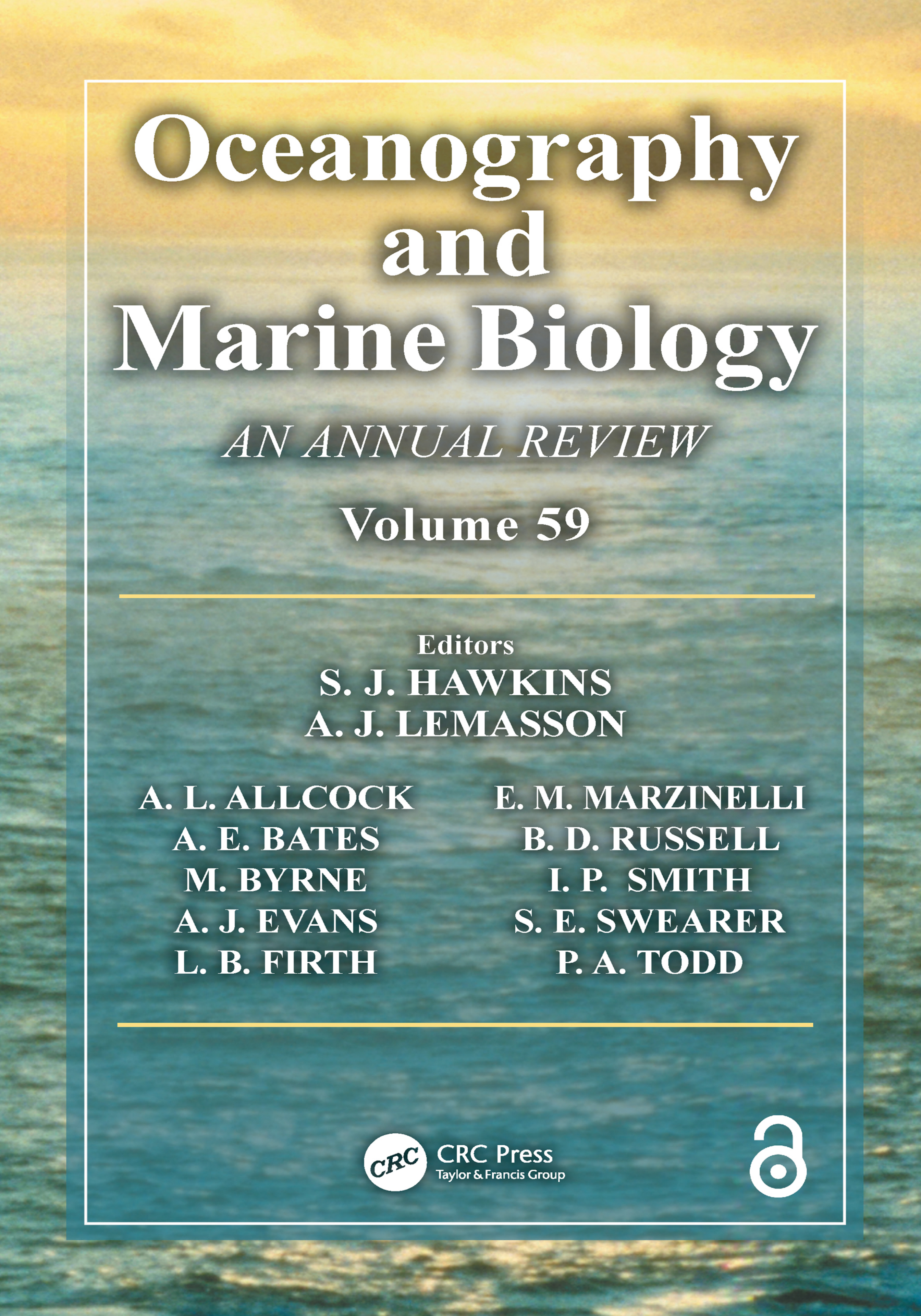

Oceanography and Marine Biology

AN ANNUAL REVIEW

Volume 59

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Preface

Oceanography and Marine Biology: An Annual Review remains one of the most cited sources in marine science and oceanography. The ever-increasing interest in work in oceanography and marine biology and its relevance to global environmental issues, especially global climate change and its interaction with other impacts, creates a demand for authoritative refereed reviews summarizing and synthesizing the results of recent research. If you are interested in submitting a review for consideration for publication in OMBAR, please email a provisional title and brief topic outline to the Editor-in-Chief, Prof. Stephen Hawkins, at S.J.Hawkins@soton.ac.uk. For nearly 60 years, OMBAR has been an essential reference for research workers and students in all fields of marine science. This volume considers such diverse topics as the phylogeography of marine mussels, the Great Barrier Reef Expedition of 1928–29, Mediterranean marine caves, macromedusae in eastern boundary currents, marine biodiversity in Korea, epifaunal assemblages, phase shifts in subtidal communities, responses of copepods to climate change and development of a geo-ecological carbonate reef system model to predict responses of reefs to climate change. Seven of the nine peer-reviewed contributions in Volume 59 (1, 2, 3, 4, 5, 6, 7 and 9) are available to read as Open Access PDF under a Creative Commons Attribution-Non Commercial-No Derivatives 4.0 license. The links can be found on the book's Routledge web page at https://www.routledge.com/book/9780367685225. An international Editorial Board ensures global relevance by commissioning reviews and guiding expert peer review, with editors from Australia, Canada, Hong Kong, Ireland, Singapore, and the United Kingdom. The volumes of this series find a place in the libraries of not only marine laboratories and oceanographic institutes, but also universities worldwide. The editors thank the hard work of the referees in improving these reviews. We also wish to acknowledge the help and support of the team at Taylor & Francis (Alice Oven, Damanpreet Kaur, and Marsha Hecht) and codeMantra (Sathya Devi).

Prof. Stephen J. Hawkins
(Editor-in-Chief) on behalf of the Editorial Board

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MEDITERRANEAN MARINE CAVES: A SYNTHESIS OF CURRENT KNOWLEDGE

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Abstract Marine caves are biodiversity reservoirs and refuge habitats, harbouring rare species and living fossils. The Mediterranean Sea hosts more than 3000 caves, which are among the most studied in the world. This review aims to synthesize and update knowledge of Mediterranean marine caves. Their biota includes few obligate cave-dwelling organisms, but many cryptobiotic or crevicular (crevice-dwelling) and bathyphilic (preferring deep-water) species that secondarily colonize caves. A total of 2369 taxa have been reported from 404 caves in 15 countries, with several species new to science described in recent decades. Dramatic environmental gradients generate a zonation of the biota, with up to six faunal zones and two main biocoenoses. Biotic cover and biomass are strongly reduced inside caves, due to hydrological confinement and trophic depletion. The food web is based on suspension-feeders, but motile carnivores play a role in the importation of organic matter from outside. Lack of primary production, faunal affinities and microbial metabolism make marine caves readily accessible models of deep ocean ecosystems. Future research should focus on filling regional (e.g. south-eastern Mediterranean) and thematic (e.g. microbes, meiofauna, macro-infauna) gaps in fundamental knowledge, and on management measures. Marine caves have low ecological resilience and harbour many species of conservation interest, but are threatened by seawater warming, local human impacts and non-indigenous species.

Keywords: Marine Caves; Benthic Habitats; Biodiversity; Conservation; Mediterranean Sea

Introduction

Rocky reefs, coastal cliffs and coral reefs around the world harbour cavities of various sizes at or below sea level, and therefore contain marine water (Colantoni 1978). These ‘marine caves’ are a quantitatively trivial fraction of the marine environment but hold a great scientific and ecological importance, as they represent a major reservoir of marine biodiversity (Gerovasileiou & Voultsiadou 2012, Gerovasileiou et al. 2016a) and provide ecosystem services to humans (Salomidi et al. 2012).

Land caves have played a major role in the life and evolution of humans: over the centuries, they have offered shelter to humans and their domestic animals, and have been important for religion and culture; today, they provide opportunities for sport adventures, with research and scientific knowledge fostered by these activities. On the contrary, marine caves began to be explored much later and explicitly for scientific reasons. After early attempts in the eighteenth century, when the Italian

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naturalist Filippo Cavolini reached submerged caves near Sorrento (Bay of Naples, Italy) with the aid of rudimentary equipment (Bianchi & Morri 2000), the scientific community addressed the study of marine caves especially in the middle of the twentieth century, motivated by the expectation of extraordinary new findings: “we will show you … things you did not even dream about” (Riedl 1978). The ensuing discovery of the many peculiarities and the natural heritage value of marine caves gave birth to the awareness of the need for their conservation, as they turned out to be unique and vulnerable habitats threatened by multiple global and local pressures (Montefalcone et al. 2018). The first instances of protection date back to the 1970s (Sarà 1974, 1978) but only recently have led to concrete initiatives (at least in Europe and the Mediterranean) by the Habitats Directive of the European Union and by the Mediterranean Action Plan of the United Nations Environment Programme. About two-thirds of the Mediterranean marine protected areas include marine caves (Abdulla et al. 2008).

The rocky coasts of the Mediterranean Sea are particularly rich in marine caves (Hofrichter 2002, Giakoumi et al. 2013), whose geology, biology and ecology have been studied with continuity for several decades (Riedl 1966, Cattaneo & Pastorino 1974, Harmelin et al. 1985, Bianchi et al. 1996, Cicogna et al. 2003, Gerovasileiou et al. 2015a). Environmental issues about Mediterranean marine caves have been recently tackled to evaluate their health status (Rastorgueff et al. 2015a) and to evidence threats (Gerovasileiou et al. 2016b, Nepote et al. 2017, Montefalcone et al. 2018). Thus, Mediterranean marine caves are perhaps the best known of the world ocean (Gerovasileiou & Voultsiadou 2016) and may offer paradigms and theory to students of marine caves from other geographic regions.

This review aims to synthesize and update existing knowledge about Mediterranean marine caves, to evaluate the current scientific knowledge and to illustrate the need for the protection of, and research on, these habitats: only a small number of caves have been explored and, mostly, in a superficial and incomplete manner, while it is likely that many caves are as yet undiscovered. We largely based our review on previous reviews, often written in language other than English (e.g. German: Riedl 1966, French: Harmelin et al. 1985; Italian: Bianchi et al. 1996; Greek: Gerovasileiou 2014) and therefore less accessible to the international audience. Recent additions have been possible thanks to a large number of publications dispersed in various scientific journals and in the grey literature, and to a recent Turkish volume (Öztürk 2019). The bulk of our text derives, with modification, from a desktop study prepared for the Regional Activity Centre for Specially Protected Areas of the United Nation Environment Programme Mediterranean Action Plan (Gerovasileiou & Bianchi 2020).

Marine caves and cave biota

The term ‘cave’ is commonly used to describe an opening into a natural underground or underwater hollow, which is large enough for a human to enter (Gunn 2004, Romero 2009). Caves can be horizontal, vertical or a combination of both, and their long dimension (i.e. length or depth) is greater than the cross-sectional dimensions at the entrance (Gunn 2004, Gerovasileiou et al. 2016a). They are formed by different processes in various rock types, such as dissolution of bedrock by water circulating through fissures and pores (‘solution’ or ‘karsts’ caves), fracturing, differential non-dissolution erosion, lava tubes and talus caves among rock falls. In marine caves (also known as ‘littoral’ or ‘sea caves’), the mechanical action by the waves may also be important (Riedl 1966, Colantoni 1978, 1994, Gunn 2004). Thus, different classification schemes and terminologies exist with regard to their origin and formation process (speleogenesis), type of host rock and water regime, while local terms exist in several cases (e.g. ‘Vrulja’ in Croatia for underground streams discharging below sea level – see Surić et al. 2010). Bianchi et al. (1996) defined ‘marine cave’ as a cavity of various origins, entirely or partly occupied by the sea, accessible to humans, which has significant horizontal and volumetric development: a possible criterion is that the ratio between the numbers expressing the total volume (in m^3) and the entrance area (in m^2) must be greater than 1, and that the width of the entry must not exceed the internal average.

A standard glossary, based on existing terminology for marine cave systems and their biota, has recently been developed by the Editorial Team of the World Register of marine Cave Species (WoRCS) database (see Gerovasileiou et al. 2016a, 2020). Marine caves belong to several types (Figure 1). They can be assigned to two main categories according to their submersion level: 'submerged', completely below the water level; and 'semi-submerged', extending above and below the sea surface, and thus more exposed to and affected by sea-surface dynamics. Cave morphology can also be variable, with the most conspicuous types being blind-ended caves (ending as a cul-de-sac), tunnels (opening to entrances at two or more ends), pits (vertical caves with negligible horizontal passages) or more complex morphologies, consisting of arrays of intersecting passageways that form distinctive patterns (Riedl 1966, Palmer 1991, Field 1999, Hofrichter 2002, Gerovasileiou et al. 2016a). The term 'anchialine' or 'anchihaline' derives from the Greek word '*άγχίαλος*' (= near the sea) and is used to characterize environments that are supplied with saline or brackish groundwater of marine origin, through an underground connection to the sea (Stock et al. 1986, Gerovasileiou et al. 2016a). The marine 'marginal caves' ('Randhöhlen' in Riedl 1966 and Riedl & Ozretić 1969), which are also characterized by a subterranean connection to the sea and contain mixohaline water bodies, fall within the category of anchialine caves (Stock et al. 1986, Bianchi et al. 1996).

Cave biota can be assigned to four main ecological categories (Delamare Deboutteville 1971, Culver & Pipan 2009, Romero 2009, Culver & White 2012, Gerovasileiou et al. 2016a,

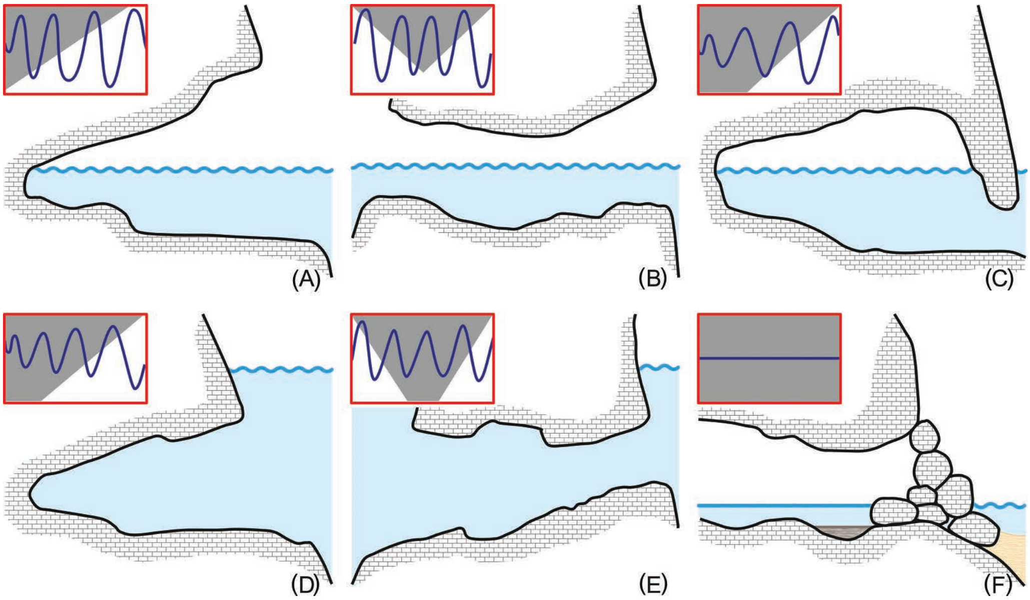

Figure 1 Basic morphological types of marine caves (in the broad sense): (A) semi-submerged blind-ended (cul-de-sac) cave; (B) semi-submerged tunnel; (C) cave with air dome; (D) submerged blind-ended cave; (E) submerged tunnel; and (F) marginal cave. Complex caves may show a combination of two or more basic types. Upper left boxes schematize the patterns of light penetration (white portions with respect to grey portions) and water movement (sinusoidal curves) inside the different types of cave. Redrawn and modified from Riedl (1966) and Hofrichter (2002).

Lunghi & Manenti 2020): ‘troglobionts’ or ‘stygobionts’ (cave-exclusives *sensu lato*), which are obligatory cavernicoles, adapted to subterranean life (e.g. by loss of pigmentation and vision); ‘troglophiles’ or ‘stygophiles’, which can live and complete their life cycle within caves, but can also be found in suitable habitats outside caves (e.g. undersides of rocks, deep waters); ‘trogloxenes’ or ‘stygoxenes’, which occur in caves, but do not complete their life cycle within caves, and periodically move outside (e.g. finding shelter within caves during daytime but leaving to forage in nearby habitats during night); ‘accidental’ (or random visitors), which may enter caves by chance (e.g. advected by currents), but can only survive in this environment for short periods of time. The prefix ‘troglo-’ should be preferred for subterranean species and ‘stygo-’ for the aquatic cave biota.

In contrast to terrestrial and anchialine caves, marine caves *sensu stricto* are not sufficiently isolated from the external environment due to the continuity of the aqueous medium (Bianchi et al. 1996). Thus, the majority of species recorded in marine caves could be characterized as stygophiles (e.g. sponges and bryozoans which also occur in dim-light environments outside caves, such as coralligenous reefs and deep waters) or stygoxenes (e.g. crustaceans and fishes exhibiting diel, also known as nychthemeral, movements into and out of caves for feeding) (Riedl 1966, Harmelin et al. 1985, Balduzzi et al. 1989, Bianchi et al. 1996, Bussotti et al. 2018). This dominance of ‘cryptobiotic’ or ‘crevicular’ (i.e. preferring cryptic habitats such as rock crevices) and ‘bathyphilic’ species in marine caves is at the root of the concept of ‘secondary troglobiosis’ (Cattaneo & Pastorino 1974) or, better, ‘secondary stygobiosis’, since these species originate from external marine environments (such as coralligenous reefs, deep rocks and small hard substrata dispersed in detrital infralittoral and circalittoral bottoms) but are commonly found in marine caves (Figure 2), and therefore become characteristic of this habitat only secondarily (Iliffe 1990). Nonetheless, a considerable number of taxa have not been – at least yet – reported from habitats other than caves and thus can be considered as exclusive to caves in the broad sense: future research, for instance in cryptic and deep-sea habitats, might show that some of these species occur in other habitats (Gerovasileiou & Voultsiadou 2012). Since the 1980s, the scientific exploration of underwater caves, and especially those of the

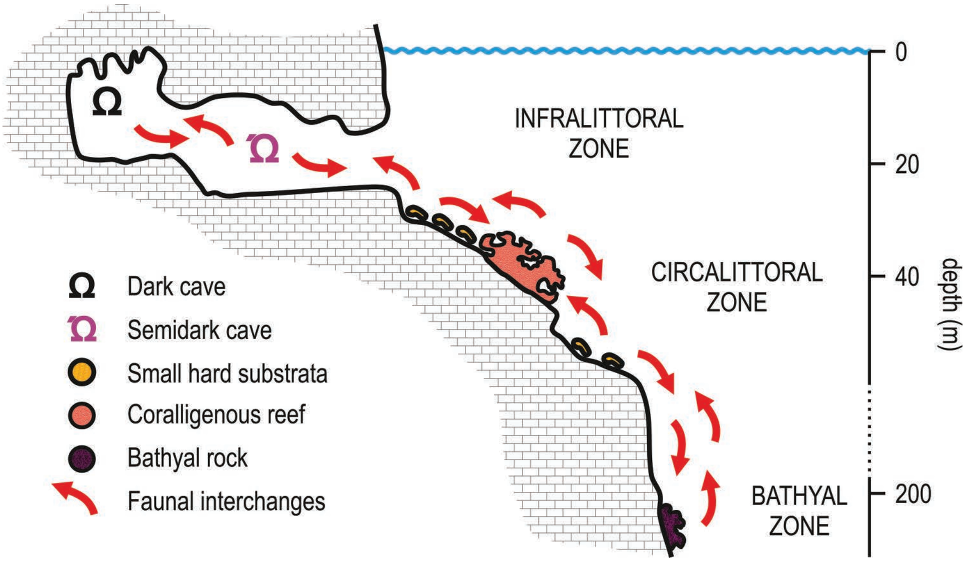

Figure 2 A schematic representation of the faunal interchanges between marine caves and the external environments, allowing cryptobiotic/crevicular and bathyphilic species to colonize the caves (secondary stygobiosis) and providing opportunity for cave species to disperse. Redrawn and modified from Harmelin (1986) and Bianchi et al. (1996).

anchialine type, has led to outstanding discoveries of novel taxa that exhibit unique adaptations to cave life (Iliffe et al. 1983, Stock 1994, Iliffe & Kornicker 2009, Gerovasileiou et al. 2016a and references therein). It is possible that some of these taxa are the result of ecological specialization from generalists that penetrated caves from external environments in the past, including 'relict species' or palaeoendemics, e.g. remnants of the (sub)tropical fauna that thrived in the Mediterranean Sea during warm periods of its history (Bianchi et al. 2012b) and found refuge and survived in cave habitats (Harmelin et al. 1985, Pérez et al. 2004). Major examples include the brachiopod *Tethyrynchia mediterranea* (Logan et al. 2004) and the serpulid *Marifugia cavatica* (Bianchi & Sanfilippo 2003).

Distribution

Rock constitutes more than half (54%) of the Mediterranean coastline (Stewart & Morhange 2009), limestone being one of the most common types (Lewin & Woodward 2009). Through time, the ongoing geological processes (e.g. karstic phenomena) in this semi-enclosed sea have resulted in the formation of a large number of more or less complex marine and anchialine cave systems (Gerovasileiou & Voultsiadou 2012). According to the latest inventory by Giakoumi et al. (2013) and the present study (Figure 3), there are more than 3000 marine caves in the Mediterranean, the majority of which are located in the eastern Adriatic, Aegean, Tyrrhenian, Provençal and Ionian coasts (Table 1), where they are sometimes densely concentrated in islands and rocky peninsulas (e.g. Aegean Archipelago, Croatian and Balearic islands, Corsica and Sardinia, Sorrentine Peninsula, Cape Palinuro, Salento).

At local or regional scales, there has been detailed mapping of marine caves in Italy (Cicogna et al. 2003), Corsica (Anonymous 2010), Croatia (Surić et al. 2010) and Greece (Sini et al. 2017). In addition, recent expeditions and baseline studies in the framework of the research projects MedKeyHabitats, MedMPAnet and LIFE BaĦAR for N2K have provided valuable information on the distribution of marine caves, their biodiversity and impending threats in previously understudied regions of the Mediterranean Sea. For example, a number of caves, tunnels and numerous

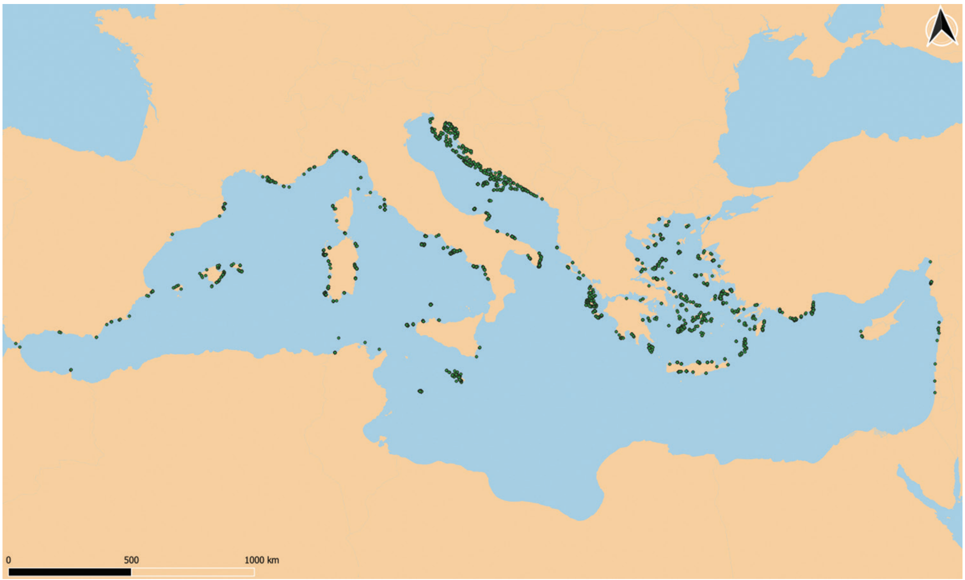

Figure 3 Distribution of known marine caves (green dots) in the Mediterranean Sea (based on data from Giakoumi et al. 2013, Sini et al. 2017 and LIFE BaĦAR for N2K project – LIFE12 NAT/MT/000845). Note the scarcity of data from the southern coasts.

Table 1 Number of marine caves recorded by Mediterranean ecoregion

Mediterranean ecoregion	Number of marine caves
Alboran Sea	24
Algero-Provençal Basin	459
Tyrrhenian Sea	581
Tunisian Plateau/Gulf of Sidra	141
Adriatic Sea	708
Ionian Sea	307
Aegean Sea	622
Levantine Sea	209

Sources: Giakoumi et al. (2013), Sini et al. (2017), LIFE BaĦAR for N2K project (LIFE12 NAT/MT/000845) and new data from this study.

small caverns were recorded in Cap des Trois Fourches and Jbel Moussa, in Morocco (Bazairi et al. 2012, 2013, 2016, Anonymous 2014) and in the island of Rachgoun, in Algeria (Ramos Esplá et al. 2016). In Lebanon, Raoucheh Cave and other caves in Ras Chekaa and Naqoura regions were studied within MedMPAnet project (Ramos-Esplá et al. 2012, 2013, 2014). Within MedMPAnet and MedKeyHabitats projects, marine caves were also recorded and studied in the Adriatic Sea: small midlittoral caves in Albania (Kashta et al. 2013) and large marine caves in the Platamuni region of Montenegro (Torchia et al. 2016a,b, Mačić et al. 2019). In Malta and Gozo Islands, the project LIFE BaĦAR for N2K shed light on numerous marine caves and tunnels (37 semi- and 52 fully submerged caves) of various sizes and depth, as well as 17 deep-water caves between 205 m and 795 m (Borg et al. 2017). A considerable number of marine caves from the Aegean and Levantine coasts of Turkey were described in a publication by the Turkish Marine Research Foundation (Öztürk 2019). The above projects and baseline studies have greatly contributed to filling regional gaps of knowledge from previously understudied marine regions and led to the proposal or even the establishment of new marine protected areas.

Given the logistic constraints involved in finding and surveying marine caves, especially the fully submerged ones, their number is assumed to be much higher at both Mediterranean and local scales, and mapping efforts are required in order to fill current distribution gaps in the eastern and southern Mediterranean regions. Detailed guidelines for compiling inventories of dark habitats, including marine caves, have recently been provided by Gerovasileiou et al. (2017a).

Most existing marine cave records correspond to shallow and/or semi-submerged caves, with a water depth that rarely exceeds 15 m, as they are generally easier to detect and access by both scientists and recreational divers. Information about deeper caves is limited, with only a small number of marine caves studied for their biota in the depth range 15–40 m (Gerovasileiou & Voultsiadou 2012, Canessa et al. 2014). However, bathymetric data are lacking in several cases. The recent study of deeper areas with the use of Remotely Operated Vehicles (ROVs) has shown that hard substrata in deeper waters can also have large overhangs and cavities. For instance, deep-water caves and large overhangs have recently been discovered in the Linosa Trough (Freiwald et al. 2009) and west of Gozo, at depths of 270–795 m, possibly dating back to the Messinian, ~5.96–5.33 Ma (Evans et al. 2016, Borg et al. 2017). However, their study is logistically difficult and constitutes a challenge for future explorations.

The biological study of Mediterranean marine caves

In contrast to terrestrial caves, their marine counterparts remained virtually unexplored until the second half of the twentieth century. Their study became possible only after the development of autonomous diving, which allowed not only cave exploration but also direct observation and sampling by marine scientists (Laborel 1960, Vacelet 1967, Riedl 1978, Cattaneo-Vietti & Mojetta 2021). Technological advances in autonomous diving, from the development of the first reliable open-circuit self-contained underwater breathing apparatus in 1942–1943 (Drach 1948) to the modern closed-circuit rebreathers (Iliffe & Bowen 2001), have facilitated underwater cave research and revealed unique fauna (e.g. Jaume & Boxshall 2005, Iliffe & Kornicker 2009).

In the Mediterranean basin, the first thorough studies of marine caves and their biota were conducted by French (Pérès & Picard 1949, 1955, Corroy et al. 1958, Laborel & Vacelet 1958, 1959), Austrian (Starmühlner 1955a,b, Abel 1959, Banse 1959, Riedl 1959a,b,c,d,e,f, 1966, Russ & Rützler 1959, Rützler 1965, etc.) and Italian scientists (e.g. Sarà 1958, 1959a, 1961a,b, 1962, 1968, 1974, 1978, Cattaneo & Pastorino 1974, Cinelli et al. 1977, Cantone et al. 1979), followed by contributions from Spanish scientists in the 1980s (Bibiloni & Gili 1982, Gili et al. 1982, 1986, Bibiloni et al. 1984), and by Croatian scientists since 2000 (e.g. Arko-Pijevac et al. 2001, Bakran-Petricioli et al. 2007, 2012, Radolović et al. 2015, Petricioli & Bakran-Petricioli 2019). Studies of marine caves in the eastern Mediterranean were published more recently by Greek (Gerovasileiou 2014, Gerovasileiou et al. 2015a and references therein, Gerovasileiou & Voultsiadou 2016, Gerovasileiou et al. 2017b, Dimarchopoulou et al. 2018) and Turkish scientists (Öztürk 2019), with contributions also from Cyprus (Guido et al. 2017a, Jimenez et al. 2019) and Lebanon (Pérez et al. 2004, Ramos-Esplá et al. 2012, Castelló et al. 2020).

A major landmark in the history of Mediterranean marine cave research was the publication of the book *Biologie der Meereshöhlen* by the Austrian zoologist Rupert Riedl (1966), which provided the first synthesis of existing knowledge acquired in the 1950s and 1960s. Much of the information came from the 'Tyrrhenia-Expedition', which started in 1952 and focused on marine caves in the region of Naples, Italy. Subsequently, important reviews about the biology of marine caves were published in France (Harmelin et al. 1985), Italy (Bianchi 1994, 2003, Bianchi et al. 1996, Cicogna et al. 2003) and the eastern Mediterranean Sea (Gerovasileiou et al. 2015a), while Gerovasileiou & Voultsiadou (2012) and Bussotti et al. (2015) provided overviews of the sponge and fish fauna of marine caves, respectively, at the Mediterranean scale.

Taxonomic studies

The first approach to the biological study of marine caves – as of other habitats – was undoubtedly a taxonomic one, an indispensable step to conduct any other type of ecological investigation. From the very first stages of marine cave research, it became evident that this peculiar habitat harbours several previously undescribed species (Sarà 1958, 1959b, Vacelet & Lévi 1958, Vacelet 1959, Sarà & Siribelli 1960, Rützler & Sarà 1962). Until today, studies in Mediterranean marine and anchialine caves are continuously bringing to light new species from various taxonomic groups: Porifera (Vacelet & Boury-Esnault 1982, 1996, Pulitzer-Finali 1983, Pansini 1984, 1996, Voultsiadou-Koukoura & Van Soest 1991, Voultsiadou-Koukoura et al. 1991, Bibiloni 1993, Boury-Esnault et al. 1995, Corriero et al. 1996, 1997a, Bavestrello et al. 1997, Muricy et al. 1998, Pansini & Pesce 1998, Vacelet & Pérez 1998, Vacelet et al. 2000, 2007, Manconi et al. 2006, Pérez et al. 2011, Pisera & Vacelet 2011, Reveillaud et al. 2012, Melis et al. 2016, Lage et al. 2018, 2019), Priapulida (Todaro & Shirley 2003), Gastrotricha (Fregni et al. 1998), Copepoda (Riera et al. 1991, Carola & Razouls 1996, Jaume & Boxshall 1996, Jaume 1997, Jaume et al. 1999, Krsinic 2005), Decapoda (Pretus 1990, Fransen 1991), Mysida (Alcaraz et al. 1986, Wittmann 2004), Thermosbaenacea (Wagner & Chevaldonné 2020), Polychaeta (Zibrowius 1968, Fassari & Mòllica 1991), Gastropoda (Warén et al. 1997, Palazzi & Villari 2001, Crocetta et al. 2020), Bivalvia (La Perna 1998, 1999), Tardigrada (Villora-Moreno 1996), Bryozoa (Hayward 1974, Silén & Harmelin 1976, Harmelin et al. 2007, Rosso et al. 2020a), Brachiopoda (Logan & Zibrowius 1994), Chaetognatha (Casanova 1986) and Pisces (Kovačić 1999).

Moreover, the study of marine cave biota revealed that these habitats harbour ‘living fossils’ (Vacelet & Lévi 1958, Pérez et al. 2004, Manconi & Serusi 2008) and deep-water species (Pouliquen 1969, Vacelet et al. 1994, Harmelin 1997, Harmelin & Vacelet 1997, Rosso et al. 2013a, Pisera & Gerovasileiou 2021), triggering further taxonomic and ecological studies. In addition to the biodiversity inventories, the notable small-scale environmental gradients in marine caves, as well as their influence on the spatial variability of biota, became a subject of research from the first pioneer bionomic studies until today.

Bionomic descriptions

In most English dictionaries, bionomy (or bionomics), from the Greek ‘*βίος*’, life, and ‘*νόμος*’, law, is synonymous with ecology. In the tradition of Mediterranean ecology, however, bionomy refers specifically to the part of ecology that studies the distribution of organisms and their assemblages along ecological gradients to identify zones and to understand the link between habitats and species (Bianchi et al. 2012a).

The typology and distribution of benthic communities in Mediterranean marine caves has been mostly studied by French, Austrian and Italian scientists. The first description of the marine cave communities was published by Pérès & Picard (1949), who studied Niolon Cave (Marseille region, France) and noticed that macroalgae (mostly Rhodophyta), which dominated at the cave entrance, were gradually replaced by sessile animals inwards (up to 90% of the wall surface cover) due to the decrease of light. In addition, despite the shallow depth of this cave (6–12 m), some species which usually develop in deeper waters were present. Some years later, in their first bionomic descriptions from the north-western Mediterranean basin, Pérès & Picard (1955) described a type of coralligenous biocoenosis developing in marine caves under the name ‘coralligène de grotte’. At this time, marine cave communities were characterized as an ‘impoverished aspect’ of the coralligenous biocoenosis while the differentiation of their fauna was attributed to the reduction of water movement and light and the development of a black coating of ferromanganese oxides on the rocky walls of their inner reaches (Vacelet 1964). The occurrence of ferromanganese oxides in dark marine caves recalls the formation of metallic nodules in deep oceanic sediments under aphotic conditions (Pérès 1967). Bianchi et al. (1986) and Allouc & Harmelin (2001) studied in detail the structure of this coating in marine caves of north-western Italy and south France, respectively.

The clear distinction of the marine cave biocoenoses from the coralligenous was based on the dominance of sessile animals versus macroalgae (Vacelet 1959, Laborel 1960, 1961). Vacelet (1959) reported that at the cave entrance, a transitional community between the photophilic algae and the coralligenous biocoenosis (also known as ‘precoralligenous’) can develop. However, according to Laborel (1961) coralligenous concretions are not the most characteristic feature of marine cave communities, which are dominated by sessile animals, *Corallium rubrum* being the most typical species. Therefore, Laborel & Vacelet (1959) described two successive assemblages that develop in marine caves along a decreasing light gradient: a transitional dim-light zone, where biotic cover decreases from 100% (at the outer zone) to 50%, with the most characteristic taxa being sponges and scleractinian corals; and a completely dark zone, dominated by serpulid polychaetes, sponges and scleractinians and where biotic cover decreases to 20% or less.

A few years later, the influential *Nouveau Manuel de Bionomie Benthique* by Pérès & Picard (1964; see also Pérès 1967), which summarized and updated the existing knowledge on Mediterranean benthic communities, described three distinct biocoenoses developing along the horizontal cave axis: the coralligenous biocoenosis (biocénose coralligène – C), which can often develop at the cave entrance; the semidark cave biocoenosis (biocénose des grottes semi-obscures – GSO), which – in the virtual absence of macroalgae – is dominated by sponges and anthozoans; and the biocoenosis of caves and dead-end passages in total darkness (biocénose des grottes et boyaux à obscurité totale – GO), which is characterized by sponges, serpulid polychaetes and motile crustaceans. Pérès (1967) highlighted that the coralligenous biocoenosis can develop both outside and inside marine caves, while several species of the semidark cave biocoenosis can be found as 'enclaves' in dark holes and crevices of the coralligenous formations. The presence of coralligenous assemblages at the entrance of submarine caves has been reported from several Mediterranean regions (e.g. Ballesteros 2006, Kipson et al. 2011, Teixidó et al. 2011, Gerovasileiou et al. 2017b).

Riedl (1966) studied marine caves with various morphologies in the Tyrrhenian Sea (Gulf of Naples) and the Adriatic coasts (Croatia), and suggested a different scheme of biological zonation, based on the distribution of hydroids, macroalgae and other taxa. Riedl's zonation scheme is typical of blind-ended caves but may not apply to marine caves with different shape. The boundaries and extent of the different zones depend on the topographic features of each cave (e.g. entrance width-to-cave length ratio, substratum inclination at the cave entrance and number of entrances), which affect light gradients and water exchange within the cave. For instance, zones generally tend to shift outwards with increasing depth, while some zones could be absent from tunnels with multiple entrances which receive more sunlight and are characterized by a higher hydrodynamic regime. Therefore, even neighbouring marine caves could exhibit biotic heterogeneity due to their different morphology and cave-specific topographic features.

Pouliquen (1972) studied marine caves in the Marseille region and concluded that the benthic biocoenoses described from marine caves in previous studies can exhibit differences, or even be absent, according to cave typology. He distinguished three types of marine caves based on their bathymetry: 'superficial caves', partly above the sea level, where no clear patterns of biological zonation occur due to their high hydrodynamic regime; 'semi-superficial caves', located at 0 to 5 m depth, which are also characterized by high hydrodynamic forces but exhibit biological zonation shaped mainly by water movement; and 'deep caves', which are located at depths greater than 10 m, where light and hydrodynamic forces decrease inwards and generate a marked biological zonation. While in the first two categories, hydrodynamics is the main factor shaping biological zonation, in the deeper caves currents and water renewal greatly depend on the cave morphology and size.

A landmark study on dark submarine caves was published by Harmelin et al. (1985), who characterized these unique environments as 'extreme habitats' and 'refuge biotopes'. According to this study, the two principal factors affecting the characteristics of the cave communities are the absence of light and the confinement, which often act in combination, generating isolation and oligotrophy. The transition from the semidark (GSO) to the dark cave biocoenosis (GO) is marked by a remarkable decrease of biotic cover, biomass and species richness (with the exception of serpulid polychaetes), the disappearance of erect growth forms and their replacement by encrusting forms. However, in this transitional zone, encrusting bryozoans (e.g. *Onychocella marioni*) often form nodules on the ceiling of the cave.

Developing some of the ideas of Harmelin et al. (1985), Bianchi & Morri (1994) postulated that beside light, hydrological confinement was the main driver of biological zonation in marine caves. The term 'confinement' relates to water renewal and the replacement of 'vital elements' (e.g. trace elements and vitamins) of marine origin, and was first introduced by Guelorget & Perthuisot (1983, 1992) for transitional coastal ecosystems (e.g. coastal lagoons). Studying 17 marine caves in Italy (Ligurian Sea, Tyrrhenian Sea, Sardinia and Sicily Channel) and four in the Maldives (Indian Ocean), Bianchi & Morri (1994) distinguished six ecological zones based on structural and functional aspects of the biotic assemblages.

Apart from the occasional attention given to biological cover, most of the above-mentioned bionomic studies provided mainly qualitative descriptions of the benthic communities in marine caves and rarely quantified spatial variability. To date, only a small number of studies have investigated marine cave benthos in a quantitative manner, using either destructive (scraped quadrats) or non-destructive (still-framed photography) methods (e.g. Cinelli et al. 1977, Gili et al. 1982, Pansini & Pronzato 1982, Balduzzi et al. 1985, 1989, Corriero et al. 2000, Martí et al. 2004a,b, Bussotti et al. 2006, Gerovasileiou & Voultsiadou 2016, Gerovasileiou et al. 2017b, Sanfilippo et al. 2017, Dimarchopoulou et al. 2018, Rosso et al. 2019, Bitner & Gerovasileiou 2021). The continuous development of photographic methodologies, including photogrammetry, has already assisted in the quantitative study and depiction of marine cave benthos and its distribution (Bianchi et al. 2004, Gerovasileiou et al. 2013, 2017a and references therein).

Almost all the above-mentioned bionomic studies have focused on hard substratum communities, while only few studies have so far investigated macro- and meiobenthos thriving in the sediments of marine caves in France, Italy and Spain (e.g. Monteiro-Marques 1981, Bianchi & Morri 2003, Akoumianaki & Hughes 2004, Todaro et al. 2006, Navarro-Barranco et al. 2012, 2013a,b, 2014, Janssen et al. 2013, Romano et al. 2018, 2020, Bergamin et al. 2020, Pino de la Torre et al. 2020).

Environmental gradients and ecosystem functioning

The dramatic environmental gradients in Mediterranean marine caves have attracted the interest of researchers since the early stages. The disappearance of light and the effect of water movement inside caves, depending on cave geomorphology (e.g. blind-ended versus tunnels; deep versus shallow), were the first abiotic parameters considered in the bionomic description of different biotic zones and biocoenoses in marine caves (e.g. Pérès & Picard 1949, 1964, Riedl 1966, Harmelin 1969, Cinelli et al. 1977, Harmelin et al. 1985, Balduzzi et al. 1989, Zabala et al. 1989, Bianchi & Morri 1994). However, only a small number of studies have investigated abiotic parameters (e.g. temperature, salinity, sedimentation rate, pH, oxygen concentration) inside marine caves, aiming at understanding species distribution patterns and ecosystem functioning (e.g. Passelaigue & Bourdillon 1985, Riera et al. 1985, Gili et al. 1986, Sgorbini et al. 1988, Fichez 1991a). The detailed study of several environmental parameters in the Grotta Marina of Bergeggi, Italy (Bianchi et al. 1986, Sgorbini et al. 1988, Morri et al. 1994a), and in marine caves of Marseille region, France (Fichez 1989, 1990a,b,c, 1991a,b,c), revealed an extreme impoverishment of the food intake observed in the more confined cave sections, which was presumed to affect community composition and ecosystem functioning (trophic depletion hypothesis). However, the exploration of marine caves with internal sulphur springs in Cape Palinuro (Italy) shed light on a unique ecosystem based on microbial chemo-litho-autotrophy, resembling deep-sea hydrothermal vents (e.g. Abbiati et al. 1992, Bianchi et al. 1994, Cinelli et al. 1994, Southward et al. 1996).

The study of matter and energy flow in Mediterranean marine caves provided a better understanding of their trophic structure and ecosystem functioning, through the development of theoretical models (Ott & Svoboda 1978, Russo & Bianchi 2003, Rastorgueff et al. 2015a). Particular animal behaviours, such as the diel horizontal migrations of swarm-forming mysids and schooling fishes, were found to have a pivotal role in mitigating trophic depletion in caves (Riera et al. 1991, Coma et al. 1997, Rastorgueff et al. 2011, 2015a,b, Bussotti et al. 2017, 2018). Nevertheless, there are still important gaps regarding the environmental status and functioning of marine cave ecosystems, since all the above studies have so far focused on a small number of caves from the western Mediterranean Sea. Such information is pivotal in order to monitor dynamics and potential changes of marine cave communities and provide evidence-based conservation.

Biodiversity

From the first pioneer taxonomic studies in Mediterranean marine caves, it became evident that they harbour several previously undescribed species. In his historical monograph, Riedl (1966) listed a total of 905 taxa, estimating that the overall diversity in Mediterranean marine caves could reach 2000 species. Many of these taxa (529 taxa belonging to 32 major groups) were recorded in marine caves of the Tyrrhenian Sea. Nearly 50 years later, updates for many taxa in Italian marine caves were provided by Cicogna et al. (2003). The study of Gerovasileiou et al. (2015a) combined information from 62 literature sources with data from primary research in 23 marine caves of the eastern Mediterranean Sea and listed 520 taxa belonging to 34 major groups. Several reviews, meta-analyses, checklists and large-scale surveys on marine cave biota have been published for particular taxa, such as sponges (e.g. Gerovasileiou & Voultsiadou 2012, Manconi et al. 2013, Grenier et al. 2018) and fishes (Bussotti et al. 2015), and for the whole Mediterranean Sea (Gerovasileiou & Voultsiadou 2014).

Overall diversity and regional patterns

The overview of 360 literature sources (peer-reviewed and grey literature) showed that 2369 taxa (compare to the 2000 species predicted by Riedl more than half a century ago), which belong to 58 major taxonomic groups, have been reported from 404 marine caves (mostly semi-submerged and/or shallow) in 15 Mediterranean countries. This census is based on data by Gerovasileiou (2014), Gerovasileiou & Voultsiadou (2014), Gerovasileiou et al. (2015a) and recent studies (e.g. Sanfilippo et al. 2017, Lage et al. 2018, 2019, Romano et al. 2018, 2020, Öztürk 2019, Rosso et al. 2019, Castelló et al. 2020). Taxa have been cross-checked and taxonomically updated using the World Register of Marine Species (WoRMS Editorial Board 2020) and the World Register for marine Cave Species (WoRCS) thematic database (Gerovasileiou et al. 2020). Taxa identified only at taxonomic ranks above species (e.g. genus, family) have been considered only when no other taxon of the same or lower rank was reported from other marine caves. Soft sediment thanatocoenoses have been excluded. However, in some cases data sources did not specify if species were found as living or dead specimens. All taxa reported from at least one Mediterranean marine cave have been considered. All cave zones (i.e. entrance, semidark and dark), types (i.e. marine caves proper, marine and brackish-water layers of anchialine caves, semi- and entirely submerged, blind-ended caves and tunnels), substrata (i.e. hard and soft sediments) and Mediterranean regions have been considered.

However, as expected, not all Mediterranean regions and taxonomic groups received the same research effort. The majority of the caves studied (93%) were located in the northern Mediterranean coasts, with Italy, France, and Spain being the main countries where marine cave research has taken place (129, 88 and 52 studies, respectively). Sponges were by far the most investigated group (160 studies), followed by anthozoans (87), polychaetes (63), bryozoans (60), decapods (43), bivalves (44) and fishes (40) (Table 2). Very few studies examined microbes, planktonic taxa and miscellaneous ‘small’ groups, such as soft substratum meio- and macrofauna. The number of species per taxonomic group and marine region was positively correlated to research effort (Figure 4), expressed as both the number of studies and caves explored (Gerovasileiou & Voultsiadou 2012, 2014, this study). Research in a greater number of marine caves in different Mediterranean regions is expected to lead to an increment in the number of species known, particularly within ‘inconspicuous’ groups (Bianchi 2007).

According to the biodiversity census for Mediterranean marine caves by Gerovasileiou & Voultsiadou (2014) and this study, the highest number of taxa (both sessile and motile) in the literature has been reported from the semidark zone of marine caves (1153), followed by the cave entrance (988) and the dark zone (848). However, for 510 taxa, cave zone was not specified in the literature sources (Table 2). Macroalgae (mostly rhodophytes) dominated in terms of species richness in the entrance zone (23% of the species), while sponges dominated in the semidark and dark zones (19% and 22.4%, respectively). Bryozoans and polychaetes were also among the richest groups in all zones. A total of 438 taxa were recorded in sediments on the cave bottom and 54 taxa in the marine and brackish-water layers of anchialine caves.

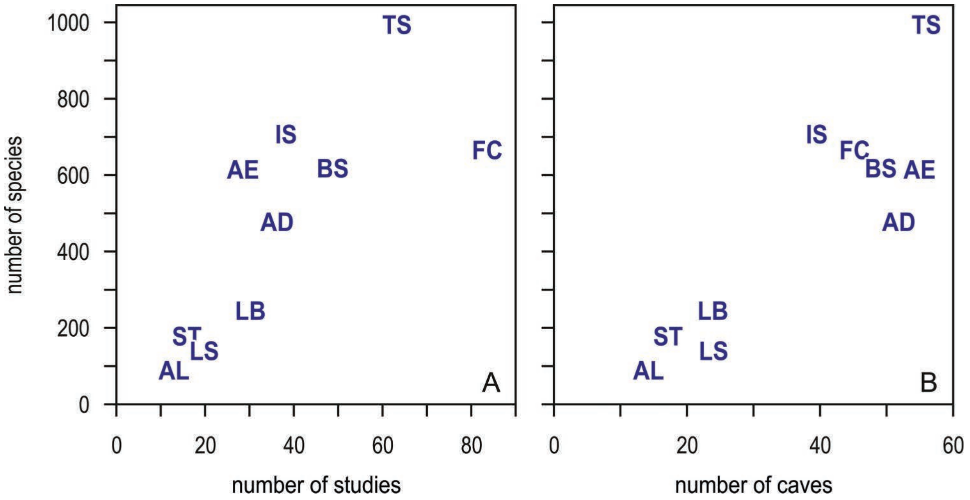

Figure 4 Relationship between cave species richness and research effort, expressed in terms of number of studies (A) and of caves investigated (B) in different Mediterranean regions. AL, Alboran Sea; BS, Balearic Sea; FC, French Coast; LS, Ligurian Sea; TS, Tyrrhenian Sea; ST, Siculo-Tunisian Strait; AD, Adriatic Sea; IS, Ionian Sea; AE, Aegean Sea; LB, Levantine Basin. Spearman's rank correlation coefficient (r_s) and probability level (p) are: r_s=0.891 and p=0.001 for A; r_s=0.748 and p=0.013 for B. Based on data from Gerovasileiou & Voultsiadou (2014), updated with recent studies.

Marine cave biota

This section provides an outline of existing knowledge (diversity patterns, frequently recorded taxa, cave-exclusive and non-indigenous species) of Mediterranean marine cave biodiversity for the main taxonomic groups (Table 2). Species are reported from a considerable number of marine caves, at the Mediterranean scale, according to data from the Mediterranean marine cave biodiversity database by Gerovasileiou & Voultsiadou (2012, 2014). Within each taxonomic group, species are listed in decreasing order by number of records. Each record represents occurrence in a different Mediterranean marine cave. All cave zones, from the entrance to the inner dark zone, have been considered.

Prokaryotes

The microbial diversity of Mediterranean marine caves has been very little studied, thus not allowing for the description of general diversity patterns. Most available studies concern the microbial mats of the famous Grotta Azzurra and Grotta Sulfurea of Cape Palinuro, Italy (e.g. Mattison et al. 1998, Canganella et al. 2002, 2007), and more recently, marine caves and cavities of Zakynthos Island, Greece (Polymenakou et al. 2018). Microbial mats have also been reported from organic-rich sediments that accumulate in shallow marine caves at Ventimiglia (Italy), following disturbances (Nepote et al. 2017) and in a shallow cave of the north Aegean Sea (Daskalaki et al. 2018). The cyanobacterium *Leibleinia gracilis* was abundant in the semidark zone of the Grotta del Mago, Ischia Island, Italy (Cinelli et al. 1977).

Microalgae

Many unicellular photosynthetic organisms can thrive under extremely dim light conditions and are thus able to penetrate marine caves (Riedl 1966). However, studies of microalgae in Mediterranean marine caves are extremely scarce. Mazzella et al. (1979) found 28 species of diatoms in the volcanic cave Grotta del Mago, Ischia Island, Italy, none of them being exclusive of the cave habitat.

Table 2 Number of taxa and studies on marine cave biota by taxonomic group, Mediterranean sector and cave zone.

	Mediterranean sectors										Cave zone			Number	Number	Proportion of
Taxonomic group	AL	BS	FC	LS	TS	ST	AD	IS	AE	LB	CE	SD	D	of studies	of taxa	Mediterranean diversity (%)
Bacteria					+		+	+				1	10	7	12	–
Bacillariophyceae					+							20	5	2	21	2.9
Foraminifera	+	+	+		+			+	+	+	7	8	10	17	106	17.7
Myzozoa								+				1	1	1	1	–
Ciliophora								+			11	16	15	2	20	–
Radiozoa								+			2	2	2	1	2	–
Phaeophyceae		+	+	+	+	+	+	+	+		33	2		20	35	13
Chlorophyta	+	+	+	+	+	+	+	+	+	+	27	4		26	30	15.8
Rhodophyta	+	+	+	+	+	+	+	+	+	+	169	30		34	182	27.7
Porifera	+	+	+	+	+	+	+	+	+	+	137	213	189	161	329	48.3
Hydrozoa		+	+	+	+	+	+	+	+	+	49	60	17	34	108	23.6
Scyphozoa		+					+		+		2	2	1	2	4	20
Anthozoa	+	+	+	+	+	+	+	+	+	+	24	26	25	92	53	32.1
Ctenophora				+					+			1		3	1	3.3
Platyhelminthes					+		+		+		3	4	3	2	36	4
Nemertea					+		+	+			3	3	3	2	9	5.2
Nematoda														3	37	5.3
Rotifera														1	2	3.4
Kinorhyncha					+		+							1	1	3.6
Priapulida								+					1	1	1	20
Gastrotricha							+	+					16	2	16	9.7
Entoprocta			+				+	+					2	4	4	21.1
Copepoda		+	+				+	+			49	38	53	17	113	28
Ostracoda			+		+							1	2	4	8	1.6

(*Continued*)

Table 2 (*Continued*) Number of taxa and studies on marine cave biota by taxonomic group, Mediterranean sector and cave zone.

	Mediterranean sectors										Cave zone			Number	Number	Proportion of
Taxonomic group	AL	BS	FC	LS	TS	ST	AD	IS	AE	LB	CE	SD	D	of studies	of taxa	Mediterranean diversity (%)
Cirripedia			+	+	+		+	+			1	1	4	13	7	17.5
Decapoda	+	+	+	+	+	+	+	+	+	+	24	44	35	43	75	19.5
Mysida		+	+	+	+	+	+	+	+		6	6	7	22	21	20.6
Thermosbaenacea		+	+										2	2	2	33.3
Facetotecta								+						1	1	–
Tanaidacea	+		+		+		+		+			3	4	6	6	14
Pentastomida								+					1	1	1	–
Isopoda	+		+		+		+	+	+	+	2	7	6	12	26	15.8
Leptostraca		+											1	2	1	16.7
Amphipoda	+	+	+	+	+				+		26	59	30	19	83	18.5
Cumacea	+		+		+							2	5	6	6	6.1
Branchiopoda								+			3	4	3	1	4	–
Pycnogonida			+		+						3	15	2	4	15	33.3
Acari					+									2	5	–
Insecta (marine)								+			1	1		1	1	0.4
Oligochaeta					+									4	2	–
Polychaeta	+	+	+	+	+	+	+	+	+	+	86	186	113	63	262	23.4
Sipuncula			+		+		+		+		2	5	3	9	6	16.7
Echiura		+		+			+		+		1		1	4	1	16.7
Polyplacophora			+		+						5			7	7	22.6
Gastropoda	+	+	+	+	+	+	+	+	+	+	68	76	39	41	139	8.9
Bivalvia	+	+	+	+	+	+	+	+	+	+	31	41	30	48	93	23.3
Caudofoveata					+							1		1	1	3.4

(*Continued*)

Table 2 (*Continued*) Number of taxa and studies on marine cave biota by taxonomic group, Mediterranean sector and cave zone.

	Mediterranean sectors										Cave zone			Number	Number	Proportion of
Taxonomic group	AL	BS	FC	LS	TS	ST	AD	IS	AE	LB	CE	SD	D	of studies	of taxa	Mediterranean diversity (%)
Cephalopoda				+			+		+		3	2		4	3	4.6
Tardigrada			+		+		+	+					1	3	31	40.3
Bryozoa	+	+	+	+	+	+	+	+	+	+	121	168	132	66	228	40.9
Brachiopoda	+	+	+	+		+	+		+	+		7	8	22	10	71.4
Phoronida									+		1			1	1	20
Chaetognatha		+	+					+			1	1	5	3	5	25
Pterobranchia			+										1	1	1	20
Echinodermata		+	+	+	+	+	+	+	+	+	17	21	17	31	36	23.4
Tunicata	+	+	+		+	+	+	+	+	+	24	24	13	37	45	19.7
Pisces	+	+	+	+	+	+	+	+	+	+	45	46	29	40	112	17.2
Mammalia	+							+	+	+	1	1	1		1	4.3
Number of studies	14	51	88	21	70	18	38	41	33	33				360		
Number of caves	15	61	48	25	59	18	54	41	58	25						
Number of taxa	92	620	671	144	1022	181	481	713	617	260	988	1153	848		2369	13.9%

Source: Updated from Gerovasileiou (2014) and Gerovasileiou & Voultsiadou (2014) with recent data.

Note: The proportion of number of taxa in marine caves against the total Mediterranean diversity for each taxonomic group was calculated based on data in Coll et al. (2010) and Rosso & Di Martino (2016) for bryozoans.

Abbreviations: AL, Alboran Sea; BS, Balearic Sea; FC, French Coast; LS, Ligurian Sea; TS, Tyrrhenian Sea; ST, Siculo-Tunisian Strait; AD, Adriatic Sea; IS, Ionian Sea; AE, Aegean Sea; LB, Levantine Basin; CE, Cave entrance zone; SD, Semidark cave zone; D, Dark cave zone.

The most common species included *Biddulphia biddulphiana*, *Amphora bigibba*, *Grammatophora serpentina*, *Licmophora gracilis*, *L. abbreviata*, *Navicula ramosissima* and *Triceratium repletum*. A number of species, such as *Cocconeis scutellum*, *Grammatophora marina* and *Rhabdonema adriaticum*, were also present in the innermost and totally dark zone. Because photosynthesis should be inhibited in the dark, it might be supposed that they were resting stages rather than active organisms; however, there are examples of cave diatoms that are myxotrophic or even heterotrophic (Lewin & Lewin 1967, Armstrong et al. 2000, Abdullin & Bagmet 2016).

Macroalgae

Macroalgae can be very abundant at the entrance zone of marine caves (Figure 5A), and in some cases, sciaphilic species penetrate further inside semidark cave sections, though with low cover (Riedl 1966, Cinelli et al. 1977, Bianchi 2003, Alongi et al. 2012, Gerovasileiou et al. 2017b, Taşkın & Akçalı 2019). A considerable number of macroalgal taxa have been reported from Mediterranean marine caves, specifically 30 Chlorophyta, 35 Phaeophyceae and 182 Rhodophyta. The most frequently reported species (all in >10 caves) were the chlorophytes *Palmophyllum crassum* (Figure 5A), *Flabellia petiolata*, *Halimeda tuna* and *Valonia macrophysa*; the phaeophytes *Halopteris filicina* and *Dictyota dichotoma*; and the rhodophytes *Peyssonnelia squamaria*, *Lithophyllum stictiforme*, *Peyssonnelia rubra*, *Plocamium cartilagineum* and *Sphaerococcus coronopifolius*. The crustose rhodophyte *Hildenbrandia rubra* was the macroalgal species that penetrated furthest in the Grotta del Mago, Ischia Islands, Italy (Cinelli et al. 1977). The same species is also very abundant in caves of Crete, Greece (V. Gerovasileiou, unpublished data).

Foraminiferans

The most widely reported foraminiferan in Mediterranean marine caves is *Miniacina miniacea* (in >20 caves), which is a sessile benthic species, clearly visible to the naked eye (Figure 5B). It can cover up to 1% of the total biotic cover (Balduzzi & Cattaneo 1985, Dimarchopoulou et al. 2018) and – together with other taxa – may contribute to bioconstructions (Ballesteros 2006, Sanfilippo et al. 2015). There are very few studies, providing scattered information, of benthic (e.g. Riedl 1966, Rosso et al. 2019) or planktonic foraminiferans (e.g. Moscatello & Belmonte 2007), in most cases identified at higher taxonomic levels (e.g. family, order). In the latest census on Mediterranean marine cave biodiversity, only 14 foraminiferan species were reported (Gerovasileiou & Voultsiadou 2014). However, recent detailed studies of benthic foraminiferans in two marine caves of Sardinia, Italy (Bergamin et al. 2018, Romano et al. 2018, 2020, E. Romano, personal communication) yielded 131 taxa in cave sediments, of which 101 were represented by living individuals. Based on these updates, the foraminiferan diversity of Mediterranean marine caves should be approximately 106 taxa (considering only living species).

Sponges

Porifera is one of the most abundant and species-rich phyla in Mediterranean marine caves (Sarà 1962, Pouliquen 1972, Corriero et al. 2000, Cadeddu 2012, Gerovasileiou & Voultsiadou 2012, 2016, Manconi et al. 2013, Grenier et al. 2018). A total of 329 sponge species from all classes (279 Demospongiae, 29 Calcarea, 20 Homoscleromorpha and one Hexactinellida), which constitute 48% of the Mediterranean sponge diversity, have been recorded from at least 185 marine caves (Gerovasileiou & Voultsiadou 2012 and unpublished data). Certain taxa seem to be highly represented in the marine cave habitat, such as homoscleromorphs (e.g. *Oscarella* spp. and *Plakina* spp.), dictyoceratids and lithistids (Vacelet 1994, Pisera & Gerovasileiou 2021). A high proportion of the marine cave sponges are Mediterranean endemics (41%), including rare species with narrow distribution range, relict species (e.g. *Petrobiona massiliana* – Figure 5B), and >30 cave-exclusives (Gerovasileiou & Voultsiadou 2012, Grenier et al. 2018). In addition, several deep-sea species were found in dark marine caves, such as the carnivorous cladhorizid *Lycopodina hypogea* and the

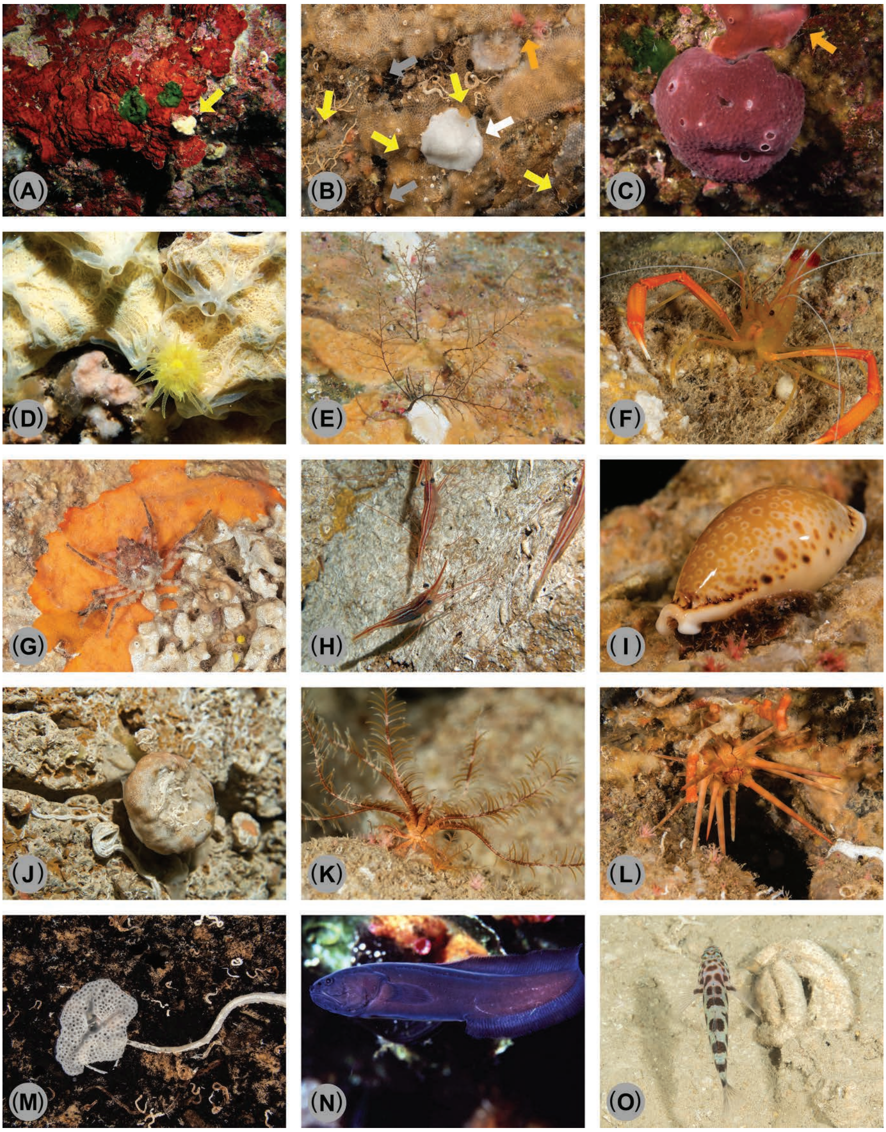

Figure 5 Characteristic species of Mediterranean marine caves: (A) the rhodophyte *Peyssonnelia rosa-marina*, the chlorophyte *Palmophyllum crassum* and nodules of the bryozoan *Rhynchozoon neapolitanum* (yellow arrow); (B) the calcareous sponge *Petrobiona massiliana* (white arrow), the foraminiferan *Miniacina miniacea* (orange arrow) and the brachiopods *Argyrotheca cuneata* (grey arrows) and *Joania cordata* (yellow arrows) on a cave wall with bryozoan encrustations; (C) the demosponges *Ircinia variabilis* and *Petrosia ficiformis* (orange arrow) and the chlorophyte *Palmophyllum crassum*; (D) the scleractinian coral *Leptopsammia pruvoti* and the demosponge *Hexadella racovitzai*; (E) hydrozoans (*Eudendrium* sp.) together with bryozoan encrustations on the walls of a submerged tunnel; (F) the shrimp *Stenopus spinosus*; (G) the spider crab *Herbstia condyliata*; (H) *Plesionika narval* shrimps on the walls of a dark cave; (I) the gastropod *Naria spurca* and the foraminiferan *Miniacina miniacea* in a semidark cave; (J) fungiform nodule formed mainly by the bryozoan *Hippaliosina depressa*; (K) the crinoid *Antedon mediterranea*, (L) the sea urchin *Stylocidaris affinis* and the bryozoan *Myriapora truncata*; (M) the didemnid ascidian *Lissoclinum perforatum* and serpulid tubes on a dark cave wall; (N) the cave-dwelling fish *Grammonus ater* in a dark cave; (O) the leopard-spotted goby *Thorogobius ephippiatus* over a muddy cave bottom. Photos by V. Gerovasileiou (A), T. Dailianis (B–M and O) and Donat Petricioli (N).

hexactinellid *Oopsacas minuta* (Vacelet et al. 1994, Vacelet & Boury-Esnault 1995). The most frequently recorded sponges (in >30 caves) in Mediterranean caves are the demosponges *Agelas oroides*, *Petrosia ficiformis* (Figure 5C), *Spirastrella cunctatrix*, *Ircinia variabilis* (Figure 5C), *Phorbas tenacior*, *Crambe crambe*, *Chondrosia reniformis*, *Axinella damicornis*, *Spongia virgultosa*, *Acanthella acuta*, *Penares euastrum*, *Terpios gelatinosa*, *Aaptos aaptos*, *Diplastrella bistellata*, *Haliclona mucosa*, *Erylus discophorus*, *Aplysilla sulfurea*, *Haliclona sarai*, *Ircinia oros*, *Cliona viridis*, *Penares helleri* and *Spongia officinalis*; the calcareous sponges *Clathrina coriacea* and *Petrobiona massiliana*; and the homoscleromorph *Oscarella lobularis*. Due to the lack of light and space-competing algae, sponges, which are generally sciaphilic animals, turn marine caves into a real 'sponge realm', with a maximum of 86 taxa recorded within a single cave (Grotte du Figuier, Marseille region). Nevertheless, most species (67%) are known from only 1–5 caves, with 34.5% reported from a single cave, thus indicating the fragmentation and individuality of the cave habitat (Gerovasileiou & Voultsiadou 2012).

Cnidarians

A total of 165 cnidarian species have been reported from Mediterranean marine caves (53 Anthozoa, 108 Hydrozoa and 4 Scyphozoa). Anthozoans represent one of the most abundant and widespread taxa in marine caves, where they can form dense facies, especially on the ceilings and walls of the semidark cave zone. Examples include the scleractinians *Leptopsammia pruvoti* (Figure 5D), *Madracis pharensis* (very abundant in the eastern Mediterranean), *Hoplangia durotrix*, *Polycyathus muellerae*, *Caryophyllia inornata* and *Astroides calycularis* (mostly in south-western Mediterranean), some of which can be also abundant in darker sections; the red coral *Corallium rubrum*, which is more common in the north-western Mediterranean; and *Parazoanthus axinellae*, which can be abundant in cave entrances or in semidark tunnels with high hydrodynamic forces (Pérès 1967, Zibrowius 1978, Gili & Ballesteros 1991, Gerovasileiou et al. 2015a). In addition, gorgonian facies (e.g. *Eunicella cavolini* and *Paramuricea clavata*) can develop at cave entrances, mostly in the western Mediterranean. The most common sea anemone in marine caves, *Cerianthus membranaceus*, is often found in the sediment of cave bottoms, in both semidark and dark zones. Hydroids prefer cave sections with good water circulation, such as entrances or tunnels (Figure 5E) (e.g. Riedl 1959b, Boero 1985, Balduzzi et al. 1989, Bianchi & Morri 1994, Morri et al. 2009). The most frequently recorded hydroid species in Mediterranean marine caves are *Clytia linearis* (Lessepsian migrant), *Campanularia hincksii*, *Clytia hemisphaerica*, *Obelia dichotoma*, *Eudendrium racemosum* and *Antennella secundaria* (all recorded in >10 caves). Interestingly, eight non-indigenous and cryptogenic hydroids have been reported in caves (Gerovasileiou et al. 2016b), mostly in the Levantine Sea (Morri et al. 2009), with the circumtropical *Clytia linearis* being the most widespread throughout the Mediterranean.

Annelids

While oligochaetes have been rarely found in Mediterranean marine caves (Akoumianaki & Hughes 2004), polychaetes have been recorded in high number (262 species), mostly on hard substrata. The most frequently reported species belong to the families Serpulidae (e.g. *Protula tubularia*, *Serpula vermicularis*, *Semivermilia crenata*, *Filogranula annulata*, *Spiraserpula massiliensis*, *Vermiliopsis labiata*, *Josephella marenzelleri*, *Filograna implexa*) and Syllidae (e.g. *Trypanosyllis zebra*, *Syllis hyalina*, *Haplosyllis spongicola*, *Syllis variegata*), which thrive on hard substrata (all recorded in >10 caves). Although none of these species are cave-exclusives (Belloni & Bianchi 1982), some serpulids can be considered typical of the cave habitat, such as *Serpula cavernicola*, *Spiraserpula massiliensis* and *Vermiliopsis monodiscus* (Zibrowius 1968, Fassari & Mòllica 1991, Bianchi & Sanfilippo 2003, Sanfilippo et al. 2017). The other serpulids found in marine caves have been assigned to four main ecological groups: sciaphilic/coralligenous taxa, deep-water taxa, shallow-shelf taxa and shelf taxa (Rosso et al. 2013a, Sanfilippo et al. 2017). Serpulids are usually the most abundant taxon, in terms of cover, in the dark cave biocoenosis, where some species tend to form dense aggregates. Approximately 60 polychaete taxa have been reported from cave sediments, with the most frequently reported species being *Chrysopetalum debile* and *Sabella spallanzanii* (in >5 caves). Some other species were found to be abundant in particular caves (e.g. *Levinsenia gracilis* in the Grotta Azzurra of Cape Palinuro, Italy). However, the small number of studies on soft substratum macrobenthos does not allow diversity patterns to be generalized.

Miscellaneous 'small' taxa

A wide variety of small-sized planktonic, macro- and meiobenthic taxonomic groups (for crustaceans see below) are represented in Mediterranean marine caves (Table 2). Due to the scarcity of studies on soft substratum macro- and meiofauna and zooplankton assemblages, there is little information about their diversity in this habitat. However, 40% of the Mediterranean tardigrade fauna has been reported from marine caves of Italy (e.g. De Zio Grimaldi & Gallo D'Addabbo 2001), while many new species belonging to 'small' invertebrate groups were found in soft sediments of marine caves of Italy and France (Casanova 1986, Villora-Moreno 1996, Fregni et al. 1998, Gallo D'Addabbo et al. 2001, Todaro & Shirley 2003). Although these species have not been found in other habitats so far, it is not sure whether they are cave-exclusives or deep-sea species (Zeppilli et al. 2018). These include the priapulid *Tubiluchus troglodytes*; the gastrotrich *Urodasys acanthostylis*; the tardigrades *Parastygarctus mediterranicus*, *Pseudostygarctus rugosus* and *Trogloarctus trionyches*; and the chaetognath *Spadella ledoyeri*.

Arthropods

A total of 375 arthropods from several taxonomic groups, mostly crustaceans, have been reported so far from Mediterranean marine and anchialine caves (Table 2). The groups with the highest number of species are Copepoda (113), Amphipoda (83), Decapoda (75), Isopoda (26), Mysida (21) and Pycnogonida (15), with all other groups comprising less than 10 taxa. The most frequently reported species (in >10 caves) were the decapods *Stenopus spinosus* (Figure 5F), *Herbstia condyliata* (Figure 5G), *Palinurus elephas*, *Palaemon serratus*, *Dromia personata*, *Galathea strigosa*, *Plesionika narval* (Figure 5H) and *Scyllarus arctus*, and the mysids *Hemimysis margalefi*, *H. speluncola* and *Siriella jaltensis*. These species move into and out of caves, with the first two mysids forming swarms, thus playing an important role in the functioning of the marine cave ecosystem. Marine cave decapods have been especially studied by Gili & Macpherson (1987), who reported 11 species from Mallorca Island, Spain, and by Manconi & Pessani (2003), who reported 24 species from 21 Italian marine caves. The high number of copepod species in Mediterranean caves derives from one study on zooplankton assemblages of Grotta di Ciolo, Italy (Moscatello & Belmonte 2007), and one study on soft substratum meiobenthos of 3PP Cave, France (Janssen et al. 2013). Nevertheless, both studies listed a considerable number of taxa which were either undetermined or identified only at high taxonomic levels, which were not considered in the census by Gerovasileiou & Voultsiadou (2014). Interestingly, 75% of the taxa found by Janssen et al. (2013) were undescribed and several had deep-sea affinities. In addition, many new copepods, decapods and a thermosbaenacean species, probably all cave-exclusive, were found from marine and anchialine caves of the Adriatic Sea, the Balearic Islands and south France (e.g. Pretus 1990, Fransen 1991, Jaume & Boxshall 1996, Jaume 1997, Jaume et al. 1999, Wagner & Chevaldonné 2020). The molecular study of mysids in several marine caves from different Mediterranean regions by Rastorgueff et al. (2014) revealed at least four cryptic *Hemimysis* taxa still undescribed. The above results indicate that further studies on planktonic, hyperbenthic and meiobenthic fauna in marine and anchialine caves would shed light on new crustacean diversity. Seven non-indigenous and cryptogenic crustaceans have been found in Mediterranean marine caves (Gerovasileiou et al. 2016b), with the Indo-Pacific shrimp *Urocaridella pulchella* being the most recent addition, having been reported from Aegean and Levantine caves (Digenis et al. 2021).

Molluscs

Several studies showed that Mediterranean marine caves harbour a rich malacofauna and especially (micro)gastropods (e.g. Starmühlner 1968, True 1970, Cantone et al. 1979, Cattaneo 1981, 1982, Cattaneo-Vietti & Russo 1987). Molluscs are represented in Mediterranean caves by 243 species, mostly gastropods (139) and bivalves (93). Other classes are represented with fewer than 10 species (seven Polyplacophora, three Cephalopoda and one Caudofoveata). The most frequently reported species are the nudibranch *Peltodoris atromaculata*, which grazes on the cyanobacteria of the sponge *Petrosia ficiformis*, the bio-eroding bivalves *Lithophaga lithophaga* and *Rocellaria dubia* and the spiny file clam *Lima lima* (all in >10 caves). The gastropods *Naria spurca* (Figure 5I) and *Luria lurida*, included in Annex II (List of endangered or threatened species) of the Bern Convention and the SPA/BD Protocol of the Barcelona Convention, are more commonly observed in caves than elsewhere (Bianchi 2003). Radolović et al. (2015) reported unusually high abundance of the gastropod *Homalopoma sanguineum* in the Y-Cave of Croatia. In the dark part of caves with terminal air domes, the deep circalittoral bivalve *Neopycnodonte cochlear* was seen forming thick encrustations on rocky walls just below the water surface in marine caves of Salento and the Sorrentine Peninsula (Italy) and of Croatia (C.N. Bianchi, personal observations in 1979, Cattaneo-Vietti & Russo 1987, Arko-Pijevac et al. 2001, Novosel et al. 2002, Onorato et al. 2003). Some mollusc species were first described from marine caves, such as the gastropods *Hyalogyra zibrowii*, *Skeneoides digeronimoi* and *Ocenebra vazzanai*, and the bivalves *Asperarca magdalenae*, *Neolepton discriminatum* and *Lucinoma spelaeum* (Warén et al. 1997, La Perna 1998, 1999, Palazzi & Villari 2001, Crocetta et al. 2020). Nevertheless, it remains unknown if these species are exclusive cave dwellers or if they simply prefer cryptobiotic and deep-water environments which are not easily sampled (Crocetta et al. 2020). A total of 15 non-indigenous and cryptogenic molluscs (eight bivalves and seven gastropods) were recorded in Mediterranean marine caves, mostly in Lebanon, such as *Brachidontes pharaonis*, *Spondylus spinosus* and *Chama pacifica*, which seem to have replaced native habitat-forming bivalves that were present in the past (Crocetta & Russo 2013, Crocetta et al. 2013a,b, Gerovasileiou et al. 2016b).

Brachiopods

Brachiopoda exhibit a particular preference for marine caves, often developing in large populations on the ceiling of the dark sections (Logan et al. 2004, Bitner & Gerovasileiou 2021). Out of the 14 brachiopods occurring in the Mediterranean Sea, nine to ten (64–71%) have been found in marine caves. The most frequently recorded species are *Joania cordata* (Figure 5B), *Argyrotheca cuneata* (Figure 5B), *Novocrania anomala* (although some records could actually belong to the congeneric species *N. turbinata* – see Bitner & Gerovasileiou 2021), *Argyrotheca cistellula*, *Tethyrhynchia mediterranea* and *Megathiris detruncata*. The rhynchonellid *Tethyrhynchia mediterranea* was first described from marine caves of southern France and Tunisia (Logan & Zibrowius 1994) and has not been recorded from other habitats to date. *Novocrania anomala* can be found in considerable numbers, cemented on dark cave walls and ceilings (Logan et al. 2004, Radolović et al. 2015, Rosso et al. 2019). Several brachiopod shells can be found in sediments of the cave bottom as thanatocoenoses, having detached from the cave ceiling (Taddei Ruggiero 1994, Bergamin et al. 2020, Pino de la Torre et al. 2020).

Bryozoans

Bryozoans are among the dominant phyla in Mediterranean marine caves, in terms of both cover and species richness (Harmelin 1985, 1986, 2000, Rosso et al. 2019). In the Mediterranean Sea, marine caves are the single habitat richest in bryozoans, hosting 228 species (Gerovasileiou & Voultsiadou 2014, Rosso & Di Martino 2016, Rosso et al. 2019). Most species are cheilostomes (181), followed by cyclostomes (37) and ctenostomes (10). Despite their small number, ctenostomes are represented with a slightly higher species percentage in marine caves compared to other habitat types (4.5 versus <2%), possibly due to the availability of special microenvironments offered by some sponges (Rosso & Di Martino 2016). Within caves, the highest bryozoan cover has been observed in the transitional zone between the semidark and dark cave biocoenoses, where several encrusting taxa (e.g. *Onychocella marioni* and *Hippaliosina depressa*) may develop multilayered structures (Figure 5J) (Harmelin 1985, 2000, Harmelin et al. 1985, 2003, Rosso et al. 2013a, 2015, 2019, 2020b). The most frequently reported species in Mediterranean marine caves (>10 caves) are the cheilostomes *Myriapora truncata*, *Celleporina caminata*, *Crassimarginatella maderensis*, *Aetea truncata*, *Cribrilaria radiata*, *Escharina vulgaris*, *Reteporella grimaldii*, *Chlidonia pyriformis*, *Caberea boryi*, *Cribrilaria innominata*, *Glabrilaria pedunculata*, *Fenestrulina malusii*, *Adeonella calveti*, *Escharoides coccinea*, *Margaretta cereoides*, *Reptadeonella violacea*, *Schizotheca fissa* and *Schizoretepora serratimargo*; and the cyclostomes *Crisia sigmoidea*, *Disporella hispida*, *Diplosolen obelius*, *Harmelinopora indistincta*, *Annectocyma major* and *Crisia pyrula*. Several bryozoan species were first described from Mediterranean marine caves (e.g. Hayward 1974, Silén & Harmelin 1976, Harmelin et al. 2007, Rosso et al. 2020a). According to Harmelin (1986), the bryozoan fauna of dark caves exhibits affinities with that of other crevicular microhabitats (e.g. coralligenous concretions), undersides of small hard substrata and deep-sea habitats. Rosso et al. (2013a) distinguished five ecological categories of bryozoans in marine caves of Sicily: cave species, sciaphilic and/or coralligenous taxa, deep-water taxa, shallow-shelf taxa and shelf taxa. Non-indigenous taxa and new species with Indo-Pacific affinities have been recorded in marine caves of Lebanon (Harmelin et al. 2007, 2009, 2014a,b).

Echinoderms

The echinoderm fauna of Mediterranean marine caves is represented by 36 species in total. The most frequently reported taxa (>10 caves) are the sea urchin *Arbacia lixula*, which can occasionally enter shallow caves, and the brittle star *Ophiothrix fragilis*. Echinoderms are never abundant in caves except for some ophiurids (e.g. *Amphiura chiajei* and *Ophioderma longicaudum*) and, to a lesser extent, asteroids (Tortonese 1978). The crinoid *Antedon mediterranea* (Figure 5K) is abundant in the Grotta Azzurra of Cape Palinuro, Italy (Bianchi et al. 1994, Cinelli et al. 1994). The same species and the sea urchin *Stylocidaris affinis* (Figure 5L) have been also observed in relatively high abundance in some marine caves of Crete, Greece (V. Gerovasileiou, personal observation).

Tunicates

A total of 45 tunicate species have been recorded in Mediterranean marine caves, mostly Ascidiacea, except for two undetermined salps that had drifted in from the outside (Moscatello & Belmonte 2007). The most frequently reported ascidians are *Halocynthia papillosa* (18 caves) and *Microcosmus vulgaris* (7). *Pyura vittata* was also mentioned as a typical species of the semidark cave biocoenosis by Pérès (1967). Didemnids can be also common in eastern Mediterranean marine caves (Figure 5M) (V. Gerovasileiou, unpublished data). The rare species *Rhodosoma callense*, which has the shape of a box with an articulated lid, was found and redescribed, after its first description in the nineteenth century, in two marine caves of Marseille region (France) by Monniot & Zibrowius (1999). Some non-indigenous species (e.g. *Herdmania momus*, *Phallusia nigra* and *Symplegma brakenhielmi*) have been recorded in eastern Mediterranean caves (Gewing et al. 2014, Gerovasileiou et al. 2016b). Certain colonial species (e.g. *Clavelina* spp.) can locally form patches (Bianchi 2003).

Fishes

Mediterranean marine caves are used as shelters by several fish species (Riedl 1966, Bussotti et al. 2002, 2003, 2015, 2017, Bussotti & Guidetti 2009, Gerovasileiou & Voultsiadou 2014, Gerovasileiou et al. 2015a,b, Bilecenoğlu 2019); juveniles, in particular, find refuge from predators (Balduzzi et al. 1980). A total of 112 fish species have been reported from different sections of Mediterranean marine caves, including sporadic visitors. According to Bussotti et al. (2015, 2017) fishes in marine caves can be assigned to three main ecological categories: (1) species typically inhabiting marine caves, such as *Gammogobius steinitzi*, *Grammonus ater* (Figure 5N) and *Didogobius splechtnai*; (2) species associated with cryptic habitats (e.g. crevices and fissures), also frequently found in caves, such as *Apogon imberbis*, *Conger conger*, *Corcyrogobius liechtensteini*, *Epinephelus marginatus*, *Scorpaena* spp. (*S. notata* and *S. porcus* are more common in the western Mediterranean, while *S. maderensis* is more common in the eastern basin), *Sciaena umbra*, *Serranus cabrilla*, *S. scriba*, *Phycis phycis* and *Thorogobius ephippiatus* (Figure 5O); and (3) several nectobenthic species inhabiting rocky reefs that can occasionally be found in caves, but usually close to the entrance (e.g. *Coris julis*, *Diplodus* spp., *Sarpa salpa* and *Symphodus* spp.). The cardinal fish *Apogon imberbis* is by far the most frequently reported and abundant species in marine caves, contributing to the mitigation of trophic depletion through its diel inside–outside migrations. One of the most recent additions to the Mediterranean cave fish fauna is the deep-water Messina rockfish *Scorpaenodes arenai* that was photographed for the first time by a scuba diver in a submerged cave (26–31 m) of Zakynthos Island, Ionian Sea, Greece (Tsiamis et al. 2015), and non-indigenous species of Indo-Pacific origin (e.g. *Sargocentron rubrum*, *Pempheris rhomboidea* and *Pterois miles*) in caves of the eastern Mediterranean Sea (Gerovasileiou et al. 2016b, and unpublished data by V. Gerovasileiou and C.N. Bianchi).

Birds and mammals

Some seabirds and rock pigeons (*Columba livia*) that inhabit the rocky coasts often find refuge, especially at the time of nesting, in the subaerial part of large semi-submerged caves, but none can be considered as typical (Cattaneo & Pastorino 1974; Galli & Spanò 2003, V. Gerovasileiou, personal observations).

Among mammals, the Mediterranean monk seal *Monachus monachus* is one of the most emblematic species to use this habitat (Mo 2003). There is historical evidence of the use of caves by this species: in Italy, for instance, many traditional marine cave names, such as ‘Grotta delle Sirene’ (= Mermaids Cave) or ‘Grotta del Bue Marino’ (= Sea Ox Cave), derive from the (past) occurrence of monk seals there. However, the bibliography of these last two centuries indicates a progressive increase in the use of coastal caves with entrances having limited human access. It has therefore been speculated that the species use of this habitat, to rest, moult, give birth and nurse pups, has been an adaptation to the intense human persecution to which it has been exposed since classical antiquity (Voultsiadou et al. 2013). The species uses coastal caves with underwater or semi-submerged entrances, provided that these are characterized by emerged internal beaches or rocky platforms on which the species may haul out (Reijnders et al. 1997). Caves used by monk seals for breeding have specific characteristics: they need to be well protected from wind and waves and human disturbance in order to guarantee pup survival. This implies the presence of factors such as an entrance with a protective barrier against strong waves, a long entrance corridor, a well-sheltered shallow internal pool, beaches that are always above high tide level and a chamber with a wide beach or with a highly inclined beach (Gücü et al. 2004, Karamanlidis et al. 2004, Dendrinos et al. 2007).

Some bat species (e.g. *Miniopterus schreibersii*, *Myotis blythi*, *Tadarida teniotis*) find refuge in the subaerial part of semi-submerged caves and tunnels, often in large populations (Galli & Spanò 2003, Mačić et al. 2019 and V. Gerovasileiou, personal observation).

Bionomy

Bionomic framing and heterogeneity

Environmental gradients in marine caves are dramatic (Morri et al. 1994a): within a few metres, there are variations of light, water movement and trophic input, which, in the external environment, can take place within tens or even hundreds of metres (Sarà 1978, Bianchi 1994). These environmental

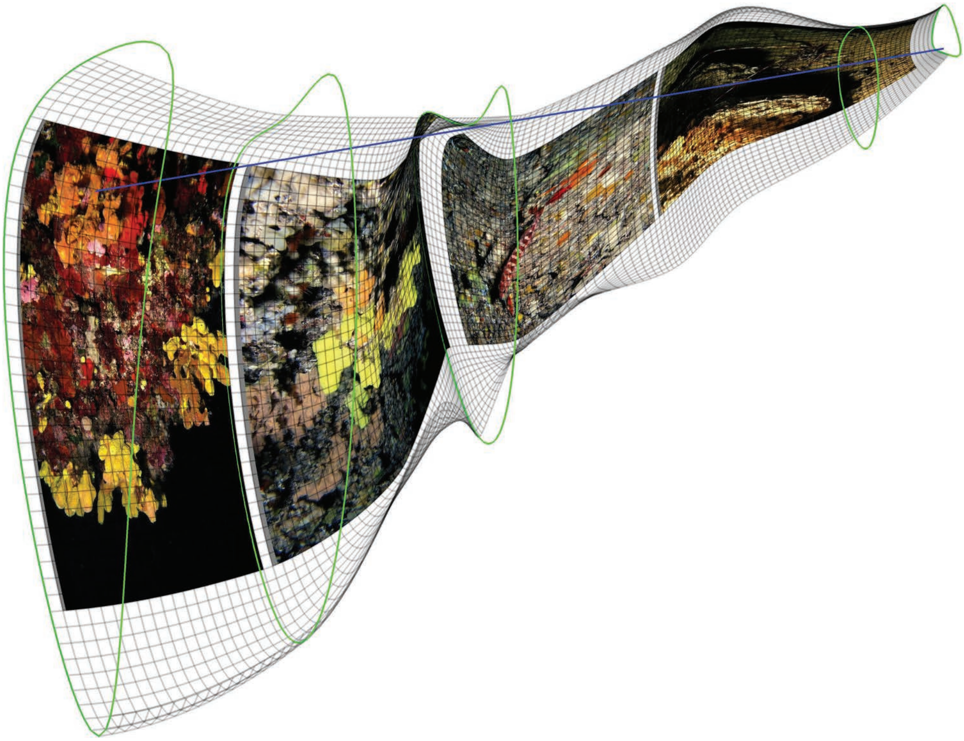

Figure 6 Ecological zonation in a blind-ended cave (24–40 m depth, Agios Vasilios Cave, Lesvos Island, Greece), depicted on a three-dimensional model. Representative images of different communities are superimposed on the cave model. From left to right, the coralligenous biocoenosis of the cave entrance is gradually replaced by the intermediate, animal-dominated semidark and the inner dark cave biocoenoses, respectively. Biotic cover decreases and erect growth forms (e.g. sponges, bryozoans and corals) are replaced by encrusting sponges and serpulids. Green circles represent cross-sections of the cave, providing a three-dimensional perspective to the model. The blue line represents the start-to-end cave axis (22 m long). Visualization was made with 'cavetopo' software (Gerovasileiou et al. 2013). For detailed descriptions of sessile benthic communities in this cave, see Gerovasileiou & Voultsiadou (2016), Gerovasileiou et al. (2017b), Sanfilippo et al. (2017), Rosso et al. (2019), and Bitner & Gerovasileiou (2021).

gradients generate a marked zonation of cave communities (Figure 6), and thus, species are not distributed homogeneously inside caves, but generally prefer distinct sections (Bianchi et al. 1996, Bianchi & Morri 1999).

In addition to the general patterns and trends of ecological zonation, small-scale variability can be so high that in some cases, heterogeneity between opposite walls or nearby sites within a cave can be higher than between nearby caves with similar morphology (Bussotti et al. 2006, Gerovasileiou & Voultsiadou 2016). This idiosyncratic pattern, also known as 'individuality', has been attributed to the cave-specific (micro)topography and the associated environmental gradients and modifications in trophic or larval supply, but might be also due to stochastic biological patchiness (Riedl 1966, Balduzzi et al. 1989, Benedetti-Cecchi et al. 1997, Martí et al. 2004a, Bussotti et al. 2006, Gerovasileiou et al. 2013, 2017b, Sempere-Valverde et al. 2019). The presence of microhabitats and unique features (e.g. sulphur springs, freshwater springs, bioconstructions and secondary openings) within caves could further increase heterogeneity, as they often support distinct communities and peculiar species (Bussotti et al. 2006, Gerovasileiou et al. 2017a).

As the first ecological and bionomic studies in Mediterranean marine caves took place mostly in the north-western Mediterranean, the first bionomic descriptions by pioneer researchers largely reflected regional conditions and knowledge. The gradual exploration of marine caves towards insular, southern and eastern sectors of the Mediterranean basin allowed for comparisons, revealing a non-negligible biogeographic heterogeneity, with several taxa having a restricted distribution range or being common in some regions but absent from others (Gerovasileiou & Voultsiadou 2012, Bussotti et al. 2015, Gerovasileiou et al. 2015a).

The biotic zones of Riedl

Riedl (1959b, 1966) distinguished six biotic zones, based on species replacement across the outside-inside gradient of blind-ended caves (Figure 7):

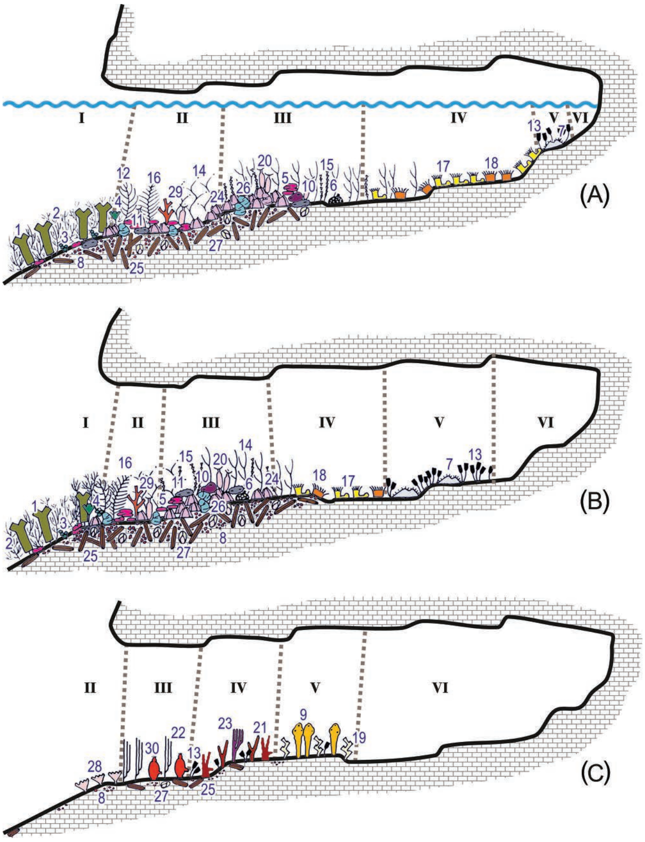

Figure 7 Biotic zones in semi-submerged caves (A), in infralittoral (B) and circalittoral (C) submerged caves according to Riedl (1966). The inner zones can occur close to the cave entrance as the depth increases. I: algal dominated zone, II: entrance zone, III: anterior zone, IV: central zone, V: posterior zone and VI: 'empty quarter'. For simplicity and graphical clarity, organisms have been schematically illustrated only on the cave floor, but walls and ceilings are also colonized: 1 *Dictyopteris*; 2 *Cystoseira*; 3 *Halimeda*; 4 *Flabellia*; 5 encrusting Rhodophyta; 6 *Clathrina*; 7 *Petrobiona*; 8 *Cliona*; 9 *Axinella*; 10 *Petrosia*; 11 *Ircinia*; 12 *Pennaria*; 13 *Campanularia*; 14 *Eudendrium*; 15 *Dynamena*; 16 *Aglaophenia*; 17 *Parazoanthus*; 18 Dendrophylliidae; 19 other Scleractinia; 20 *Cornularia*; 21 *Corallium*; 22 *Eunicella*; 23 *Paramuricea*; 24 Balanidae; 25 *Lithophaga*; 26 *Ostrea*; 27 *Rocellaria*; 28 *Reteporella*; 29 *Myriapora*; and 30 *Halocynthia*. Redrawn and modified from Riedl (1966).

(I) Phytal-Schattengebiet (shady phytal zone),

(II) Höhlen-Eingangsgebiet (cave entrance zone),

(III) vordere Bestandsgebiete (anterior cave zone),

(IV) zentrale Bestandsgebiete (central cave zone),

(V) hintere Bestandsgebiete (posterior cave zone),

(VI) das ‘leere Viertel’ (the ‘empty quarter’ – a nearly azoic zone).

In the phytal zone, the abundance of algae decreases in parallel with the decrease of light, while the sessile fauna dominates towards the inside. The zonation of the different faunal groups depends primarily on the gradients of light and water movement in the entrance area and in the anterior cave zone. For the majority of groups, the abundance is higher in the central cave zone, but is also greatly influenced by the inclination of the substratum. In the posterior zone, under complete darkness and calm waters, the inclination of the substratum (and hence the sedimentation) constitutes the most important factor. Finally, the ‘empty quarter’ (Figure 8) is characterized by the almost total absence of fauna, the bare rock and the great distance from the entrance: its existence is determined by the scarcity of food supplies, the deterioration of water quality and possible freshwater infiltrations.

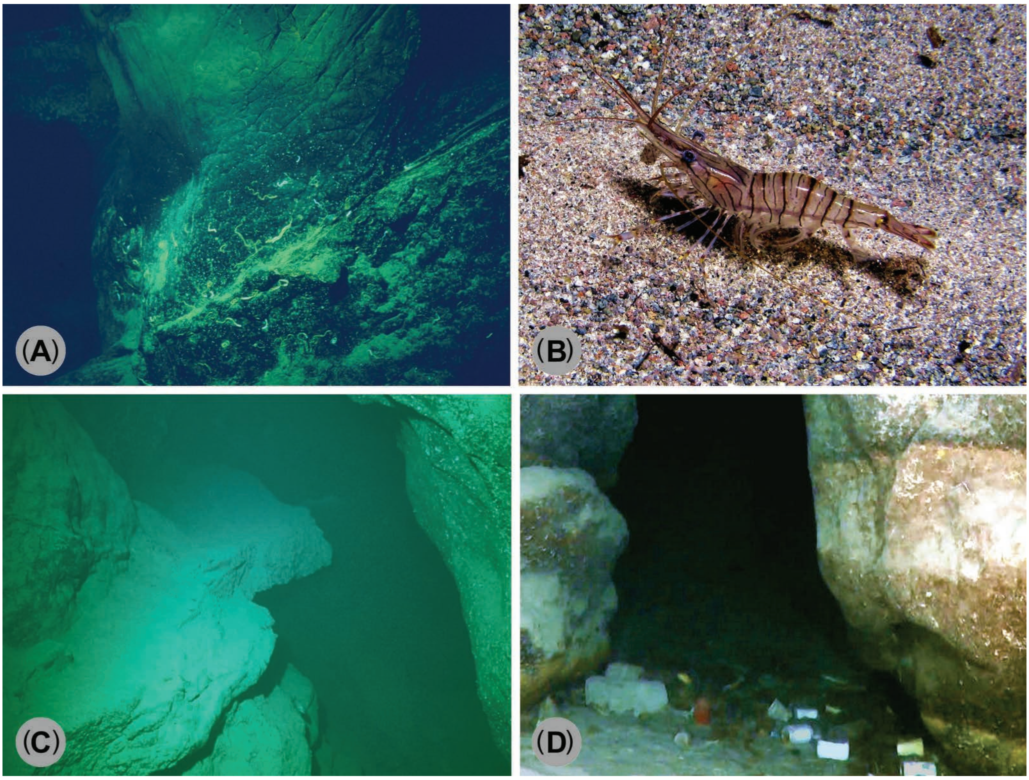

Figure 8 Aspects of the so-called leere Viertel (= empty quarter), the farthest reach of dark caves. (A) Layer of black metallic oxides and scanty serpulids on a rock wall; (B) the shrimp *Palaemon serratus* is one of the few representatives of the motile fauna; (C) the deposit of fine sediment on subhorizontal rocks hampers the settlement of sessile organisms; (D) lack of water movement may favour the accumulation of anthropogenic litter. Photos by C.N. Bianchi (A, C, D) and V. Gerovasileiou (B).

Comparing different marine caves, three main aspects were considered important in determining the zonation of the biotic zones: depth, size and shape of the cave. As for depth, deep-water caves exhibit a marked decrease in flora and fauna, with fauna being concentrated near the entrance, while the 'empty quarter' is more extensive than in shallow caves. It is also possible to observe the reduction of the phytal assemblage and changes in the composition of the inner assemblages. As for the size of the cave, the 'empty quarter' is larger in wide and morphologically complex caves with narrow entrance, while it may even be absent in small caves.

However, according to Riedl, the most important factor for the distribution of the biota is the shape of the caves. In tunnel-shaped caves, where there is constant water movement and light can be very variable, it is difficult to identify a clear zonation pattern and some zones can be absent. In addition, Riedl observed that benthic assemblages similar to those of caves can also be found outside, under roofs and overhangs, suggesting a pivotal role for light.

The cave biocoenoses of Pérès & Picard

Due to the great influence of the French school on Mediterranean marine ecologists, the model of cave zonation by Pérès & Picard (1964) has been the most widely followed and accepted to date. Knowledge about the composition and structure of the two basic cave biocoenoses – the semidark cave biocoenosis or GSO (from the French 'grotte semi-obscure') and the dark cave biocenosis or GO (from the French 'grotte obscure') – has been completed and updated thanks to current data from different Mediterranean regions.

The semidark cave biocoenosis

The semidark cave biocoenosis is typically found at (or in proximity to) the entrance of caves and even under caverns and overhangs that, topographically speaking, would not be characterized as true caves. The distinction of the GSO biocoenosis from that of the coralligenous, to which it was first assimilated, is due to Laborel (1960, 1961), who first pointed out its originality. The distinctive feature of this biocoenosis is the fact that it is dominated by sessile animals (e.g. sponges, anthozoans and bryozoans), although some sciaphilic macroalgae (e.g. the chlorophyte *Palmophyllum crassum* and some encrusting rhodophytes) may occur in certain caves.

Sponges form distinctive facies in semidark caves (Figure 9A–C), where they are the most species-rich group (Vacelet 1994). In semidark caves, the most frequently recorded sponge species, ordered according to the decreasing number of records, are *Agelas oroides*, *Petrosia ficiformis*, *Spirastrella cunctatrix*, *Chondrosia reniformis* and *Phorbas tenacior* (Gerovasileiou & Voultsiadou 2012). Some sponges (e.g. *Petrosia ficiformis*) can be often discoloured due to effect of reduced light on their associated cyanobacteria. The sponge *Aplysina cavernicola* has also been described as a typical species of this biocoenosis in the north-western Mediterranean basin (Vacelet 1959), although the distinction from the closely related, photophilic species *A. aerophoba* has been questioned (Voultsiadou-Koukoura 1987). Sponges of the class Homoscleromorpha (e.g. *Oscarella* spp. and *Plakina* spp.) can also have considerable cover in some caves (Gerovasileiou & Voultsiadou 2016, Grenier et al. 2018).

Three anthozoan facies have been recorded in the semidark cave biocoenosis (Figure 9D–F), mostly on ceilings and overhangs (Pérès 1967, Zibrowius 1978): (1) facies with scleractinians, such as *Leptopsammia pruvoti*, *Madracis pharensis* (more common in the eastern Mediterranean), *Hoplangia durotrix*, *Polycyathus muellerae*, *Caryophyllia inornata* and *Astroides calycularis* (mostly in southern sectors of the western Mediterranean); (2) facies with the red coral *Corallium rubrum*, found also in shallow water in the north-western Mediterranean Sea, but only deeper (below 50 m) in the north-eastern basin; and (3) facies with *Parazoanthus axinellae*, which can be found close to the entrance or in semidark tunnels with high hydrodynamics (more common in the western Mediterranean Sea and the Adriatic Sea). Facies with erect bryozoans (e.g. *Adeonella* spp. and *Reteporella* spp.) may also develop within this biocoenosis (Pérès 1967, Ros et al. 1985).

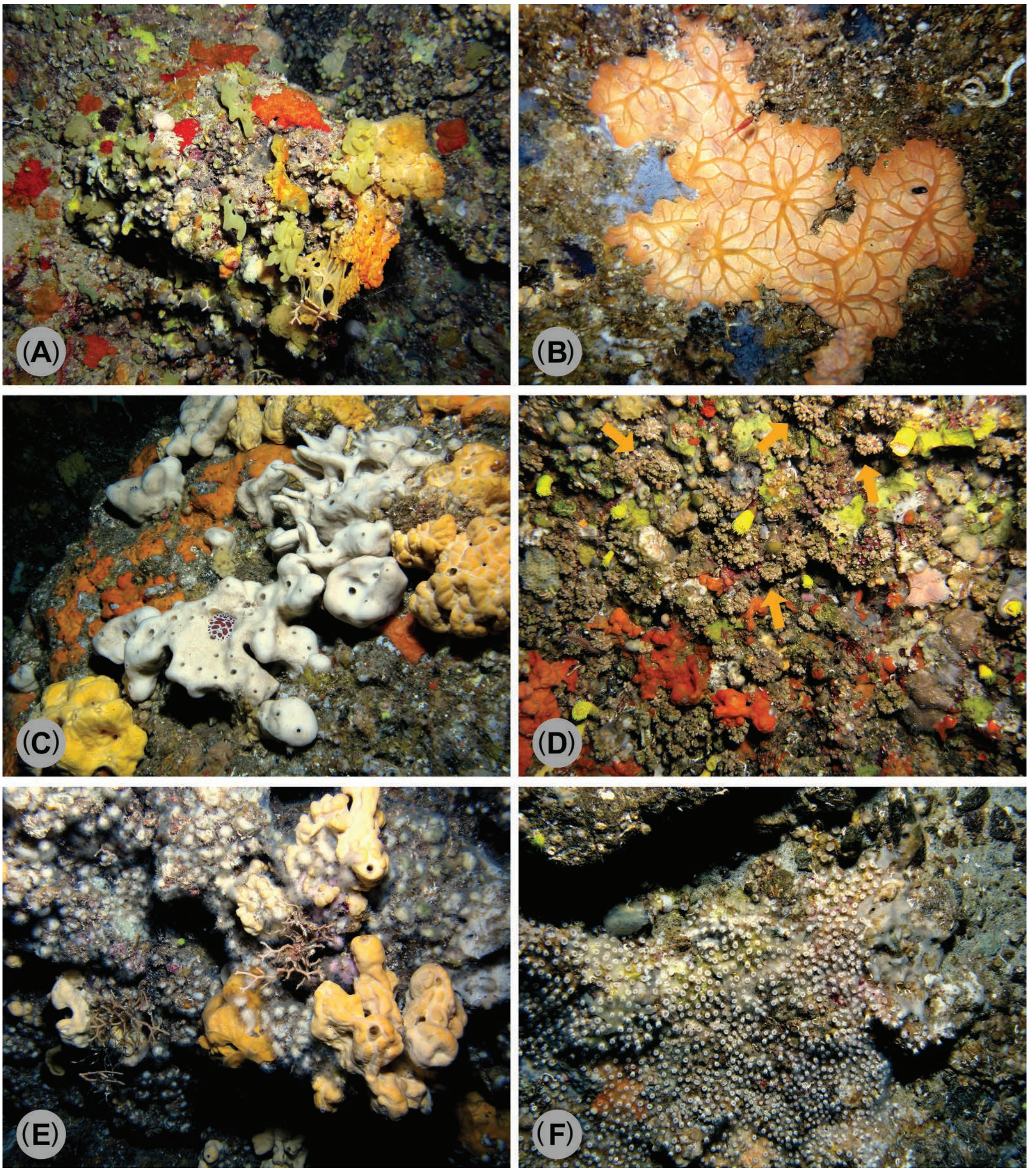

Figure 9 Typical aspects of the semidark cave biocoenosis dominated by sponges (A–C) and anthozoans (D–F): (A) *Oscarella* spp. and encrusting sponges; (B) *Spirastrella cuncatrix* (red) and *Phorbas tenacior* (pale blue) crusts; (C) discoloured *Petrosia ficiformis* (white) preyed upon by the nudibranch *Peltodoris atromaculata*, *Agelas oroides* (massive orange) and *Spirastrella cunctatrix* (orange-red); (D) facies of the scleractinian corals *Hoplangia durotrix* (orange arrows) and *Leptopsammia pruvoti* (yellow corals); (E) facies of the scleractinian *Madracis pharensis*, *Agelas oroides* and the erect bryozoan *Adeonella pallasii*; (F) facies of the scleractinian *Polycyathus muellerae*. Photos by V. Gerovasileiou.

Finally, the facies of impoverishment are numerous: their composition varies according to the nature of the factor generating the impoverishment of the assemblages (e.g. intense water movement). For example, in very shallow-water caves, many species characteristic of this biocoenosis can be absent, and hydroids (e.g. *Eudendrium armatum*) are particularly developed. High sedimentation rates, causing the excess of mud, can lead to the dominance of erect sponges (especially *Axinella* spp.).

The dark cave biocoenosis

The dark cave biocoenosis develops in the inner sections of blind-ended caves. The shift from the semidark to the dark cave biocoenosis is evidenced through a sharp decrease in biotic cover, species richness, biomass and three-dimensional complexity (Pérès 1967). However, Harmelin et al. (1985) observed that in tunnel-shaped caves with constant water movement, biotic cover can reach 100% even in the totally dark zone (Figure 10).

Laborel & Vacelet (1959) described a transitional zone between GSO and GO biocoenoses, where sponges and scleractinians are still abundant but the biotic cover decreases, and a black coating appears on the rock. Nodular and crest-like bryozoan formations often develop in this transitional zone (Harmelin 1985, Harmelin et al. 1985), although in some cases, they are also present in the dark cave biocoenosis (Balduzzi et al. 1989, Rosso et al. 2019).

The rock in dark cave sections is usually sparsely colonized by sponges, serpulid polychaetes, bryozoans and brachiopods (Figure 11A–D) (Pérès 1967). The most common sponges are *Petrosia ficiformis* (usually discoloured), *Petrobiona massiliana* (more common in the western Mediterranean Sea), *Chondrosia reniformis* (usually discoloured), *Diplastrella bistellata*, *Penares* spp. and *Haliclona mucosa* (Pérès 1967, Gerovasileiou & Voultsiadou 2012). Some deep-water species have been recorded in sublittoral dark caves, regardless of depth, such as the hexactinellid (glass) sponge *Oopsacas minuta*, which has been reported from caves of Marseille region and Croatia (Harmelin et al. 1985, Vacelet et al. 1994, Bakran-Petricioli et al. 2007). Serpulid polychaetes are among the dominant taxa in the dark cave biocoenosis, the most typical species being *Filogranula annulata*, *Janita fimbriata*, *Metavermilia multicristata*, *Serpula cavernicola*, *Spiraserpula massiliensis* and *Vermiliopsis monodiscus* (Zibrowius 1968, Sanfilippo & Mòllica 2000, Bianchi & Sanfilippo 2003). Although not exclusive to caves, the serpulid *Protula tubularia* often forms aggregates of several tubes (Figure 11C–D). The most typical, although not always abundant, bryozoans in dark caves are *Desmeplagioecia violacea*, *Ellisina gautieri*, *Glabrilaria pedunculata*, *Harmelinopora indistincta*, *Liripora violacea* and *Setosella cavernicola* (Harmelin 1969, 1985, 1986, 1997, 2000, Rosso et al. 2019, 2020a). Brachiopods occurring in dark caves include *Argyrotheca cistellula*, *A. cuneata*, *Joania cordata*, *Novocrania anomala* and *Tethyrinchia mediterranea* (Logan et al. 2004, Bitner & Gerovasileiou 2021). *Novocrania anomala*, in particular, is often found in high numbers, cemented on cave walls and ceilings (Figure 11B) (Radolović et al. 2015).

Several motile species often find shelter in dark caves, such as the mysids *Hemimysis margalefi* and *H. speluncola*, the decapods *Scyllarides latus* (Figure 11E), *Stenopus spinosus* (Figures 5F and

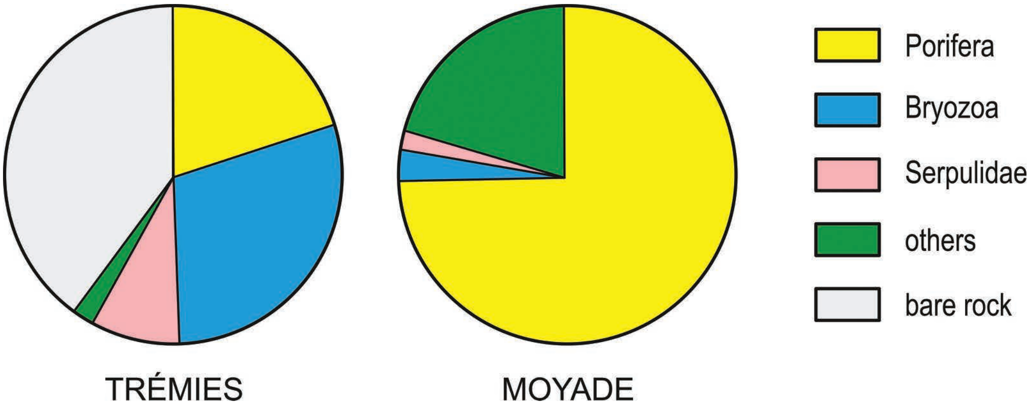

Figure 10 Per cent biological cover in two submerged marine caves of the Marseille region, France. Trémies is a blind-ended cave, and Moyade is a tunnel-shaped cave. Redrawn and modified from Harmelin et al. (1985).

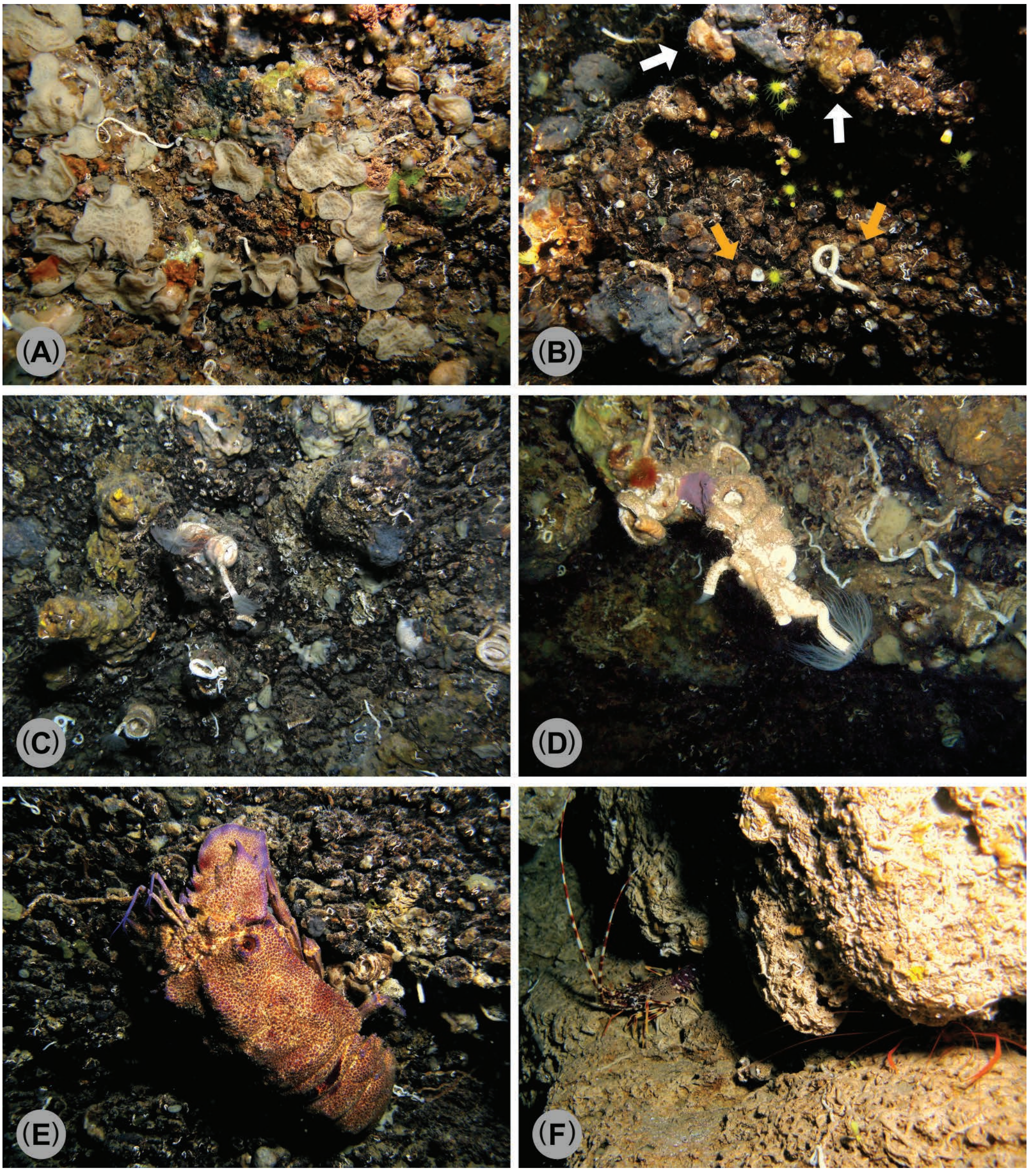

Figure 11 Aspects and species of the dark cave biocoenosis: (A) assemblage of the encrusting sponges *Plakina bowerbanki* (whitish-brownish), *Dendroxea lenis* (greyish-blue), *Hexadella* spp. (bright yellow and pale pink) and *Timea unistellata* (dull orange); (B) bryozoan nodules (white arrows), *Novocrania turbinata* brachiopod aggregations (orange arrows), *Dendroxea lenis* sponges (greyish-blue) and scleractinians *Leptopsammia pruvoti* (yellow); (C) coiled doughnut-like tube formations of the serpulid worm *Protula tubularia* and encrusting sponges (*Dendroxea lenis* and *Plakina* spp.); (D) biostalactite formed by the serpulid *Protula tubularia* and skeletons of other taxa; (E) the slipper lobster *Scyllarides latus*; (F) the decapods *Palinurus elephas* (left) and *Stenopus spinosus* (right) in a crevice of a cave wall. Photos by V. Gerovasileiou.

11F), *Palinurus elephas* (Figure 11F), *Plesionika narval* (Figure 5H; more frequent in southern and eastern Mediterranean regions), *Galathea strigosa* and *Herbstia condyliata* (Figure 5G), and the fishes *Apogon imberbis* and *Grammonus ater* (Figure 5N) (Pérès 1967, Ros et al. 1985, Bussotti et al. 2015, Gerovasileiou et al. 2015b).

The confinement zones of Bianchi & Morri

Similarly to Riedl (1966), Bianchi & Morri (1994) and Morri (2003) distinguished six ecological zones, but rather than species replacement they considered change in growth forms, trophic guilds, three-dimensional structure and biotic cover (Figure 12).

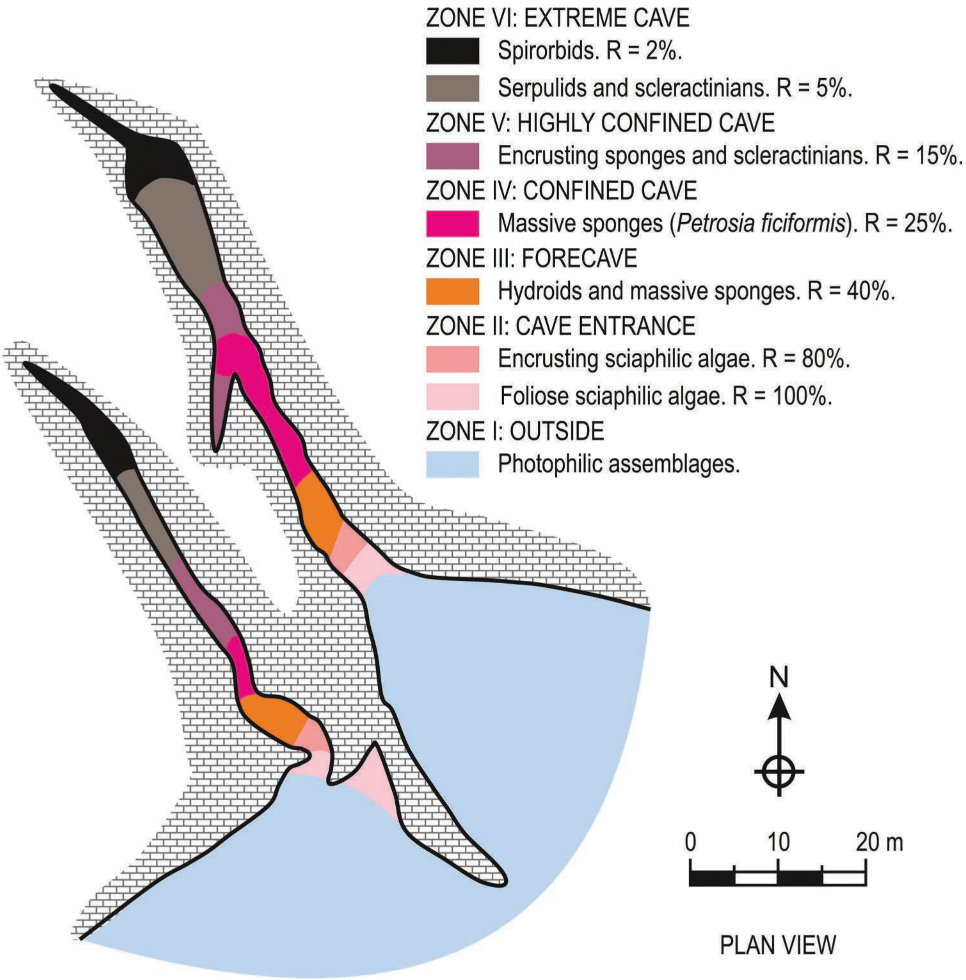

Figure 12 Zonation of the biotic assemblages of the twin caves named ‘Grotte del Bue Marino’, in the Gorgona Island (Tyrrhenian Sea, Italy) according to the confinement gradient. Cave depth is 6.5 m at the entrance and reaches 0 m in the terminal tract. R = percent cover. Redrawn and modified from Bianchi & Morri (1994) and Morri (2003).

Zone I corresponds to the ‘periphery’ of the marine cave ecosystem, consisting of the external assemblages developing close to the cave entrance; according to depth and substratum slope, they may be photophilic or sciaphilic.

Zone II represents the cave entrance and still resembles the previous zone, sharing several structural elements.

Zone III is the forecave, located shortly after the cave entrance, where macroalgae disappear and the benthic communities acquire the typical cave appearance, dominated by sessile epifauna.

Zone IV corresponds to the confined part of the cave, lacking passive suspension-feeders and dominated by submassive sponges.

Zone V encompasses highly confined sections of the cave: biotic cover is distinctly lower than 100%, and the community is composed by a thin layer of mostly encrusting organisms (sponges, bryozoans, serpulids and scleractinians).

Zone VI is an extreme environment with scattered serpulids, scleractinians and sponges; the biotic cover is lower than 10%.

A major interest of the zonation model of Bianchi & Morri is the fact that it is relatively independent of the taxonomic resolution, and can be therefore equally applied to caves of the Mediterranean or other seas: for instance, it has been tested successfully in coral reef caves of the Maldives by Bianchi & Morri (1994).

Soft substratum communities

Cave sediments are predominantly muddy, thus resembling certain deep (circalittoral or bathyal) soft bottoms, but they often include a coarse fraction, made of either mineral, coming from the outside, or biogenic, originating from fallen fragments of skeletons and calcareous shells of the organisms (e.g. scleractinians, serpulids, molluscs, bryozoans and brachiopods) present on the cave walls and ceiling (Monteiro-Marques 1981, Bianchi & Morri 2003, Rosso et al. 2013b, Pino de la Torre et al. 2020) or even from external shallow-water habitats (Di Geronimo et al. 1993). In the Grotta Marina of Bergeggi (Italy), for example, the sediments consist essentially of gravel near the outside and in the tunnel-shaped sections, and of fine sand and mud in more internal and terminal sections (Bianchi et al. 1986) (Figure 13). Thus, cave floors can represent an enclave of soft bottom within the rocky coastal system.

However, soft substratum communities of Mediterranean marine cave floors have not been studied as intensively as hard substratum ones, and there is very little information on their composition and affinities with their counterparts living outside the caves. A recent overview of 307 studies on Mediterranean marine caves showed that only 15% provided at least some pieces of information

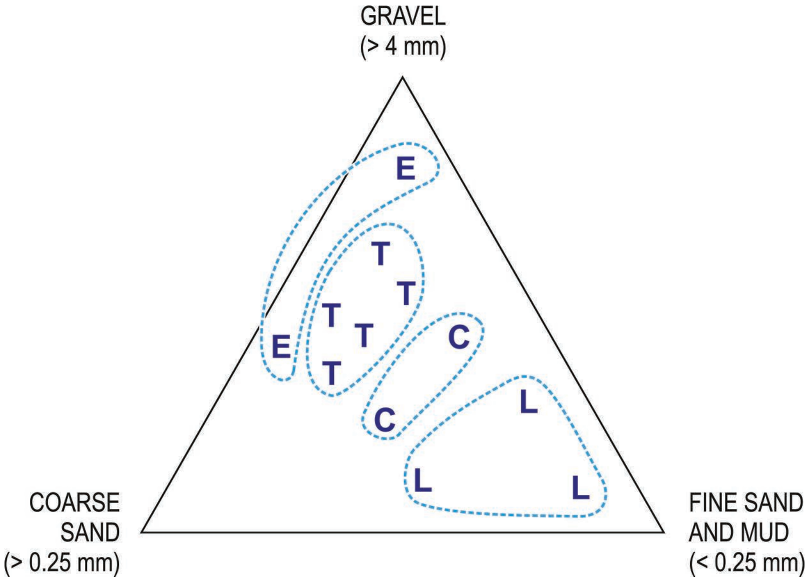

Figure 13 Ternary diagram of sediment grain size in different zones of the Grotta Marina of Bergeggi, Italy. Sediments were sampled with a diver-held corer. E=entrances; T=tunnel-shaped parts; C=lateral chambers; L=inner ‘lakes’. Redrawn and modified from Bianchi et al. (1986).

on soft substratum biodiversity (including single species records, e.g. *Cerianthus membranaceus*) (Gerovasileiou & Voultsiadou 2014). According to the latter overview and updated knowledge, a total of 438 taxa have been recorded in cave sediments, mainly foraminiferans (101 species, only living material considered), bryozoans (79 taxa on detached fragments, including non-living material), polychaetes (59 taxa), bivalves (48 taxa, although it was not always specified if they were found living or dead), amphipods (33 taxa), tardigrades (31 taxa), copepods (23 taxa) and gastrotrichs (16 taxa).

A small number of studies specifically focused on the structure of soft sediment fauna in marine caves of France, Italy and Spain (Monteiro-Marques 1981, Akoumianaki & Hughes 2004, Todaro et al. 2006, Navarro-Barranco et al. 2012, 2013a,b, 2014, Janssen et al. 2013, Pino de la Torre et al. 2020). The above studies evidenced idiosyncratic patterns in each cave, so that the structure of soft-bottom communities inside marine caves is difficult to generalize.

Macrobenthos

Monteiro-Marques (1981) studied the soft sediment macrofauna in three caves of the Marseille region (Grotte du Figuier, Grotte des Trémies, and Grotte de Jarre) and found 27 species (11 polychaetes, 10 molluscs, 3 sipunculids, 2 echinoderms and 1 crustacean). The most abundant species was the sipunculid *Onchnesoma steenstrupii*, otherwise reported from bathyal muds. The assemblage was characterized by species linked to heterogeneous sediments, rich in coarse elements, such as the bivalve *Gouldia minima* and the polychaete *Aponuphis bilineata*. However, the abundance of several indicator taxa of unstable environmental conditions was noted, such as the bivalve *Corbula gibba* and the polychaetes *Spio multioculata* and *Lumbrineris latreilli*.

Akoumianaki & Hughes (2004) studied the distribution of macroinfauna in a very peculiar cave, the Grotta Azzurra of Cape Palinuro (Italy). Its peculiarity derives both from the presence of sulphur hydrothermal springs, mainly located in the inner dark chamber of the cave (Southward et al. 1996), and from the efficient water exchange allowed by the large dimensions and the width of the entrances (Bianchi et al. 1998). A total of 97 species were recorded, specifically 55 polychaetes, 17 molluscs, 12 crustaceans, 4 sipunculids, 2 echinoderms and 7 other taxa (Anthozoa, Oligochaeta, Nemertea, Pycnogonida, Enteropneusta, Brachiopoda and Ascidiacea). In all sampling stations, polychaetes dominated in terms of both abundance and species richness. The most abundant species in the cave sediment were the polychaete *Levinsenia gracilis* (62%), the sipunculid *Onchnesoma steenstrupii* (14.6%), the polychaete *Paradoneis lyra* (7.2%) and the ophiurid *Amphiura chiajei* (4.9%). Species richness and density varied across cave sections, indicating differences at a scale of a few metres. However, there was no clear inward decline of abundance, biomass or diversity, suggesting that the chemosynthetic inputs in the inner cave chamber provide an additional trophic supply, thus having a positive effect on benthic assemblages. The abundance of taxa which are considered as indicators of environmental instability (e.g. the polychaetes *Paradoneis lyra*, *Levinsenia gracilis* and several species of the family Capitellidae, and the bivalves *Corbula gibba* and *Thyasira flexuosa*) indicated the excess of organic matter enrichment, similarly to the sediments in marine caves of Marseille region (Monteiro-Marques 1981).

In addition to the infauna, an abundant epifauna (fixed or sedentary) was found in the Grotta Azzurra floor, such as the bivalve mollusc *Pinna nobilis*, the tubiculous polychaetes *Phyllochaetopterus socialis* and *Sabella pavonina*, the echinoderms *Antedon mediterranea*, *Stylocidaris affinis* and *Ophioderma longicaudum* (Figure 14A) (Bianchi & Morri 2003). Bianchi et al. (1994) suggested that this unusual abundance of suspension-feeding and detritivorous epifauna was related to the chemosynthetic production by the sulphur bacteria in this particular environment.

Certain large tube-dwelling or burrowing anthozoans can be also common on the sedimentary bottoms of marine caves (Morri et al. 1991). *Cerianthus membranaceus* is known from several Mediterranean caves (Figure 14B). *Arachnanthus oligopodus* has been reported in the Grotta delle Corvine, in Salento (Denitto et al. 1999). A population of *Halcampoides purpureus* is known from the Grotta della Cala di Mitigliano, in the Tyrrhenian Sea (Boero et al. 1991).

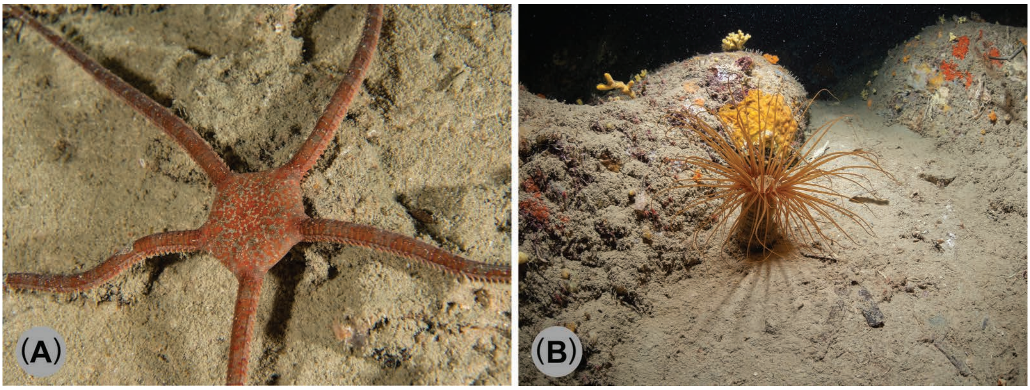

Figure 14 Typical epifaunal invertebrates on soft cave sediments: (A) the detritivorous brittle star *Ophioderma longicaudum*; (B) the tube-dwelling anemone *Cerianthus membranaceus*. Photos by T. Dailianis.

There have been recent studies of the soft substratum macrofauna of Mediterranean marine caves along the coasts of Granada (Alboran Sea, Spain). Navarro-Barranco et al. (2013a,b, 2014) investigated six caves which covered a wide depth range (6–30 m), and compared the crustacean fauna in sediments of the cave interior and adjacent external sites. None of the species exhibited a significant preference for caves, although amphipods of the genus *Harpinia* dominated inside the marine caves. In all caves, external sediments, which were coarser, had higher species richness. Diversity was significantly lower inside caves, where the percentage of silt and clay was significantly higher. However, this was not the case for abundance, which was low only in deeper caves, while in the shallower ones, the total number of individuals was lower outside caves. This is possibly related to the fact that shallow caves provide a more stable environment, protected from waves, winds and storms which affect the external sites to a greater degree. In addition, while the structure of the crustacean assemblage in external sites was quite similar (47.4% Bray–Curtis similarity), internal cave sites showed high variability and strong individuality (4.9% Bray–Curtis similarity), suggesting that these assemblages are influenced by many and complex factors (e.g. sediment granulometry, heavy metals concentration, organic matter and nitrogen concentration).

Meiobenthos

Meiobenthos has been rarely studied in Mediterranean marine caves. Specifically, only a few studies have investigated spatial variability of meiobenthos, on soft (e.g. Todaro et al. 2006, Janssen et al. 2013, Ape et al. 2016, Romano et al. 2018, 2020) and hard substrata (Russo et al. 2015), while taxonomic studies have brought to light several new species of tardigrades, gastrotrichs and a priapulid, possibly having deep-sea affinities (Zeppilli et al. 2018 and references therein).

Todaro et al. (2006) studied meiofauna in three dark sites of the Grotta di Ciolo (Salento, Italy), at horizontal distances of 55, 75 and 90 m from the entrance. A high diversity was found, including representative taxa of 12 major groups, with a total density of 656 and 1069 individuals per 10 cm^2 in November and June, respectively. Nematodes were the most abundant taxon, followed by harpacticoid copepods, priapulids, polychaetes and gastrotrichs, which were found in both seasons. Turbellarians, nemertines, ostracods, tanaids, oligochaetes, tardigrades and amphipods were also found, but with very low densities and/or sporadically. The community structure was quite different along the cave sites (e.g. priapulids were the second most abundant taxon in the first station), with small seasonal variation. Mean density of the total meiofauna, and particularly of harpacticoid copepods, decreased inwards, thus indicating that meiobenthic community is structured in accordance with the trophic depletion hypothesis.

Janssen et al. (2013) studied the meiofauna of the sediments of the 3PP Cave (Marseille region, France) at three sampling stations (entrance, middle and blind end). Meiofauna was assigned to 14 major taxa. Nematodes were the most abundant taxon, followed by copepods, priapulids and annelids. Kinorhynchs, ostracods, tardigrades and rotifers were also observed but in lower numbers. Six other taxa (i.e. Acari, Amphipoda, Bivalvia, Gastrotricha, Isopoda and Loricifera) were represented by single specimens. The community composition, based on presence/absence of major taxa, did not vary among stations. Nevertheless, individual densities and copepod diversity decreased inwards, and tardigrades were restricted to the inner parts of the cave. Copepods were assigned to 27 families and 90 species, 75% of which were undescribed. There were significant quantitative and qualitative differences in the composition of copepod assemblages between the three stations, at the family, genus and species levels. Some harpacticoid taxa, known from the deep sea (e.g. *Marsteinia*, *Ancorabolina*, *Paranannopus*, *Nematovorax* and Argestidae), were recorded in the cave, and the assemblage of the inner cave end was classified as 'abyssal', highlighting the faunal affinities between marine caves and the deep sea (Figure 15).

The meiofauna of the sediments of two caves in Ustica Island (Sicily, Italy) was poorer and scarcer than the one outside the cave and included different taxa (Ape et al. 2016). Nematodes, in particular, were represented in the dark sections of the caves by the exclusive species *Anticoma acuminata*. Availability of organic matter (i.e. phytopigment concentration) influenced meiofaunal distribution and composition inside the caves, while bacteria represented the most important food source for nematodes.

Studies on benthic foraminiferans in two marine caves of Orosei Gulf (Sardinia), Bel Torrente (BT) and Bue Marino (BM), showed that benthic foraminiferans may live in cave environments, even at a considerable distance from the entrance, while their distribution and community structure is affected by environmental gradients (Bergamin et al. 2018, Romano et al. 2018, 2020). In the BT cave, benthic foraminiferans were found as far as 330 m from the cave entrance, while the inner sections were totally barren (Romano et al. 2018). A total of 106 species were recorded (76 species had living individuals), with the most abundant being *Gavelinopsis praegeri*, *Nodulina dentaliniformis*, *Eggerelloides advenus* and *Ammonia inflata*. In the BM cave, benthic foraminiferans were found along the first 450 m of the cave (Romano et al. 2020). In total, 108 species were found (52 species had

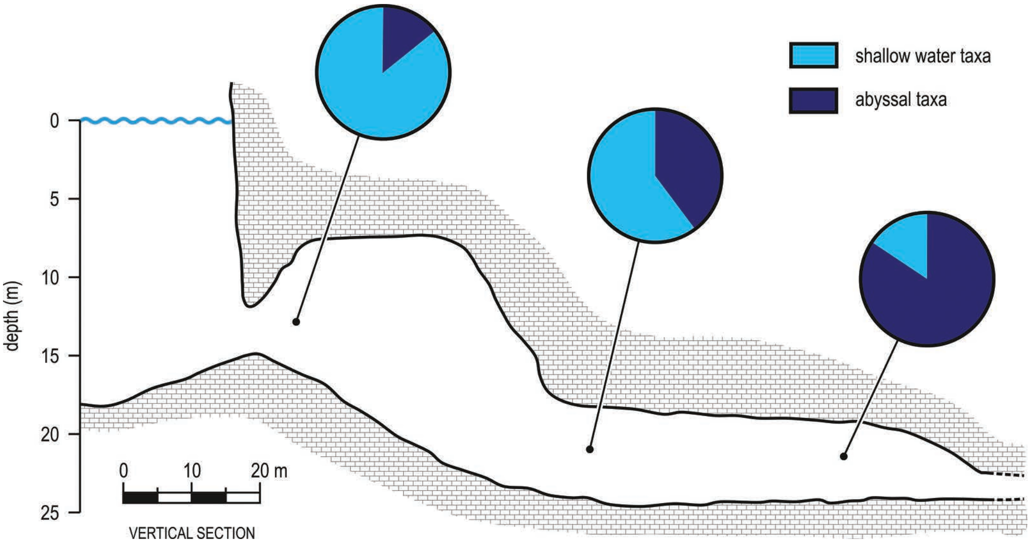

Figure 15 Proportion of copepod species with affinity for shallow or abyssal waters in different zones of the 3PP Cave of Marseille region, France. Redrawn and modified from Janssen et al. (2013).

living individuals), with the most abundant being *Nouria polymorphinoides*, *Eggerelloides advenus*, *Rosalina bradyi* and *Gavelinopsis praegeri*. None of the recorded species are cave-exclusive, and the colonization of caves probably took place through transport from the open sea of juvenile specimens in a cryptic stage (Bergamin et al. 2018). Common taxa from external coastal areas were found only close to the entrance, while inside the caves foraminiferans were exclusively epifaunal clinging/attached or opportunist infaunal species, which tolerate a wide range of environmental parameters, possibly generated by episodic freshwater inflow (Romano et al. 2018). In both caves, density and species diversity decreased inwards and were associated with gradients of physicochemical parameters. More specifically, salinity was found to affect the assemblage structure, and water acidification was suggested to cause a shift from a calcareous hyaline-dominated assemblage to an agglutinant-dominated one (Romano et al. 2018). In the BM cave, three ‘ecozones’ were identified (i.e. entrance, confluence and a transitional ecozone), while foraminiferans were absent from the inner cave zones (Romano et al. 2020). All the ecozones were characterized by the presence of hyaline, porcelaneous and agglutinated taxa, which however had different relative abundances in each ecozone. In the entrance ecozone, hyaline taxa dominated, while agglutinated taxa were more abundant in the two other ecozones. Porcelaneous taxa covered only a minor percentage of the total assemblage in all ecozones. A single species, *Nouria polymorphinoides*, was extremely abundant in the confluence ecozone, perhaps exhibiting opportunism in response to the high input of plant debris after a period of high rainfall (Romano et al. 2020).

Environmental and biological gradients

A striking characteristic of marine cave communities is that they present a marked zonation due to steep environmental gradients, even within a scale of a few metres. Gradients are recognizable in both physicochemical factors and biological aspects.

Main environmental gradients

Light availability

The decrease of light obviously plays a pivotal role in shaping community structure and species distribution in marine caves, constituting a limiting factor for the development of macroalgae and thus providing vital space for the development of sciaphilic sessile invertebrates (Pérès & Picard 1949, Riedl 1966, Cinelli et al. 1977, Balduzzi et al. 1989, Corriero et al. 2000, Martí et al. 2004a, Gerovasileiou et al. 2017b). Light level has been traditionally used for distinguishing the two marine cave biocoenoses, those of semidark and dark caves, respectively (Pérès & Picard 1964). Although threshold values for light intensity in these two cave zones are often arbitrary, it has been suggested that the limit for algal development is around 0.5–1% of the surface illumination (Riedl 1966) while, according to Harmelin et al. (1985) and Bianchi et al. (1986), animal-dominated communities develop in cave sections where light intensity is <1% of the sunlight at the sea surface and the dark cave biocoenosis develops where light levels are lower than 0.01% of the sea-surface levels, respectively. Observations and measurements made by Southward et al. (1996) at the entrance of the Grotta Azzurra of Cape Palinuro showed that with light equal to 17% of that of surface, the assemblages are still dominated by photophilic algae, in particular by Phaeophyceae (*Dictyota*). At 3%, the assemblage becomes sciaphilic, dominated by Rhodophyta (*Peyssonnelia* and encrusting coralline algae), while below 0.8%, the assemblage consists exclusively of sessile animals, with sponges, hydroids, scleractinians, bryozoans and colonial ascidians (Figure 16). Of course, the decrease in ambient light depends not only on the distance from the entrance, but also on the topographic position (e.g. floor, walls or ceiling).

According to Passelaigue (1989), the decrease in light intensity in shallow marine caves is similar to that occurring from 50 to 400 m depth in the open sea. As expected, light intensity decreases

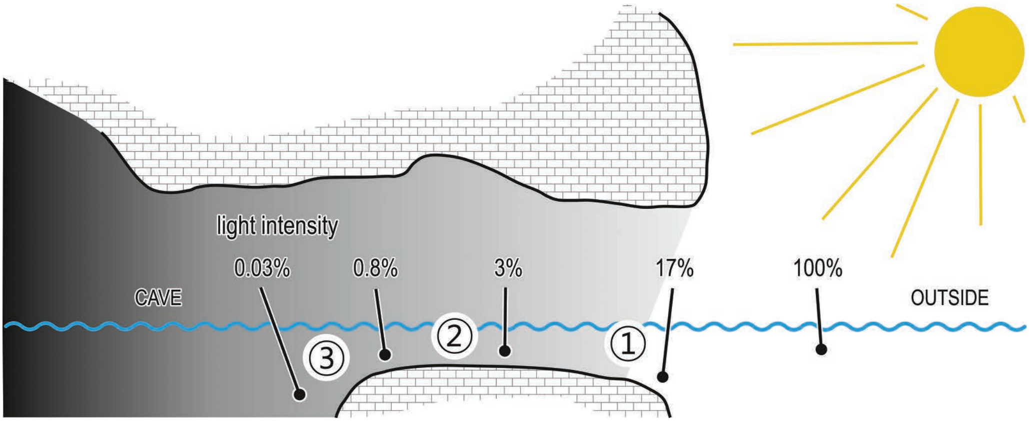

Figure 16 Reduction in light intensity and biological zonation at the entrance of the Grotta Azzurra of Cape Palinuro, Italy. Light intensity is expressed as a percentage of the surface value. (1) Community of photophilic algae; (2) sciaphilic algal assemblage (encrusting rhodophytes); (3) exclusively animal assemblage. Redrawn and modified from Southward et al. (1996) and Morri & Bianchi (2003).

with depth (e.g. shallow versus deep caves) and is affected by cave-specific topographic features. According to Riedl (1966), the exposure to light of a marine cave is affected by five factors: surface illumination, depth, orientation with respect to the cardinal points (i.e. aspect), vertical angle of the plane of the entrance and slope of the main axis of the cave. The entrance width to cave length ratio, and the position and number of entrances and secondary openings can also affect light intensity in caves. Thus, entrance zones in shallow semi-submerged caves and tunnels with multiple openings receive more sunlight compared with submerged blind-ended caves, and within caves, ceilings and overhangs tend to be darker compared to vertical walls, even when they are located at the same distance from the entrance (Riedl 1966, Pouliquen 1972, Bianchi & Morri 1994, Martí et al. 2004a, Gerovasileiou et al. 2017b).

Water circulation and associated parameters

The study of tunnel-shaped caves shows that the absence of light is not the only driver for the development of the dark cave biocoenosis, since biotic cover may be remarkably high throughout the length of the cave, even reaching 100% of the hard substratum in dark zones (Riedl 1966, Harmelin 1969, Harmelin et al. 1985). Therefore, it has been argued that water circulation constitutes an important key factor for determining the structure and type of benthic communities in marine caves (Riedl 1966, Harmelin et al. 1985, Gili et al. 1986, Balduzzi et al. 1989, Zabala et al. 1989).

According to Fichez (1991c), water residence time in marine caves ranges from one day at the entrance zone to over eight days in the inner confined sections. Based on current measurements and accurate topographic data, which allowed the cave geometry to be reconstructed, Bianchi et al. (1998) calculated the water balance of the Grotta Azzurra (Tyrrhenian Sea, Italy). In the tunnel-shaped section of the cave, water exchange was caused by the flow between the two opposite entrances. With a slightly rough sea, water was completely renewed in less than half an hour, while during calm weather conditions, the complete replacement took a few hours. In the blind end of the cave, water was exchanged only by diffusion. A particle of water that travels along the entire perimeter of the chamber would take more than 2.5 hours under calm seas but only 15 minutes in the presence of a current speed of 10 $cm \cdot s^{-1}$. Should we accept that the water turnover rate is an adequate estimate of confinement, these calculations indicate that not even the blind-ended part of the Grotta Azzurra is confined. This result suggests that confinement depends not only on the shape of the cavity (blind-ended or tunnel-shaped) but also on its size: large caves with wide chambers are less affected by confinement, as the presence of large masses of water probably allows the formation of density gradients and internal currents.

The study of Grotta Marina of Bergeggi (Ligurian Sea, Italy) by Morri et al. (1994a) showed that water movement affects a series of parameters which define the quality of seawater, such as temperature, salinity, oxygen concentration, pH and sedimentation rate. The role of these parameters has been investigated in several publications (e.g. Passelaigue & Bourdillon 1985, Riera et al. 1985, Gili et al. 1986, Sgorbini et al. 1988, Fichez 1991a). For example, Gili et al. (1986) studied a submerged cave in Medes Islands (Catalonia, Spain) and showed that salinity, temperature, density, dissolved oxygen, chlorophyll *a* and pigments inside did not differ significantly from those outside the cave due to the constant water exchange.

Water circulation also affects biotic parameters such as the removal of catabolites, larval dispersal and food supply (Balduzzi et al. 1989). It has been calculated that there is a close relationship between the cave volume and available nutritional reserves: in the absence of water renewal, a cave of 10 m^3 has reserves for 1 hour and a cave of 1 m^3 for only 8 minutes (Riedl 1966). Thus, due to the limited amount of autochthonous primary production, cave communities greatly depend on external food supply. Since benthic communities in caves are dominated by suspension-feeders, this food will essentially be represented by the organic substance suspended in the water. These considerations lead to the trophic depletion hypothesis, which states that cave fauna in more confined environments with limited water circulation will have a significantly lower food intake (Zabala et al. 1989, Bianchi et al. 2003).

Current speed

Long-term measurements of water movement in Mediterranean Sea caves are lacking, although there have been a few short-term studies (normally over periods of less than 24 hours). These few examples measured unidirectional flows, especially in tunnel-shaped caves, but different wave regimes are likely to cause significant variability in water movement patterns inside caves with complex morphologies. Pansini & Pronzato (1982) and Balduzzi et al. (1989) estimated water movement in the blind-ended Grotta della Cala di Mitigliano (Tyrrhenian Sea, Italy), using plaster balls, whose dissolution rate is proportional to the agitation of the water. Using this same method, and applying the empirical formula $v = 3.65 \times (M/B - 1)$ (where v is the equivalent velocity in $cm \cdot s^{-1}$, M is the % weight loss of the balls after 24 hours, and B is the % weight loss of the reference balls, placed in still water), Sgorbini et al. (1988) calculated the equivalent current speed in the Grotta Marina of Bergeggi (Ligurian Sea, Italy). Due to the general tunnel-like shape of this cave, the flow (as indicated by release of dye from the plaster balls) was unidirectional from sections with the shallowest water depth to the deepest. Current speed varied little throughout the cave (12–20 $cm \cdot s^{-1}$), except in internal 'lakes' and lateral chambers where water flow was significantly slower (Figure 17). In the same cave, Morri et al. (1994a) found a significant positive correlation between the values of equivalent current speed and the amount of biological cover observed on the cave walls. Bianchi et al. (1998) measured the current speed in the Grotta Azzurra (Tyrrhenian Sea, Italy) using magnetic induction current meters and found that during calm sea conditions, the current was directed towards south-east with a velocity of <2 $cm \cdot s^{-1}$. During slightly rough sea conditions, with winds blowing from the north-east quadrant, current inside the cave was directed towards south-west with a velocity of 6–10 $cm \cdot s^{-1}$. Faster currents are expected with greater wave height.

According to Riedl (1966), the intensity of water movement at a specific point in a cave depends on four factors: coast exposure and profile, depth, form and nature of the substratum. Riedl (1966) suggested that the development of typical cave communities requires a water agitation of no more than 2–10% of that of the surface. The shape of the cavity can accelerate (narrows) or slow down (widenings) the motion of water, which is reflected in the distribution of indicator taxa (e.g. hydroids) or the occurrence of erosional features in the rock. Several studies have suggested that the reduced sponge morphological diversity (i.e. dominance of encrusting growth forms) and species diversity

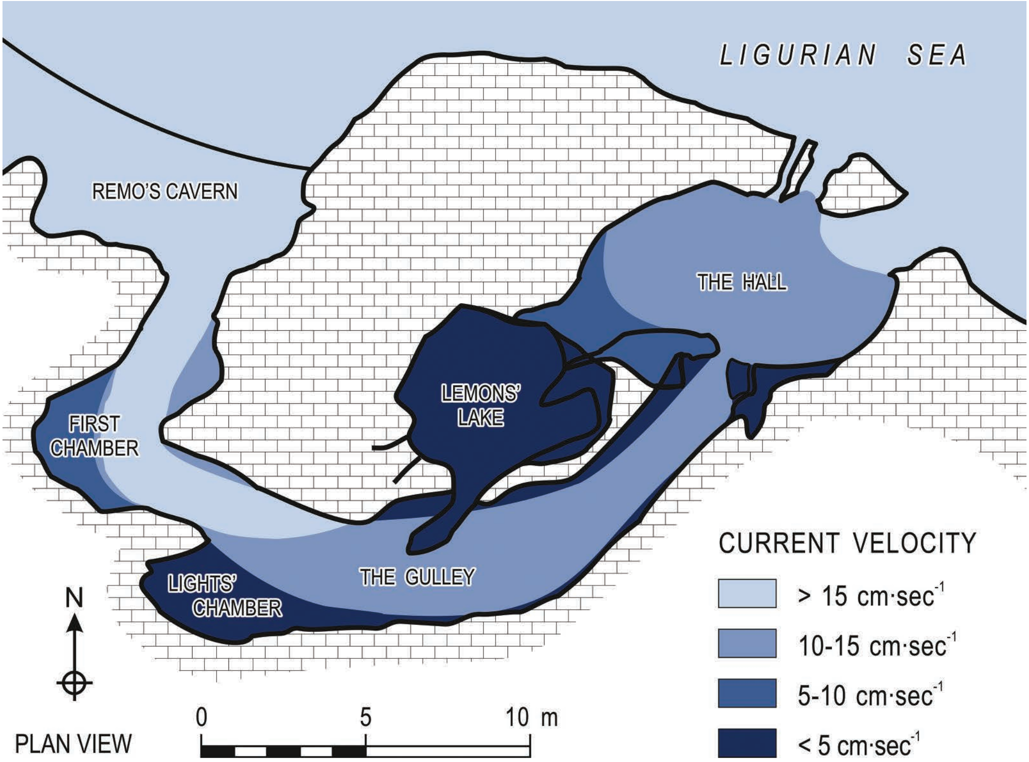

Figure 17 Current equivalent velocity in different zones of the eastern branch of the Grotta Marina of Bergeggi, Italy. In the tunnel-shaped part of the cave, the flow is mostly directed towards south-east. Redrawn and modified from Bianchi et al. (1986) and Montefalcone et al. (2018).

in the intermediate corridors of marine caves are related to the locally stronger flow rates due to the Venturi effect (i.e. the velocity of a fluid increases as the cross-sectional area decreases), which is caused by the cave narrowing (Pansini et al. 1977, Bell 2002, Gerovasileiou & Voultsiadou 2016).

Water temperature

Water temperature inside marine caves depends on several parameters, such as geographical location, local environmental conditions, water circulation, exposure to the open sea, cave morphology and bathymetry, presence of internal springs and freshwater infiltrations. Water temperature difference between the inner sections of marine caves of Marseille region (France) and the external environment could reach up to 7 °C, with temperature fluctuations being greater in the entrance zone (Pouliquen 1972, Harmelin et al. 1985, Passelaigue & Bourdillon 1985). Bianchi et al. (1986) took monthly temperature measurements in the Grotta Marina of Bergeggi (Italy): the innermost portions of the cave exhibited less variable temperatures (14–20 °C) all year-round with respect to the entrance zone (12.5–22.5 °C) (Figure 18). Martí et al. (2004a) studied a semi-submerged cave in Cabrera Island (Balearic Islands, Spain) and a submerged cave in Medes Islands (Catalonia, Spain) and found no differences in water temperature between different cave zones or seasons (June and November) within each cave (the average temperature was 19 °C in the Cabrera cave and 17 °C in the Medes cave). On the other hand, Radolović et al. (2015) measured water temperature in the shallow horizontal Y-Cave (Dugi Otok Island, Croatia), using data loggers year-round (August 2003 to July 2004) and found water stratification despite the fact that the cave is shallow and exposed to the open sea. More specifically, they observed the retention of different water bodies in different parts

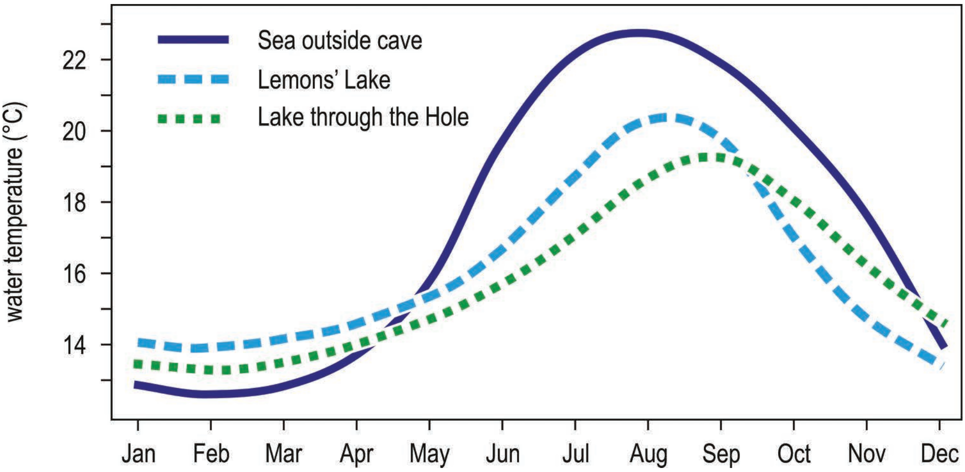

Figure 18 Annual trends of monthly water temperatures in the sea outside and in the highly confined inner 'lakes' of the Grotta Marina of Bergeggi, Italy. Redrawn and modified from Bianchi et al. (1986).

of the cave: a colder water layer on the bottom of the cave interior during summer, attributed to the cave morphology; brackish water (18–22 PSU) on the sea surface in an intermediate semi-submerged chamber during summer; and warmer water (>15 °C) in upper parts of the cave during winter, possibly due to the mixing of freshwater and seawater. Romano et al. (2020) studied two marine caves in Sardinia, Bel Torrente and Bue Marino and found that their mean water temperature was 24.9±0.5 °C and 24.2±0.2 °C, respectively, in the summer of 2014, whereas it was 19.7±0.4 °C and 17.0±0.3 °C, respectively, in the spring of 2015.

The 3PP Cave near Marseille, France, provides a good illustration of the role of cave morphology in thermal stratification of water inside caves. The cave slopes downwards from the entrance, which, in combination with the presence of a berm at the entrance (3 m above the ceiling and 10 m above the bottom of the internal chamber), is responsible for a rare pattern of thermohaline stratification: the inner cave chamber is filled with cold, density-trapped seawater which remains at a nearly constant temperature all year (12.8–14.5 °C) compared with external water at the same depth (13.0–24.7°C in 1991) (Vacelet et al. 1994, Harmelin 1997). These conditions, combined with the darkness and oligotrophy in the inner cave, allow for the colonization of deep-sea species, such as the hexactinellid sponge *Oopsacas minuta*, whose propagules are upwelled from the nearby Cassidaigne Canyon (Vacelet et al. 1994, Harmelin & Vacelet 1997).

The maximum water temperatures recorded from caves of the Marseille region, which slope upwards from the entrance, reach up to 24 °C, usually for relatively short periods (Chevaldonné & Lejeusne 2003). For example, while temperature inside the descending 3PP Cave remains low year-round, temperature fluctuations inside Jarre Cave follow those of the external environment, occasionally rising to 24 °C (2001–2002 data). In the eastern Mediterranean Sea, water temperature in shallow semi-submerged caves of the Aegean Sea (Greece) can reach 26–28 °C during summer, while it is lower (18–23 °C) in deeper, entirely submerged caves (2010–2018, unpublished data by V. Gerovasileiou). In shallow caves of Lebanon that receive freshwater input, temperature in the seawater layer reached 27–28 °C while in the freshwater layer, it was 21 °C (September 2002 and July 2003, data in Pérez et al. 2004). In a marine cave in the Levantine coasts of Turkey (Antakya Bay), water temperature was 28 °C at the entrance of the cave and 21–22 °C in the terminal chamber, where an internal freshwater spring is present, while in winter, temperature at the entrance is about 16 °C and 21 °C in the terminal chamber (Turan et al. 2019).

Freshwater input

In some caves, freshwater infiltrations (usually sporadic or seasonal) in the inner and upper portions (e.g. cave ceilings of inner chambers with an ascending profile) are responsible for the local impoverishment or even disappearance of sessile benthos and the creation of azoic zones (Riedl 1966, Pouliquen 1972, Balduzzi et al. 1985, Harmelin et al. 1985, Radolović et al. 2015). Harmelin et al. (2003) reported that salinity at the bell-shaped ceiling of the inner chamber of Bagaud Cave (Port-Cros, France) ranged from 5.3 to 22.85 PSU (in March and September, respectively) while its values at the entrance and outer chamber were 38.1–38.4 PSU. In the most confined parts of the Grotta Marina of Bergeggi (Italy), the infiltration of rainwater through the karstic network creates inner 'lakes' where the salinity can fall to 13.6–17.6 PSU during calm seas, to acquire a near normal marine salinity of 34.9–37.5 PSU during periods of greater wave action, which causes complete water renewal in the whole cave (Bianchi et al. 1986).

The occurrence of some rare sessile taxa and bioconstructions only in a small number of caves with freshwater input is possibly related to either salinity gradients or the provision of organic material and nutrients. Such cases include the rare scleractinian *Guynia annulata* in marine caves of Marseille region and Crete (Zibrowius 1978), the development of 'biostalactites' by the serpulid *Protula tubularia* in caves of Italy, Greece and Cyprus (Belmonte et al. 2009, 2020, Guido et al. 2014, 2017a, 2019a,b, Sanfilippo et al. 2015, 2017, Ingrosso et al. 2018, Jimenez et al. 2019, Rosso et al. 2021, V. Gerovasileiou, unpublished data), and lithistid sponges in shallow marine caves of Greece (Pisera & Gerovasileiou 2018, 2021 and unpublished data by V. Gerovasileiou). This association between dense populations of lithistids, originating from adjacent deep-water populations whose propagules were upwelled to shallow caves with freshwater influx, is probably explained by the rich silicate content in water (up to 11 times higher than outside caves and comparable to deep seawater at several hundred metres depth), delivered to the caves by freshwater sources, that promotes the development of these hypersilicified sponges (Pisera & Gerovasileiou 2021).

Seasonal freshwater floods were also found to affect the distribution and assemblage structure or benthic foraminiferans in marine caves of Sardinia (Bergamin et al. 2018, Romano et al. 2018, 2020).

Sedimentation

Cave walls in highly confined chambers with a little water movement, walls with positive inclination in proximity to the muddy bottom, protuberances and cavities on vertical walls and rocky boulders on the cave floor are often covered with a thin layer of sediment (Figure 8C). These surfaces are usually colonized only by a small number of sessile taxa which can tolerate high levels of sedimentation (Laborel & Vacelet 1958, Pouliquen 1972, Zabala & Gili 1985, Gerovasileiou & Voultsiadou 2016, Gerovasileiou et al. 2017b, Dimarchopoulou et al. 2018, Sempere-Valverde et al. 2019). For instance, erect growth forms (e.g. sponges *Axinella* spp.), which often develop on walls covered by a sediment layer, can better cope with high sedimentation rates since their body shape helps to avoid clogging of their aquiferous system (Bibiloni et al. 1989, Gerovasileiou & Voultsiadou 2016). High rates of sedimentation were the main factor affecting polychaete distribution in a marine cave of the Sorrentine Peninsula, Tyrrhenian Sea, Italy (Belloni & Bianchi 1982).

Biological gradients

In response to the steep environmental gradients, almost all structural parameters used to describe the organization of biological communities also exhibit gradients from the entrance to the interior of caves (Harmelin et al. 1985, Balduzzi et al. 1989, Martí et al. 2004a, Gerovasileiou & Voultsiadou 2016, Gerovasileiou et al. 2017b).

Biological cover and abundance

One of the most widely used parameters for the quantification of benthic community patterns on hard substrata is the biotic cover, i.e. the percentage of substratum occupied by living organisms, as a measure of organismal abundance. From values around 100%, typical of the external environment, biotic cover progressively decreases and can even approach zero in the terminal sections of blind-ended caves, where the sessile fauna is almost absent, except for some serpulids (Riedl 1966, Harmelin et al. 1985, Balduzzi et al. 1989, Bianchi & Morri 1994, Gerovasileiou et al. 2017b). Based on biotic cover, Laborel & Vacelet (1959) distinguished two zones within the dark cave biocoenosis: zone 1, with a cover of 50–80%; and zone 2, with a cover of 10–40%, respectively. In blind-ended caves, the decrease of cover appears to be related to the decrease of light from the semidark to the dark cave section, and to the reduction of water movement within the inner dark section (Figure 19A–B). On the other hand, in tunnel-shaped caves with constant water renewal, biotic cover could reach 100% of the hard substrata even in the totally dark zone (Figure 19C) (Harmelin 1969, Harmelin et al. 1985). Therefore, cave topography greatly affects zonation patterns of biotic cover (Balduzzi et al. 1989, Morri et al. 1994a, Gerovasileiou et al. 2017b, Dimarchopoulou et al. 2018).

The only existing study on hard substratum meiofauna has shown that while abundance decreased from the entrance to the middle part of the Grotta di Ciolo (Salento, Italy), there was a small increase towards the inner dark zone of the cave (Russo et al. 2015). Regarding macro- and meiofauna in sediments of the cave floor, the few existing studies have shown contrasting results: thus, spatial patterns of abundance cannot be generalized.

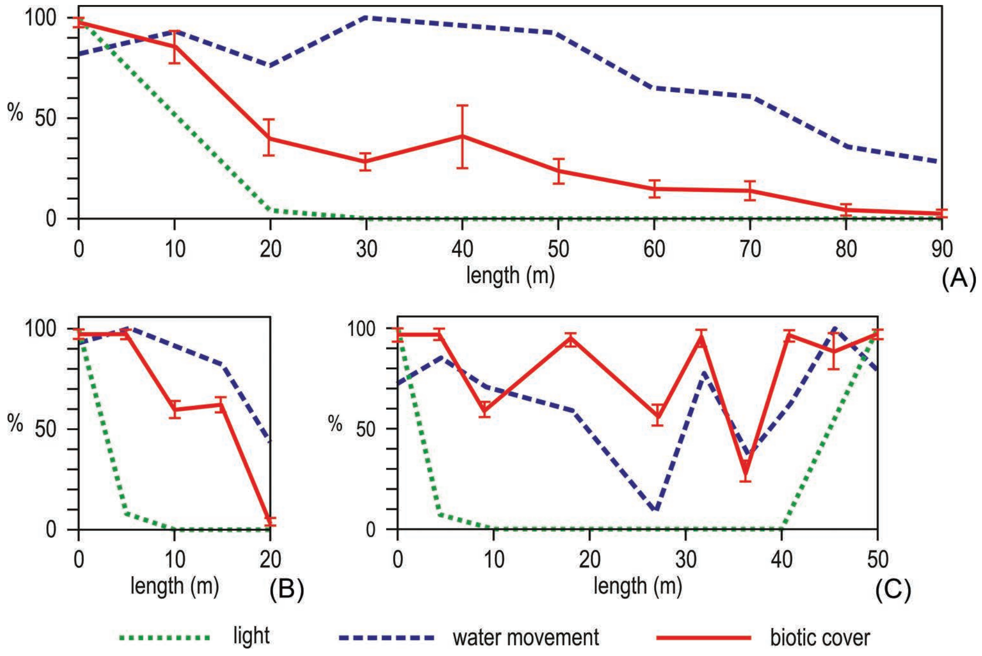

Figure 19 Differences between blind-ended caves (A, B), independently of their length, and tunnel-shaped caves (C), considering light penetration, water movement intensity and biotic cover (mean ± standard error), from the entrance to the innermost portions of the caves. Light and water movement are expressed as percentage of the maximum value measured. (A) Grotta della Cala di Mitigliano (Tyrrhenian Sea); (B) and (C) Grotta Marina of Bergeggi (Ligurian Sea). Redrawn and modified from Morri & Bianchi (2003), based on original data by Balduzzi et al. (1989) and Morri et al. (1994a).

Diversity

Species number and Shannon–Wiener (H') diversity decrease inwards, especially in blind-ended caves, in a similar way to biotic cover (Pansini et al. 1977, Balduzzi et al. 1989), although the trends are often irregular due to the patchiness of benthos (Harmelin 1985, Harmelin et al. 1985). For example, Balduzzi et al. (1989) observed a gradual decrease in the number of species in the Grotta della Cala di Mitigliano (Tyrrhenian Sea, Italy), a blind-ended cave over 80 m long, with sessile species number shifting from 60 to 10 (Figure 20). However, in several studies, diversity increased from the well-lit entrance to the semidark sections and then decreased inwards (Sarà 1962, Cinelli et al. 1977, Corriero et al. 1997b, 2000, Bell 2002, Gerovasileiou & Voultsiadou 2016, Dimarchopoulou et al. 2018), or even kept increasing to the innermost cave sections (Martí et al. 2004a,b), which were characterized by rich animal-dominated communities. Such divergent patterns were generally attributed to cave-specific topographic features which generate gradients of abiotic and biotic features.

Of course, these trends vary with the taxon under consideration, different groups dominating in different cave sections.

Regarding macroinfauna and meiofauna, the few existing studies have shown contrasting results, and thus, spatial patterns of diversity cannot be generalized. Macroinvertebrate assemblages

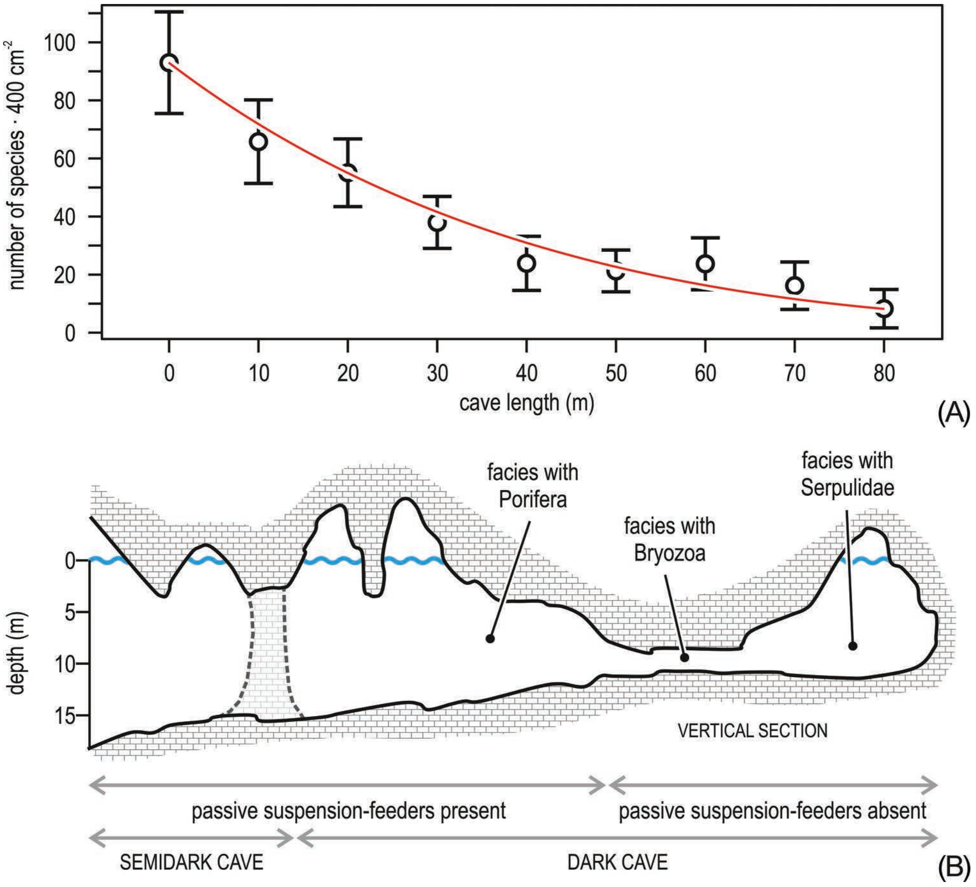

Figure 20 Decrease in species richness (A) and ecological zonation (B) in the blind-ended cave of the Cala di Mitigliano, Italy. Redrawn and modified from Balduzzi et al. (1989), Bianchi et al. (1996) and Morri & Bianchi (2003).

associated with sponges in marine caves in Lesvos Island, Aegean Sea (Gerovasileiou et al. 2016c) and hydrozoans in the Alboran Sea (Navarro-Barranco et al. 2014) were found to exhibit an inwards decrease in species richness.

Biomass

Although biomass (i.e. the quantity by weight of living matter per unit area) has rarely been measured in marine caves, a sharp decrease from the entrance towards the cave interior has been evidenced, as for biotic cover and diversity (True 1970, Gili et al. 1986, Fichez 1989, 1990b, Zabala et al. 1989). Gili et al. (1986) studied a blind-ended cave in the Medes Islands (Catalonia, Spain) and found that biomass, expressed as ash-free dry weight per square metre, decreased from the entrance (0.26 $kg \cdot m^{-2}$) to the inner portion (0.08 $kg \cdot m^{-2}$). Measurements carried out in the Grotte des Trémies (Marseille region, France) by Fichez (1989) showed that from the semidark to the dark cave zones, there was a >90% reduction in biomass. Specifically, the infaunal biomass declined from 3.4 ± 0.4 $g \cdot m^{-2}$ to 0.3 ± 0.2 $g \cdot m^{-2}$, while the epifaunal biomass declined from 305.1 ± 33.6 $g \cdot m^{-2}$ to 29.7 ± 22.0 $g \cdot m^{-2}$.

Volumetric stratification

Increasing confinement and subsequent oligotrophy towards the innermost dark cave sections causes a reduction in size and a selection of morphological groups, with the progressive replacement of erect growth forms by encrusting ones inwards (Harmelin et al. 1985, Bianchi & Morri 1994, Rastorgueff et al. 2015a, Gerovasileiou & Voultsiadou 2016, Gerovasileiou et al. 2017b). In marine caves of the north-western Mediterranean basin, sessile benthic communities at the entrance and outer cave zones are typically characterized by a well-developed upper layer that is taller than 1 dm (Figure 21), with gorgonian species (e.g. *Eunicella cavolini* and *Paramuricea clavata*) protruding into the water column for >0.5 m (Harmelin et al. 1985, Morri & Bianchi 2003). In the semidark cave sections, the height of the upper layer reduces to a maximum of 10–20 cm in the case of well-developed populations of red coral (*Corallium rubrum*). In the inner cave sections, the benthic community may appear monolayered, even in the case of 100% substratum cover, but in the transitional zone to the dark zone, it can have a thickness of a few centimetres due to the formation of bryozoan nodules (Harmelin et al. 1985, Harmelin 2000, Rosso et al. 2019). Finally, in a dark cave, sessile communities are mostly encrusting, and the upper layer usually does not exceed 1 cm in height (e.g. serpulid tubes whose terminal part arises from the substratum into the water column in order to escape the boundary layer stagnation) (Morri & Bianchi 2003). In the eastern Mediterranean basin, where large cnidarians are typically absent from the outer cave zones, the upper biotic layer may be formed by massive/tubular and arborescent sponges (Gerovasileiou et al. 2016c, 2017b).

A biological scale of hydrological confinement

As pointed out by Guelorget & Perthuisot (1983, 1992), hydrological confinement is a complex and rather abstract quantity, which cannot be accurately expressed with numbers. Confinement is mainly a hydrodynamic notion, essentially related to water exchange, but measurements of current speed and estimates of water budget in different Italian caves demonstrated that it definitely depends on both shape and size of the cavity (Morri 2003). Similarly to what had been already done for coastal lagoons by Guelorget & Perthuisot (1983, 1992), Bianchi & Morri (1994) defined a biologically based confinement scale for marine caves, taking into consideration three easily quantifiable biological parameters: (1) the structural and functional composition, as expressed by the dominant growth forms and trophic guilds, respectively; (2) the spatial organization, and above all the presence of an upper layer in the vertical development of the species assemblage; and (3) the total biotic cover of the substratum. Bianchi & Morri (1994) carried out a first test of the biological confinement scale in the Grotte del Bue Marino in the Island of Gorgona (Leghorn, Italy), two parallel caves with a predominantly subhorizontal development. The morphological characteristics of these caves, and

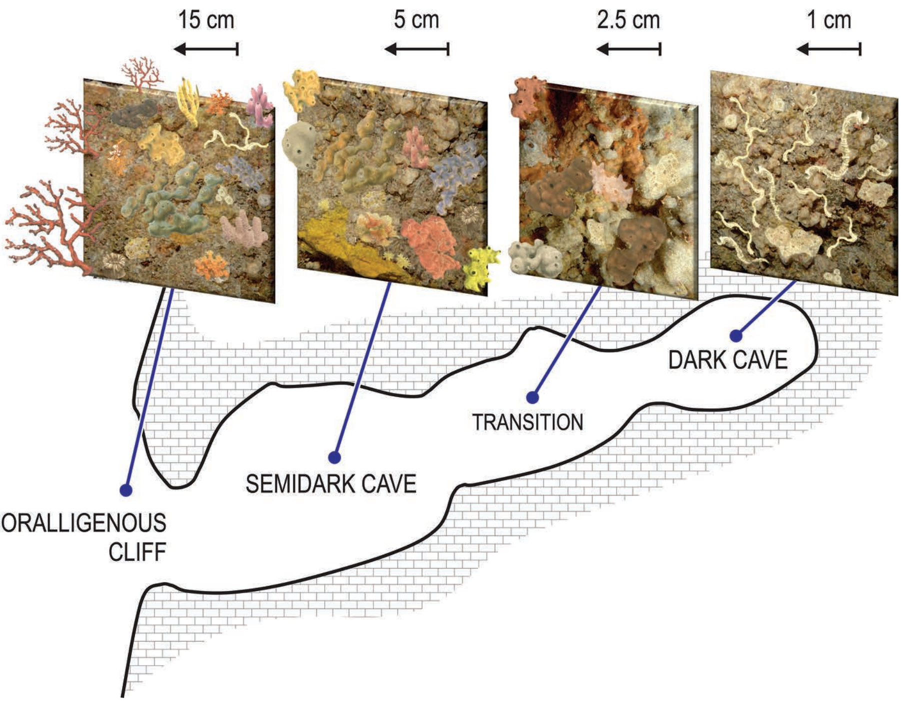

Figure 21 Loss of three-dimensional complexity in the biotic cover of blind-ended marine caves. Erect growth forms higher than 15 cm characterize the coralligenous biocoenosis at the cave entrance and are replaced by massive organisms typically not exceeding 5 cm height in semidark caves; in the transitional zone, when present, bryozoan nodules and submassive sponges may reach 2.5 cm height, whereas the dark cave biocoenosis is inhabited by encrusting organisms that may only arise 1 cm from the substratum (e.g. the terminal parts of serpulid tubes). Redrawn and modified from Harmelin et al. (1985). Animals illustrated as examples have been taken from original drawings by Toni Llobet (Ballesteros & Llobet 2015).

specifically the fact that they both have a simple linear development and blind-ended shape, can be considered as paradigmatic conditions of hydrological confinement. In addition, the fact that these are two adjacent 'twin' cavities appeared advantageous to compare directly the biological zonation observed (Figure 12):

- Degree 0 is located upstream of zone I, in the external environment.
- Degree 1 corresponds to the transition between zones I and II, at the cave entrance, and is marked by the simplification of the assemblage structure, especially by the reduction of the upper layer.
- Degree 2 is recognizable by the radical modification of the assemblage (disappearance of macroalgae), which begins to exhibit a typical cave appearance, and is situated between zones II and III.
- Degree 3 lies between zones III and IV and is indicated by the disappearance or extremely low abundance of passive suspension-feeders, especially the erect ones.
- Degree 4, between zones IV and V, corresponds to the disappearance or severe decrease of massive forms.
- Degree 5 witnesses the disappearance of sheet-like encrusting forms, between zones V and VI.
- Degree 6 is reached when all sessile fauna disappears.

Anchialine caves are characterized by highly confined conditions, beyond degree 6 of the scale above.

Ecosystem functioning

Trophic depletion

With the exception of the few caves that host chemosynthetic bacteria and the entrance sections where algae may be present, semidark and dark cave assemblages are sustained by secondary production only, due to the lack of light and the consequent absence of photo-autotrophic organisms (Riedl 1966). Even if algal filaments reach the inner semidark and dark sections of marine caves, advected by currents or waves, they fail to survive due to the lack of light (Moscatello & Belmonte 2007). Therefore, marine cave assemblages typically depend on the input of matter and energy from the external environment. By drawing their nourishment from the water column, suspension-feeders (active and passive) are the secondary producers that assimilate organic matter and energy coming from outside the cave, where it was produced, and make it available to higher trophic levels inside (Ott & Svoboda 1978, Bibiloni et al. 1984, Balduzzi et al. 1989, Bianchi 1994, Rastorgueff et al. 2011, 2015a). This explains their qualitative and quantitative dominance, which is a typical feature of all marine caves (Ott & Svoboda 1978, Bibiloni et al. 1984, Bianchi 1985). The maintenance of the marine cave ecosystem greatly depends on the input of suspended particulate organic matter in the water, which in turn depends on the water exchange in the cave. Thus, the most confined caves or cave sections will have much lower food availability (oligotrophy) and, consequently, an impoverished community in terms of species richness, biotic cover, abundance and biomass (Harmelin et al. 1985, Zabala et al. 1989, Fichez 1990b, Bianchi & Morri 1994, Bianchi et al. 1996). Trophic depletion makes ecosystems in confined dark caves highly oligotrophic, similar to those of the deep sea (Harmelin et al. 1985). The trophic depletion hypothesis was illustrated in the Grotta Marina of Bergeggi, Italy (Bianchi et al. 1986, Morri et al. 1994a), and in marine caves near Marseille, France (Fichez 1989, 1990a,b,c, 1991a,b,c). The extreme impoverishment of the dietary intake observed in the confined zones of the caves occurs through both the quantitative decrease of the nourishment (e.g. lower absolute quantity, reduction of the supply) and its qualitative degradation (e.g. high carbon/nitrogen ratio, greater proportion of complex compounds, decrease in the percentage of sugars, decrease in the ratio between chlorophyll *a* and phaeopigments) (Bianchi & Morri 1999).

Decrease in food quantity

The amount of total particulate matter, as well as the organic carbon and nitrogen it contains, decreases significantly from the semidark to the dark zone of marine caves (Bianchi et al. 2003). This decrease occurs both directly, due to the progressive sedimentation of the suspended particles, and indirectly, through their capture by passive suspension-feeders (Fichez 1991c, Palau et al. 1991, Garrabou & Flos 1995, Rastorgueff et al. 2011, 2015a). The abundance of the suspension-feeders on cave walls and ceilings is responsible for the decrease in the content of carbohydrates, lipids and proteins in the innermost cave zones. The water that reaches these areas has lost more than half of its original content of organic matter, and thus, the suspended particles reaching these areas do not provide enough energy to support an abundant benthic fauna. The situation can change during the spring season, when the warming of the open sea generates a rapid mixing of the waters with concomitant new influx of organic matter, in particular of phytoplankton (Fichez 1989, 1990b). The importance of phytoplankton in the suspended particulate material that penetrates the cave can be easily deduced from the measurement of the concentration of chlorophyll *a* in the water. In fact, in the absence of light, it cannot increase, while its decrease represents a direct index of trophic depletion. The measurements carried out in the Grotta Marina of Bergeggi (Ligurian Sea, Italy)

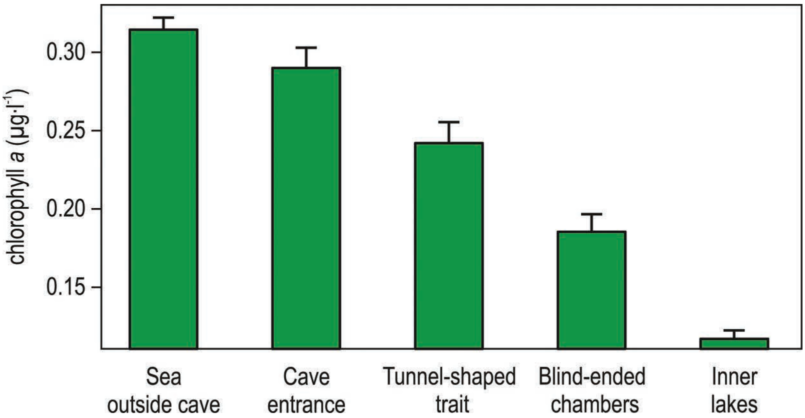

Figure 22 Chlorophyll *a* concentration in different zones of the Grotta Marina of Bergeggi, Italy. Redrawn and modified from Bianchi et al. (2003), based on data in Morri et al. (1994a).

by Morri et al. (1994a) showed that the concentration of chlorophyll *a* remains close to the typical values of the external marine environment near the entrance (Figure 22); it decreases slightly in the tunnel section, and more markedly in the blind-ended chambers of the cave, reaching very low values in the inner 'lakes'. In this case, therefore, trophic depletion seems to correspond well with the hydrological confinement gradient (Bianchi & Morri 1994).

Degradation of food quality

Moving from a semidark cave to a dark cave, not only does the total amount of organic matter decrease, but its composition changes also, with a reduction in the nutritional value of organic matter (Table 3).

- The ratio between the carbon content and the nitrogen content (C/N ratio) is an index of the nutritional value of the organic matter. Food with high carbon and little nitrogen content (e.g. cellulose) is less nutritious than food that is proportionally richer in nitrogen (e.g. proteins). Both in the Grotte des Trémies (Marseille region, France) and in the Grotta Marina of Bergeggi (Liguria, Italy), the C/N ratio tends to increase inwards (Figure 23), indicating a decrease in the food value of the suspended particulate matter (Morri et al. 1994a).

Table 3 Values of some indicators of quantity and quality of the trophic input in the Grotte des Trémies, near Marseille, France

Indicator	Semidark cave	Dark cave
Total particulate (µg·L^{-1})	1711±33	1263±48
Organic carbon (µg·L^{-1})	81.8±9.0	44.4±2.7
Organic nitrogen (µg·L^{-1})	9.3±1.2	4.3±0.3
C/N ratio	8.8±0.2	10.3±0.1
Carbohydrates (mcal·L^{-1})	123±20	48±6
Proteins (mcal·L^{-1})	187±16	89±5
Lipids (mcal·L^{-1})	312±41	135±11
Simple/complex organic matter ratio	4.1±0.6	2.3±0.1
Chlorophyll/phaeophytin ratio	256.4±159.5	5.9±0.9

Source: From Bianchi et al. (2003), based on the elaboration of data taken from Fichez (1989).

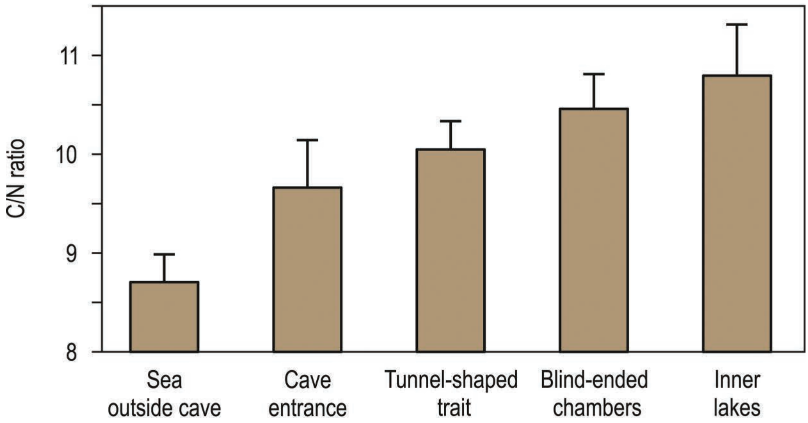

Figure 23 Food quality (expressed as carbon/nitrogen ratio), in different zones of the Grotta Marina of Bergeggi, Italy. Redrawn and modified from Bianchi et al. (2003), based on data in Morri et al. (1994a).

In both caves, the C/N ratio is lower than 17, a threshold value for animal consumption (Russel-Hunter 1970, Cocito et al. 1990). The study of the C/N ratio in the suspended particulate matter of two marine caves of Marseille region by Rastorgueff et al. (2011) showed that the ratio was higher at the entrance of Jarre Cave compared to the mid-cave and cave end, due to the rapid accumulation of organic matter (seagrass and macroalgal detritus) just inside the entrance. The high C/N value inside the 3PP Cave indicated the accumulation of refractory material close to the cave end. Regarding the C/N ratio in the particulate organic material, there were no differences between the external and internal waters of the two caves, indicating a rather fresh organic material, but in lower quantity inside the caves.

- The ratio between simple and complex organic matter can be halved in the inner cave sections, indicating a sharp decline in the quality of food available to consumers. Specifically, while the quantity of carbohydrates, proteins and lipids, which form an easily degradable fraction of the organic matter, decreases inwards, the proportions of heteropolycondensates, geopolymers, marine humic substances and other complex organic molecules, which are very resistant to degradation, increase (Bianchi et al. 2003).
- The ratio between the amount of chlorophyll and that of phaeophytin represents a further index of the quality of the suspended organic substance originating from primary production. In dark marine caves, chlorophyll is short-lived and rapidly degrades to phaeophytin. Thus, high values of this ratio will characterize ‘fresh’ vegetal organic matter, rich in live phytoplankton cells, while lower values will indicate detrital vegetal matter (Fichez 1990c). Between the semidark and the dark cave zones, the chlorophyll/phaeophytin ratio can decrease by two orders of magnitude, indicating the qualitative degradation of the food available to primary consumers inwards (Bianchi et al. 2003).

Strategies to mitigate trophic depletion

Cave biota respond to trophic depletion with a series of adaptations. Some species present physiological adaptations, such as scarce food specialization, allowing the exploitation of all possible resources (including decomposing organisms which died inside the cave), and resistance to starvation, which allows survival under an irregular and unpredictable food intake (Bibiloni et al. 1984, Culver 1985). In addition, there are also strategies that implicate the functioning of the entire cave ecosystem, rather than the physiological response of individual species. Bianchi et al. (2003)

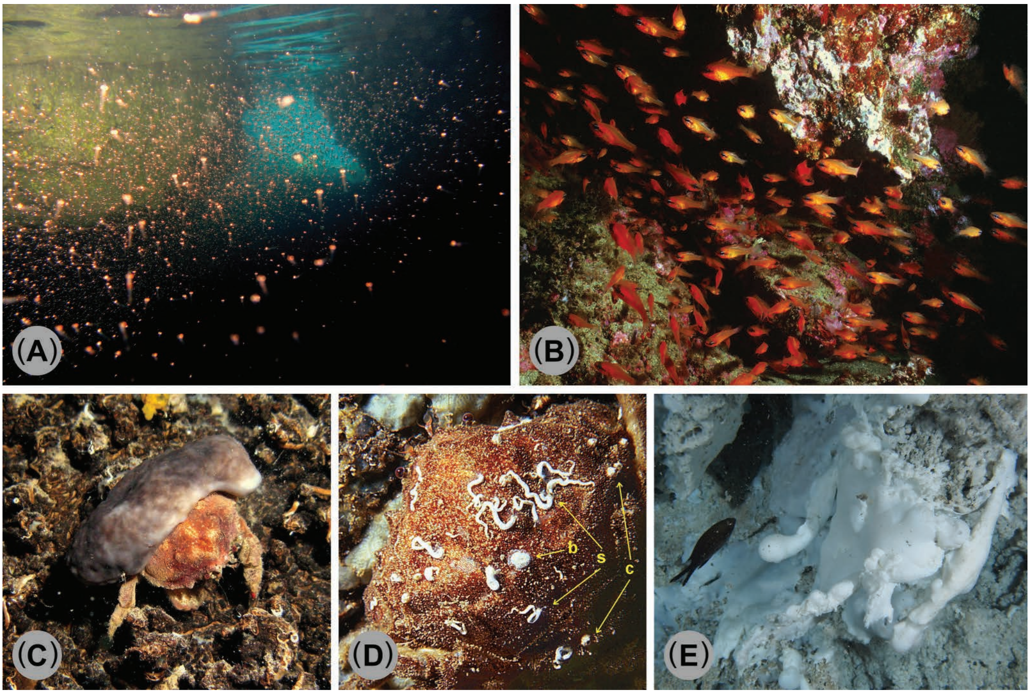

Figure 24 Main strategies to mitigate trophic depletion in Mediterranean marine caves: (A) swarm-forming mysids and (B) the cardinal fish *Apogon imberbis*, which perform nychthemeral (day–night) migrations; (C) *Dromia personata* is called 'sponge crab' due to its habit to carry the sponge *Chondrosia reniformis* on its carapace for camouflage, while the carapace of old individuals (D) may also be settled by small sessile epibionts (b = bryozoans; c = cirripeds; s = serpulids), which are therefore allowed foraging outside the cave and dispersing their propagules (epibiosis and phoresy); (E) foam-like microbial structures providing potential trophic sources for consumers such as the fish *Chromis chromis* (chemo-litho-autotrophy). Photos by V. Gerovasileiou (A and C), C.N. Bianchi (B and D) and T. Dailianis (E).

identified three principal mechanisms: diel migrations (Figure 24A and B), epibiosis and phoresy (Figure 24C and D), and chemo-litho-autotrophy (Figure 24E).

Diel migrations Motile species exhibiting diel migration patterns significantly affect the flow of energy in the marine cave ecosystem since they mitigate oligotrophy by importing organic matter. Some stygoxene species of crustaceans and fishes find shelter within caves during daytime but forage outside the cave at night. This role has been studied mostly in swarm-forming mysids (Figure 24A) and in the cardinal fish *Apogon imberbis* (Figure 24B) (Riera et al. 1991, Coma et al. 1997, Rastorgueff et al. 2011, 2015a,b, Bussotti et al. 2017, 2018). Different species of mysids form swarms of different sizes. For instance, *Hemimysis speluncola* forms swarms of millions of individuals, *H. margalefi* swarms have thousands of individuals, while *H. lamornae mediterranea* can congregate in tens to hundreds of individuals (Rastorgueff et al. 2015a and references therein). During their stay in the cave, they release faecal pellets, which increase the internal trophic load (Coma et al. 1997, Rastorgueff et al. 2011). They can also be preyed on by sessile carnivores, such as the sponge *Lycopodina hypogea* (Vacelet & Boury-Esnault 1995, Rastorgueff et al. 2011, 2015b), the actiniarian *Halcampoides purpureus* (Boero et al. 1991) and cerianthids (Rastorgueff et al. 2011, 2015a), among others. The cardinal fish *Apogon imberbis*, which is the most abundant (up to 1800 individuals per 100 m^2) and common fish in Mediterranean marine caves (Bussotti et al. 2002, 2003, 2015, 2017, 2018), can also be an important vector of organic matter, mitigating trophic depletion inside caves. This fish shelters inside caves during the day but feeds on small invertebrates (e.g. crustaceans and annelids) in rocky beds and *Posidonia* meadows at night.

Epibiosis and phoresy Large decapod crustaceans that move between the cave and the external marine environment create an opportunity for transport (phoresy) of sessile organisms. The crab *Dromia personata*, for example, is commonly called 'sponge crab' due to its habit of carrying on its carapace fragments of sponges (in caves usually *Chondrosia reniformis* and *Petrosia ficiformis*) (Figure 24C). The crab picks the sponge fragments up just for camouflage, but the sponge regenerates rapidly, survives for long periods on the crab, and can reproduce both sexually and asexually (McLay 1983, Voultsiadou-Koukoura & Koukouras 1993). Many small sessile taxa, such as serpulids, bryozoans and barnacles, can settle as epibionts on the carapace of old individuals of *Dromia personata* (Figure 24D). These sessile suspension-feeders, thanks to the phoretic transport, are able to feed outside at night, thus bypassing the hydrological confinement gradient and avoiding the trophic depletion conditions inside caves. These epibionts, besides participating in the horizontal transfer of organic matter, can represent a source of larvae capable of maintaining pseudo-populations of stygophilic taxa in caves, thus contributing to their biodiversity (Bianchi et al. 2003).

Chemo-litho-autotrophy Explorations at Cape Palinuro, Tyrrhenian Sea, brought to light caves with sulphidic hydrothermal springs (Abbiati et al. 1992, 1994). These springs convey water full of sulphurs which, being warm, unsalted, and therefore less dense, floats over the seawater and accumulates in the vault of the cave. At the interface between the marine water layer and the hydrothermal waters, a permanent chemocline is formed (Figure 25). The vault of the cave is populated by well-adapted prokaryotes (*Beggiatoa*-like bacteria), which form extensive mats and are responsible for oxidizing sulphides to sulphates (Mattison et al. 1998, Canganella et al. 2002, 2007). From this oxidation, sulphur bacteria draw energy for their metabolism, which is therefore chemo-litho-autotrophic. Thus, there is a primary source of production, not photosynthetic, but native to the cave, similar to what has already been seen in some terrestrial caves (Sarbu et al. 1996).

The profound influence that the sulphur bacterial production has on the marine cave ecosystem has mostly been studied in the Grotta Azzurra of Cape Palinuro (Tyrrhenian Sea, Italy). This production constitutes 31% of the available total particulate organic matter, thus representing an additional source of food and energy for a benthic community of consumers that is indeed unusually rich and abundant (Figure 26) (Abbiati et al. 1992, Bianchi et al. 1994, Cinelli et al. 1994, Southward et al. 1996, Airoldi & Cinelli 1997). Some species of sessile suspension-feeders, such as the sponge *Geodia cydonium* and the scleractinian *Astroides calycularis*, exhibit gigantism, which is probably

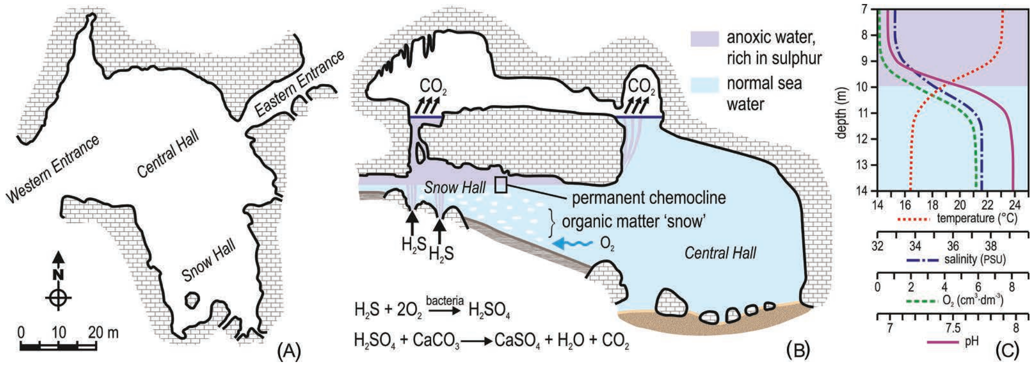

Figure 25 Sulphur-bacterial metabolism in the so-called 'Sala della Neve' (= Snow Hall) of the Grotta Azzurra of Cape Palinuro, Italy. (A) Plan view of the cave, with main cave zones indicated; (B) transverse section across the tunnel-shaped Central Hall (to the right) and the blind-ended Snow Hall (to the left), and hypothetical scheme of the sulphur chemistry; (C) vertical profiles of selected hydrological parameter across the chemocline. Redrawn and modified from Bianchi et al. (1996, 1998, 2003).

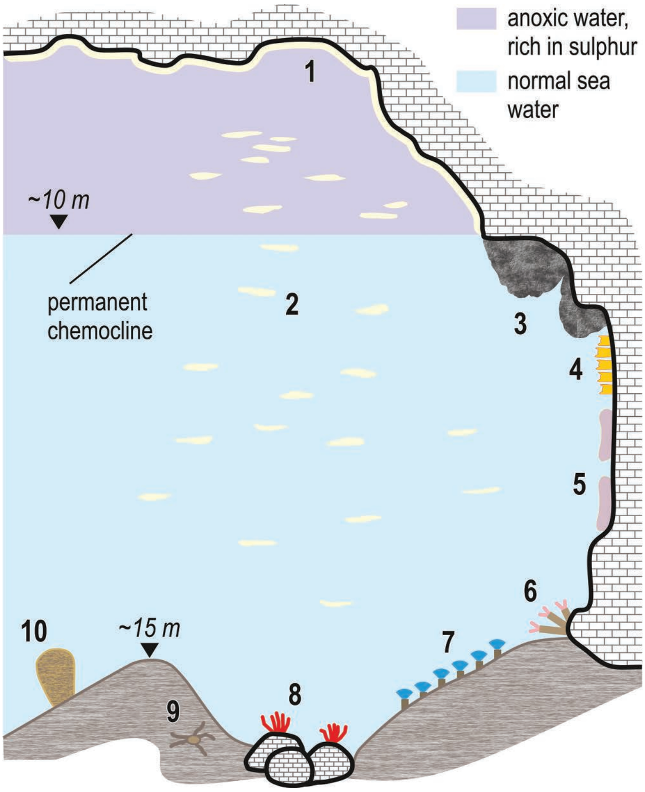

Figure 26 Biological sketch of the so-called ‘Sala della Neve’ (= Snow Hall) of the Grotta Azzurra of Cape Palinuro, Italy. 1: Sulphur-bacterial mat; 2: flakes of organic matter of bacterial origin; 3: *Geodia cydonium*; 4: *Leptopsammia pruvoti*; 5: *Petrosia ficiformis*; 6: *Phyllochaetopterus socialis*; 7: *Sabella pavonina*; 8: *Antedon mediterranea*; 9: *Ophioderma longicaudum*; and 10: *Pinna nobilis*. Redrawn and modified from Bianchi & Morri (2003).

related to the greater availability of food (Morri et al. 1994b). Other sessile taxa, such as the polychaete *Phyllochaetopterus socialis* and the hydroid *Eudendrium armatum*, ‘garden’ bacteria near their feeding appendices. Motile species, such as the sea urchin *Arbacia lixula* and the nudibranch *Doriopsilla areolata*, cross the chemocline, penetrating for short stretches into the anoxic waters above, to graze on sulphur bacterial filaments. The consumers dwelling on the cave floor, which are either suspension-feeders (e.g. the polychaete *Sabella pavonina*, the bivalve *Pinna nobilis* and the crinoid *Antedon mediterranea*) or detritivores (e.g. the ophiuroid *Ophioderma longicaudum*), also take advantage of the ‘snow’ of bacterial organic matter that falls from the ceiling in the form of white flakes, which is the origin of the name ‘Sala della Neve’ (= Snow Hall) given to this part of the Grotta Azzurra (Bianchi et al. 2003).

During a recent study on the marine cave biodiversity of the National Marine Park of Zakynthos Island (Ionian Sea, Greece), several marine caves (semi- and entirely submerged), small cavities and fissure systems located at a depth range of 0–25 m, were found to be densely colonized by egg-shaped, foam-shaped and filamentous microbial organisms, that were characterized by a strong smell of hydrogen sulphide gas (Polymenakou et al. 2018). Anaerobic enrichment cultures indicated strong methanogenesis. The studied caves were sparsely colonized by sessile invertebrates, but during underwater observations by V. Gerovasileiou, some fishes (e.g. *Chromis chromis*) were apparently feeding on white microbial aggregates advected by the excurrent water flowing from cavities and fissures (Figure 24E). Further study is required in order to investigate the trophic structure and function of these ecosystems, which are probably more widespread than previously thought.

Analogies with deep-sea ecosystems

Apart from few exceptions, the export of organic matter from marine caves to external environments is normally negligible, as are the sedimentation losses. Virtually all of the organic material present in marine caves is processed and remineralized through aerobic processes, with high efficiency (Fichez 1990b, 1991a,c, Bianchi et al. 1996). Fichez (1991a) measured benthic oxygen uptake and carbon cycling in the Grotte des Trémies (Marseille region, France) and found that while in the outer semidark zone of the cave anaerobic pathways accounted for 14% and aerobic pathways for 86% of the total benthic metabolism, the inner dark zone was a strongly carbon-limited ecosystem, where the degradation of organic carbon occurred only through aerobic processes (Figure 27).

The low respiration rates in the dark end of the cave were similar to values recorded in oligotrophic deep-sea environments (1000–2000 m depth). These characteristics make marine caves an exemplary oligotrophic (Fichez 1990a,b,c) and heterotrophic (Riedl 1966) ecosystem, similar to deep-sea ecosystems (Fichez 1989), where – in the absence of light and primary production – matter and energy are imported from shallow habitats due to drifting or gravity (Bianchi et al. 2003).

In those marine caves that have sulphur springs, the dependence of their ecosystem on chemolitho-autotrophic production recalls ecosystems that exist at great depth near hydrothermal vents on mid-oceanic ridges (Bianchi et al. 2003).

There are several other aspects that marine cave ecosystems have in common with those of the deep sea (Zibrowius 1971, Harmelin et al. 1985, Boury-Esnault et al. 1993, Vacelet et al. 1994, Harmelin & Vacelet 1997). One of the most characteristic examples is the formation of metal

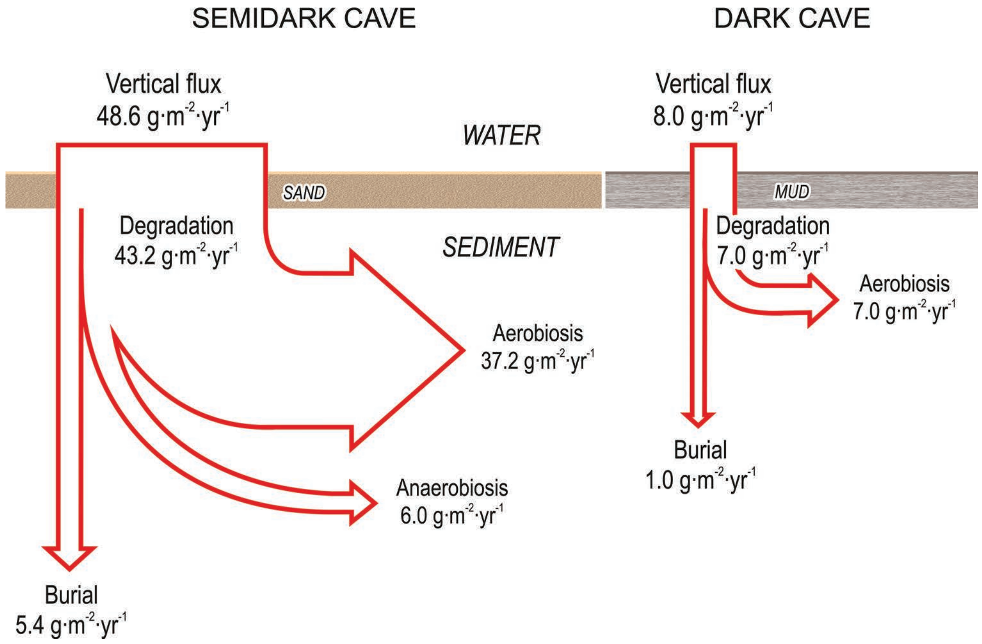

Figure 27 Organic carbon cycle at the water–sediment interface in the semidark and dark sections of the Grotte des Trémies (Marseille region, France). Organic carbon fluxes are expressed in $g \cdot m^{-2} \cdot yr^{-1}$, arrow width being roughly proportional to the amount of carbon flux. Redrawn and modified from Fichez (1991a).

patinas and nodules (Figure 8A), essentially iron and manganese oxides, which give blackish colour to the rocks and walls of the more confined dark sections of submerged caves (Laborel & Vacelet 1958, Bianchi et al. 1986, Allouc & Harmelin 2001). Their formation probably relates to bacterial metabolism, under particular physical–chemical conditions that characterize both the deep-sea and the cave environments. Therefore, confined dark caves constitute an easily accessible model or ‘mesocosm’ for the study of deep marine ecosystems (Harmelin & Vacelet 1997), which occupy over half the surface of our planet.

Trophic organization

Theoretical models on the trophic organization of Mediterranean marine cave ecosystems have been developed by Ott & Svoboda (1978), Russo & Bianchi (2003) and Rastorgueff et al. (2015a). Organic matter supply in marine caves consists principally of particulate organic matter (POM), which is usually a mixture of phytoplankton, land-derived and anthropogenic material carried to the sea by river run-off, and sewage outflow or even matter percolating through the cracks and fissures of bedrock (Rastorgueff et al. 2011, 2015a). A further contribution comes from motile organisms (i.e. crustaceans and fishes) which move outside–inside caves, on either a diel or occasional basis, leaving their faecal pellets or their remains (Figure 28).

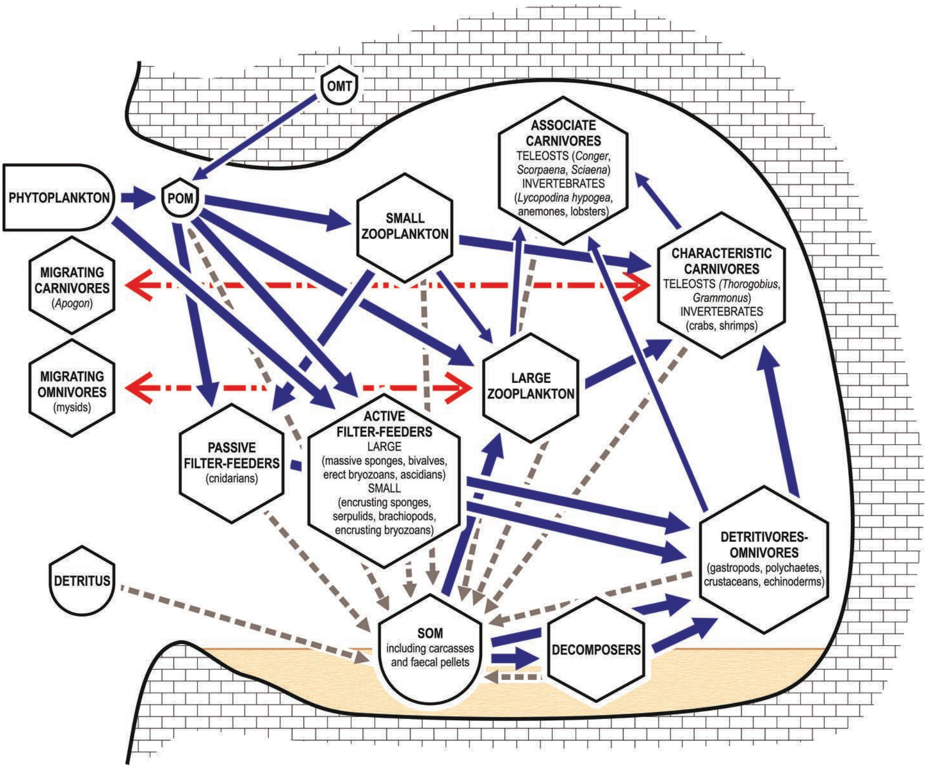

Figure 28 A simplified model of the structure and functioning of the Mediterranean marine cave ecosystem. Solid arrows denote organic matter fluxes, their thickness being roughly indicative of the assumed intensity of the fluxes. Dashed arrows represent the detrital organic matter reaching the cave floor. Horizontal dash-dotted arrows indicate nychthemeral horizontal migration of mysids and the cardinal fish *Apogon imberbis*, which may input organic matter into the cave. OMT: organic matter of terrestrial origin; POM: particulate organic matter; SOM: sedimentary organic matter. Redrawn and modified from Ott & Svoboda (1978), Russo & Bianchi (2003) and Rastorgueff et al. (2015a).

As primary producers are generally absent from inside marine caves, the major trophic-behavioural categories (Ott & Svoboda 1978, Russo & Bianchi 2003, Rastorgueff et al. 2015a) are the secondary producers (passive and active suspension-feeders), the consumers (characteristic and associate carnivores), the detritus-feeders and omnivores, the migrants and the decomposers.

Secondary producers

These are sessile animals that live by drawing directly from the organic matter imported from outside. They are suspension-feeders, either passive (e.g. cnidarians) or active (e.g. sponges, bivalve molluscs, serpulid polychaetes, bryozoans, brachiopods and ascidians). The main food resource of these taxa is plankton as well as non-living organic substance in suspension (Shimeta & Jumars 1991). Passive suspension-feeders require a higher water flow, providing nutritive particles, and thus, they are more abundant at the cave entrance and cave sections with considerable hydrodynamics, such as cave ceilings, which are characterized by more turbulent water movement (Gili & Ballesteros 1991, Russo & Bianchi 2003). Thus, their distribution towards inner cave sections is limited by water confinement, except for tunnel-shaped caves (Bianchi & Morri 1994). Active suspension-feeders are the most common and widespread taxa inside marine caves as they are comparatively less dependent on the advection of nutritive particles (Rastorgueff et al. 2015a). Many of them are colonial or modular and exhibit a wide variety of growth forms (Gerovasileiou et al. 2017b). The dominance of particular growth forms in distinct cave sections reflects an adaptation to water confinement and trophic depletion. For instance, it has been suggested that the dominance of thin encrusting sponges towards the oligotrophic inner cave sections is related to the fact that they present a more effective filtration surface/volume ratio, and thus, they can exploit the sparse particulate organic matter of the water (Bibiloni et al. 1989). All in all, secondary producers constitute the main trophic level in terms of both biomass and species richness in Mediterranean marine caves and represent the trophic substratum necessary for higher order consumers (Figure 29).

Consumers

These are animals that feed on the organic matter produced inside the cave and coming mainly from the previous level of the secondary producers. Herbivores (grazers) are generally absent from caves, due to the absence of primary producers, although echinoids from the nearby algal-dominated communities can frequently be observed grazing on plant detritus accumulated on the cave floor (Harmelin et al. 1985, Russo & Bianchi 2003). The carnivores to be found in caves include both

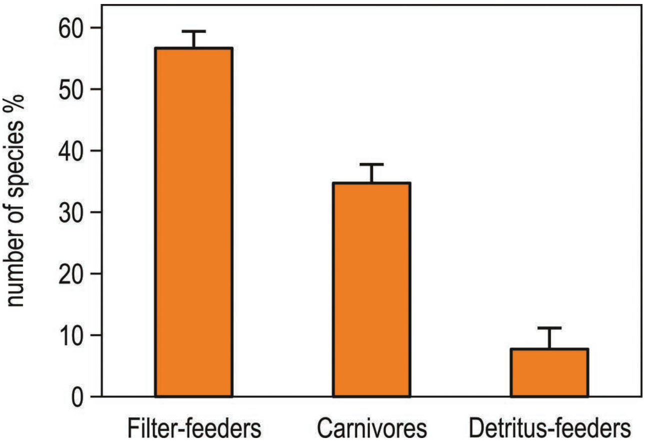

Figure 29 Qualitative dominance of trophic guilds in the polychaete assemblages of three blind-ended caves of the Sorrentine Peninsula, Italy. Redrawn and modified from Bianchi (1985).

motile and sessile forms. Motile carnivores, either stygophiles or stygoxenes, can be further categorized into characteristic carnivores, which are frequently observed in caves, although they also occur in other dark habitats, and associate carnivores, which occasionally find refuge in caves but are not characteristic of this habitat (Rastorgueff et al. 2011, 2015a). The first category includes many fish species, such as the cardinal fish *Apogon imberbis*, gobies (e.g. *Thorogobius ephippiatus* and *Gammogobius steinitzi*), the scorpion fish *Scorpaena notata*, the brotulid *Grammonus ater* and decapods (e.g. *Herbstia condyliata*, *Lysmata seticaudata*, *L. nilita*, *Palaemon serratus*, *Plesionika narval* and *Stenopus spinosus*). The associate carnivore category also includes fish species (e.g. *Conger conger* and *Phycis phycis*) and decapods (e.g. *Homarus gammarus*, *Palinurus elephas* and *Scyllarides latus*). Associate carnivores also include sessile species such as the cladhorizid sponge *Lycopodina hypogea*, the sea anemone *Halcampoides purpureus* and cerianthids (e.g. *Arachnanthus oligopodus* and *Cerianthus membranaceus*), which prey on populations of small motile taxa, such as mysids (Russo & Bianchi 2003, Rastorgueff et al. 2011, 2015a,b).

Regarding macroinfauna, the study of the gut content of soft substratum amphipods inside and outside six marine caves of Granada (Alboran Sea, Spain) showed that carnivores represented almost 60% of the amphipod species and over 80% of the abundance inside caves (Navarro-Barranco et al. 2013b). On the other hand, detritivorous amphipods were absent from cave sediments, while they dominated in adjacent external sediments. The reason behind this absence remains uncertain but could be possibly linked to physical gradients that could act as a limiting factor for the presence of detritivores or even to change of feeding behaviour under poor trophic conditions (Navarro-Barranco et al. 2013b and references therein). The study of the macroinvertebrate fauna associated with two massive-tubular sponges (*Agelas oroides* and *Aplysina aerophoba*) in two marine caves of Lesvos Island (Aegean Sea, Greece) by Gerovasileiou et al. (2016c) showed that carnivores (mainly crustaceans) dominated in terms of abundance in both sponges (especially the amphipod *Colomastix pusilla*). While carnivores dominated in terms of species richness in *Aplysina aerophoba*, deposit-feeders (mainly polychaetes) were the most species-rich feeding group in *Agelas oroides*. The trophic structure of the sponge-associated macrofauna did not change significantly across different cave sections.

Detritus-feeders and omnivores

Animals that feed on sedimented detritus, and omnivores, constitute an important component of the food chain in the marine cave ecosystem, as they make the organic matter trapped in the detritus available to other cave dwellers. Therefore, detritus constitutes an additional food source to cope with the trophic depletion in marine caves (Rastorgueff et al. 2011, 2015a). In Mediterranean marine caves, detritus-feeders and omnivores are represented by crustaceans (among which the decapods *Herbstia condyliata*, *Galathea strigosa* and *Scyllarus arctus*), gastropods, motile polychaetes and echinoderms. Large individuals of the brittle star *Ophioderma longicaudum* were found to be unusually abundant in the ‘Snow Hall’ of the Grotta Azzurra (Tyrrhenian Sea, Italy) and feeding on the ‘flakes’ of organic matter of bacterial chemosynthetic origin (Bianchi et al. 1994, Bianchi & Morri, 2003).

Migrants

In addition to swarm-forming mysids and the cardinal fish *Apogon imberbis*, other motile species, either characteristic or associate carnivores, go feeding outside at night. Examples include decapod crustaceans (e.g. *Plesionika narval*, *Palinurus elephas*, *Scyllarus arctus*, *Homarus gammarus*), cephalopods (e.g. *Octopus* spp.) and fishes (e.g. *Phycis phycis*, *Sciaena umbra*, serranids, sparids, gobies). The presence of such migrant populations, sometimes in high abundance, can represent a significant import pathway for organic matter from the outside in the form of faecal pellets, determining in certain cases local conditions for trophic improvement (Bianchi & Morri 1994, Russo & Bianchi 2003). It is not known if these species can also represent an energy loss for the cave system.

Decomposers

Little is known about decomposers (bacteria, fungi and protozoa) in marine caves, despite their very important role in the ecosystem. For example, it has been calculated that their activity produces more than 80% of the energy available in the sediments of the cave bottom (Smith et al. 1972, Zabala et al. 1989, Fichez 1991a). Important microbial mats (i.e. sulphur bacteria and mixotrophic Chrysophyceae) may develop on organic-rich sediments that accumulate in caves following disturbances (Nepote et al. 2017).

Other biotic interactions

Spatial interspecific competition

The strong environmental gradients that characterize marine caves impose a strong environmental filtering of ecological traits of the biota. Benthic taxa with similar ecological traits co-occur and functionally resemble each other in their need to respond to the same parameters. This implies that the cave ecosystem sustains a high degree of functional redundancy, thus maintaining important ecosystem processes (Gerovasileiou et al. 2017b). The dispersal of propagules from their parental habitats (inside or outside caves) is determined not only by environmental parameters (e.g. water movement) but also by larval behaviour (e.g. swimming efficiency and phototaxis), by phoresy and by a differential post-settlement survival of taxa against various environmental factors (e.g. light, food availability and spatial competition) (Benedetti-Cecchi et al. 1997, Mariani et al. 2006, Denitto et al. 2007, Moscatello & Belmonte 2007). This results in a marked spatial variability of benthic community structure and function.

Competitive interactions between different organisms significantly contribute to this spatial variability, at smaller spatial scales (e.g. different cave sections and microhabitats), where species compete for the limited available resources (Gerovasileiou et al. 2017b). One of the most characteristic examples of competition concerns availability for living space, especially at the transitional zone between the well-lit cave entrance and the semidark cave zone: sciaphilic sessile animals are competitively inferior to macroalgae, but become dominant where the reduction in light levels leads to the disappearance of the latter (Pérès & Picard 1949, Riedl 1966, Cinelli et al. 1977, Balduzzi et al. 1989, Corriero et al. 2000, Martí et al. 2004a, Gerovasileiou et al. 2017b).

The production of bioactive chemical compounds is a common defence strategy in sessile benthic taxa. Uriz et al. (1991) studied chemically mediated bioactivity in several types of benthic communities in the Balearic Archipelago and the Columbretes Islands (Spain) and found that sciaphilic and cryptic communities (i.e. the lower side of coralligenous blocks and semidark caves) harboured the highest number of bioactive species (mainly sponges, bryozoans and tunicates). The study of chemical natural toxicity in sponges, cnidarians, bryozoans and tunicates of two caves in the Medes and Cabrera islands, Spain (Martí et al. 2005, Turon et al. 2009), showed that all phyla considered included high numbers of toxic representatives. Toxicity varied significantly with season and/or cave community for sponges, cnidarians and bryozoans, although no common patterns were found for the two caves. The tunicates studied remained toxic in all seasons and communities. In the cave of Cabrera Island, the highest mean bioactivity for sponges was recorded in the innermost cave in spring. However, the highest number of bioactive sponges was found in the semidark cave community. The higher number of non-bioactive sponges in the dark cave community is possibly related to the fact that there are less interspecific contacts, due to the higher space availability. The most toxic species were the encrusting sponge *Crambe crambe* and the ascidian *Lissoclinum perforatum*. There was a negative relationship between bioactivity and sponge growth forms, with encrusting species being more toxic, suggesting either a trade-off in the allocation of energy for chemical defence and for three-dimensional growth, or that it is otherwise easier for an encrusting species to be overgrown, so it needs a stronger defence. Chemical bioactivity seemed to protect species from interspecific contact. Furthermore, toxic species generally lacked epibionts.

Santonja et al. (2018) conducted chemosensory experimental assays and found that cave-dwelling crustaceans (i.e. *Hemimysis margalefi* and *Palaemon serratus*) avoided seawater containing the chemical extracts of four sponges that are commonly found at the entrance of Mediterranean marine caves (i.e. *Aplysina cavernicola*, *Haliclona fulva*, *Oscarella tuberculata* and *Spongia officinalis*), probably due to the deterrent or toxic properties of specialized metabolites present in the sponges. On the other hand, the same cave-dwelling crustaceans were attracted by cave seawater and seawater conditioned with the sponge assemblage – in contrast to crustaceans from other habitat types – suggesting that chemical cues produced by sponges at the cave entrance could potentially guide cave-dwelling crustaceans to the entrance of caves during their diel horizontal migrations.

Therefore, chemical bioactivity of benthic invertebrates has an important role in the structuring and functioning of marine cave communities that deserves further investigation.

Ecosystem engineering

Several marine cave-dwelling taxa have the ability to create, modify or destroy benthic habitats, thus having an important ecosystem engineering role. Sessile and sedentary benthic taxa can be assigned to different categories according to their ecosystem engineering activity (Gerovasileiou et al. 2017b): ‘habitat formers’ provide habitat via their own living body; ‘constructors’ build structures with their mineral skeletons; ‘binders’ agglomerate and expand the components of the habitat framework; whereas ‘borers’ actively penetrate hard substrata via their bio-eroding activity.

Erect (arborescent or tubular) and massive sponges, anthozoans, bryozoans and other sessile taxa are habitat formers that create an upper layer which increases the three-dimensional complexity of benthic communities and support assemblages of epibionts and associated macroinfauna. Navarro-Barranco et al. (2015) studied the species composition of amphipod assemblages associated with six taxa, the sponge *Ircinia variabilis*, the anthozoans *Astroides calycularis* and *Parazoanthus axinellae*, the polychaete *Filograna implexa*, and the bryozoans *Adeonella calveti* and *Pentapora fascialis*, from Cerro Gordo Cave (Alboran Sea, Spain). In all host species, crustaceans (mostly amphipods) dominated in terms of abundance, but their assemblage structure differed significantly, with the scleractinian *Astroides calycularis* supporting the more distinctive assemblage. In the oligotrophic eastern Mediterranean Sea, erect anthozoans are absent or rare in marine caves, and thus, arborescent, massive and massive-tubular sponges, which often reach large sizes, create an upper layer in benthic communities (Gerovasileiou et al. 2015a, 2016c). The study of the macrofauna associated with the habitat-forming sponges *Agelas oroides* and *Aplysina aerophoba* in two marine caves of Lesvos Island (Aegean Sea, Greece), revealed a rich fauna comprising 86 taxa (Gerovasileiou et al. 2016c). Crustaceans dominated in terms of abundance while polychaetes were the most species rich group. Although total species richness decreased from the entrance to the innermost dark cave sections, mean density and diversity did not vary significantly, suggesting that sponges maintain their functional role as habitat formers (also characterized as ‘living hotels’ by Pearse 1950) throughout the caves by increasing habitat complexity in the impoverished inner dark cave.

Constructors are represented by several invertebrate taxa with hard body parts, skeletons or tubes, such as serpulid polychaetes, scleractinians, bryozoans, bivalves and brachiopods (Gerovasileiou et al. 2017b). The serpulid *Protula tubularia* often forms aggregates which provide the basis for the creation of ‘biostalactites’. Sponges, bryozoans, foraminiferans (e.g. *Miniacina miniacea* and *Rhizonubecula adherens*) and carbonate-forming microbes also take part in the bioconstruction process (Belmonte et al. 2009, 2020, Sanfilippo et al. 2015, 2017, Guido et al. 2016a,b, 2017a,b, 2019a,b, Rosso et al. 2021). To date, biostalactites have been discovered in dark caves of Apulia (Onorato et al. 2003, Belmonte et al. 2009, 2020, Rosso et al. 2021), Sicily (Guido et al. 2012, 2013, Sanfilippo et al. 2015) and other Italian localities (Ingrosso et al. 2018), Cyprus (Guido et al. 2017a, Jimenez et al. 2019) and Greece (Sanfilippo et al. 2017, Guido et al. 2019a,b). Another characteristic bioconstruction has the shape of small nodules and subparallel crests (approximately 2–3 cm in height), which may develop in the transitional zone between the semidark and dark cave biocoenoses, and sometimes further inside the dark cave zones (Harmelin 1985, 2000, Harmelin et al. 1985, Rosso et al. 2013a, 2015). These bioconstructions result from the concretion of several bryozoan colonies (e.g. *Onychocella marioni* and *Hippaliosina depressa* – the latter mainly in the eastern Mediterranean Sea) and other encrusting taxa (e.g. agglutinated foraminiferans, corals, serpulids and brachiopods), thus creating microstratification and a low-profile vertical structure (Harmelin et al. 1985, Rosso et al. 2019). They have been reported from marine caves near Marseille (Harmelin 1985, 2000, Harmelin et al. 2003), Sicily (Rosso et al. 2013a, 2015) and Greek islands in the Aegean and Ionian seas (Rosso et al. 2019, V. Gerovasileiou, unpublished data), those of the latter regions being smaller in size as compared to those of Marseille region. The brachiopods *Novocrania anomala* and *N. turbinata* sometimes participate into bioconstructions (Logan et al. 2004, Radolović et al. 2015, Bitner & Gerovasileiou 2021). In general, the size of the bioconstructions ranges from a few centimetres for bryozoan nodules up to 2 m for biostalactites (Onorato et al. 2003, Guido et al. 2017a, Jimenez et al. 2019, Rosso et al. 2021).

Sponges exhibit a wide variety of ecosystem engineering activities in cave ecosystems (Gerovasileiou & Voultsiadou 2012, Gerovasileiou et al. 2017b). In addition to the habitat-forming species, several others act as binders, agglomerating carbonate particles and thus expanding the habitat framework (e.g. *Geodia* spp., *Spongia virgultosa*, *Faciospongia cavernosa* and various encrusting species) together with other invertebrate taxa (e.g. bryozoans) (Ballesteros 2006, Gerovasileiou et al. 2017b).

The category of borers includes several bio-eroding and insinuating sponges (e.g. *Cliona* spp.), which often form a considerable proportion of benthic biomass in marine caves, as well as the bivalves *Lithophaga lithophaga* and *Rocellaria dubia* (Corriero et al. 2000, Ballesteros 2006, Gerovasileiou et al. 2017b). Borers penetrate actively calcareous substrata, including biogenic ones, thus creating an endolithic layer (Riedl 1966). The large amount of sponges in marine caves of Lesvos Island (Aegean Sea, Greece), and particularly of endolithic and insinuating species, was suggested to induce competition with carbonatogenetic bacteria for the same living cryptic spaces, thus preventing the development of microbialites, which are otherwise abundant in the microcavities of large biostalactites in caves of Italy and Cyprus (Guido et al. 2019a,b).

Dynamics and seasonality

Early investigations on the successional dynamics of marine caves evidenced that the development of cave communities is an extremely slow process. Harmelin (1980) used limestone plates to investigate colonization of hard substrata under dark conditions in two marine caves of the Marseille region (France): the blind-ended Trémies cave and the tunnel-shaped Moyade cave. While in the tunnel-shaped cave, 9–10 years were sufficient for colonized plates to reach a 'mature' state, with 100% of the substratum covered mainly by sponges and serpulids, in the blind-ended cave the biotic cover remained low and sponges were almost absent. These results suggest that marine caves have low ecological resilience.

The study of recruitment, settlement and primary succession of sessile benthos in the shallow, semi-submerged cave Grotta di Ciolo (Salento Peninsula, Italy), using baked clay panels, showed that while a two-year recruitment period allowed for a complete colonization of panels at the entrance zone, recruitment was very slow in the intermediate and inner dark zones, where the natural benthic communities of the cave walls were not replicated on panels (Denitto et al. 2007).

Temporal variability of marine cave communities, even on a short scale, has been rarely investigated. However, the study of sessile benthos in marine caves of Italy (Salento Peninsula) and Spain (Catalonia and Balearic Islands) showed that there are some seasonal differences in species number and cover, but they varied inconsistently with time and among caves (Martí et al. 2004a, Bussotti et al. 2006). The study of plankton assemblages along the horizontal axis of Grotta di Ciolo (Italy) revealed that the composition of the assemblage exhibited a clear seasonal cycle at the external and entrance zones of the cave, while the internal zone was differentiated, maintaining a restricted and less diverse pool of taxa throughout the year (Moscatello & Belmonte 2007). The study of soft substratum meiofauna in the same cave (three sampling stations in the dark part of the cave, at 55, 75 and 90 m from the entrance) showed that there was small seasonal variation in community structure and that the overall mean diversity did not vary with season, except for the station that was located closer to the entrance (Todaro et al. 2006). Russo et al. (2015) used artificial panels to study dynamics of hard substratum meiobenthos in the same cave, over a period of two years. As expected, taxa richness (at the family level) and the abundance of some taxa increased over time. Panel positioning seemed to affect the development of the assemblage only after the first month of deployment. However, assemblage variability of neither the artificial panels nor the natural substratum of vertical cave walls was explicable on the basis of seasonality. The study of benthic foraminiferans in two marine caves of Sardinia showed a marked reduction in foraminiferan abundance, or even disappearance, between August 2014 and April 2015, probably because of the strong freshwater flows that occurred during the rainy season, which caused the removal of superficial sediment layers (Romano et al. 2020).

A proper evaluation of ecosystem dynamics requires, as for every ecosystem, the availability of long-time series (Hampton et al. 2019), which are unfortunately rare in the Mediterranean Sea (Bianchi & Morri 2004). The Ligurian Sea (north-western Mediterranean) represents a partial exception, as historical data are available for a few caves (Bianchi et al. 2019). For instance, the sponge fauna of two semi-submerged caves was first studied in 1961–1963 (Sarà 1964) and again in 2015–2016 (Nepote et al. 2016, Costa et al. 2018). Between these studies, there was an increase in species richness and a significant change of growth forms, with massive sponges having been replaced by encrusting forms. Similar results were obtained by Parravicini et al. (2010), who compared the sessile assemblages of the Grotta Marina of Bergeggi in 1986 and 2004, i.e. before and after the summer heatwaves of 1999 and 2003 (Bianchi et al. 2019). These positive thermal anomalies (with peaks up to 4°C above the climatological mean) were suggested to have selectively killed erect and massive organisms (such as the sponge *Petrosia ficiformis*), followed by their replacement by encrusting taxa.

The Grotta Marina of Bergeggi is perhaps unique in the whole Mediterranean as it has been studied more or less regularly since the late 1970s (Bianchi et al. 1986, Sgorbini et al. 1988). The submerged part of the cave lies between the sea surface and 7 m depth, is relatively short (about 40 m), but is remarkably tortuous and morphologically complex, with both tunnel-shaped and blind-ended portions, and exhibits paradigmatic gradients of light, water movement, sedimentation and – due to freshwater infiltration – salinity (Bianchi et al. 1986). Cluster analysis of physical-chemical data, namely water temperature (°C), salinity (PSU), relative density (σ), water movement ($\mathrm{cm \cdot s^{-1}}$), light ($\mathrm{\mu W \cdot cm^{-2}}$), pH, dissolved oxygen (ppm and % saturation), organic suspended matter ($\mathrm{mg \cdot L^{-1}}$ and % of total suspended matter), C/N ratio, chlorophyll *a* ($\mathrm{\mu g \cdot L^{-1}}$), sediment mean grain size (mm), and % of fine (<0.25 mm) sediment, allowed four zones to be recognized: outer cave, main hall, shaft, and inner 'lakes' (Morri et al. 1994a). Each zone had its own biological assemblage. The outer cave was inhabited by associations of sciaphilic algae but also by typical facies of the semidark biocoenosis (Laborel 1960, Pérès & Picard, 1964), characterized by sponges, large hydroids and the anthozoan *Parazoanthus axinellae*. The main hall and the shaft harboured a typical biocoenosis of dark caves, with two different faunal zones (Laborel & Vacelet 1959). In the main hall, massive sponges (e.g. *Petrosia ficiformis*) dominated. Scleractinians (e.g. *Leptopsammia pruvoti* and *Polycyathus muellerae*) were also abundant. The motile fauna included the mollusc *Luria lurida* and the crustaceans *Dromia personata*, *Scyllarus arctus* and *Hemimysis speluncula*, the latter forming huge swarms. In the shaft, sponges were less abundant (but included *Petrobiona massiliana*). Serpulids (*Protula tubularia*, *Serpula cavernicola* and *Spirorbis cuneatus*) and brachiopods (*Argyrotheca cuneata*) were the most important elements of the sessile fauna. The motile fauna included the crustaceans

Herbstia condyliata, *Lysmata seticaudata* and *Stenopus spinosus* and the fishes *Apogon imberbis*, *Grammomus ater*, *Sciaena umbra* and *Thorogobius ephippiatus*. The inner lakes, with still water where pH fell to 7.8 and salinity to 21.2 due to freshwater infiltrations, harboured an extremely poor and rarefied assemblages, mostly characterized by scattered serpulids (*Spirobranchus polytrema*) and by the shrimp *Palaemon serratus* (Figure 8B).

The above situation remained apparently stable for about two decades. However, increased seawater temperature since the 1990s induced the substitution of the cold-water mysid *Hemimysis speluncola* by the warm-water congener *H. margalefi* (Chevaldonné & Lejeusne 2003). Such a species shift is likely to exert great influence on the energy budget of cave ecosystems (Bianchi 2007): *H. speluncola* typically forms huge swarms, while *H. margalefi* only occurs in small groups, implying a lesser role for *H. margalefi* in organic matter import from outside. Changes in the sessile assemblages led to a general homogenization of the cave communities, and the four biotic zones characterizing the cave were less distinct.

Thanks to the availability of a 30-year-long series of quantitative data (substratum cover from photo-quadrats) on the sessile communities of the Grotta Marina of Bergeggi, Montefalcone et al. (2018) evaluated ecosystem change using non-taxonomic descriptors, namely growth forms and trophic guilds, which provide information about ecosystem structure and functioning, respectively. The cave experienced a general trend of change over the years 1986 to 2013 (Figure 30A),

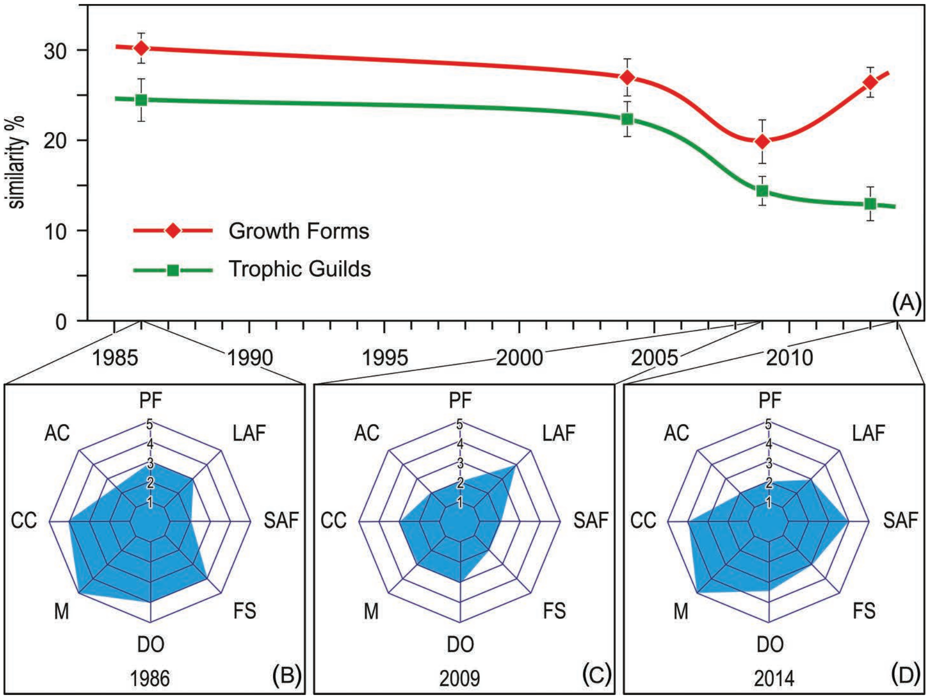

Figure 30 Changes with time in the biota of the Grotta Marina of Bergeggi (Italy). (A) Trends of average (± standard error) Bray–Curtis similarity between all the photographic samples of a given year and the 1986 centroid using non-taxonomic descriptors of the sessile assemblages: growth forms exemplify ecosystem structure, and trophic guilds represent ecosystem functioning. (B–D) Ecological quality of Bergeggi Cave in different years using the CavEBQI approach (Rastorgueff et al. 2015a), which adopts a semiquantitative scale 1–5 for eight ecological groups. PF: passive filter-feeders; LAF: large active filter-feeders; SAF: small active filter-feeders; FS: filter-feeders stratification; DO: detritus-feeders and omnivores; M: mysids; CC: characteristic carnivores; AC: associate carnivores. Redrawn and modified from Rastorgueff et al. (2015a) and Montefalcone et al. (2018).

coinciding with major local disturbances from coastal developments. The ecological quality of the cave, estimated through the ecosystem approach of Rastorgueff et al. (2015a), also underwent change (Figure 30B). Ecological group composition and structural aspects, but not functional ones, have been showing some recovery in recent years. Similar results were obtained from two caves at Ventimiglia (Italy), regularly monitored between 2010 and 2015 to assess the impact of the building of a tourist harbour (Nepote et al. 2017).

Important temporal changes have been also documented from marine caves of Spain. The comparison of photographic material collected in 1978 and 2016 from the ceiling and bottom of the submerged tunnel-shaped cave Túnel del Dofí, a popular scuba diving spot in the Medes Islands (Catalonia), revealed significant changes in benthic community structure (composition and abundance). Three-dimensional growth forms (e.g. the red coral *Corallium rubrum* and the bryozoans *Scrupocellaria* sp. and *Reteporella grimaldii*) decreased in abundance, with a concomitant increase in the abundance of encrusting sponges. The areal extent of air-pockets on the ceilings, from the air exhaled by scuba divers, increased from 0.7% in 1978 to 9.07% in 2016 (Burgués et al. 2016).

The study of sessile benthos in Cerro-Gordo submerged cave (Granada, Spain), over a decade (2007–2016), using taxonomic and morphological descriptors (i.e. major taxonomic groups and growth forms, respectively), revealed significant temporal variability in community structure and morphology in both outer and inner cave sections (Sempere-Valverde et al. 2019). During the timeframe examined, sponge cover decreased, while that of polychaetes and brachiopods increased, especially in the inner dark section. In the semidark cave section, domed morphologies also decreased through time.

The absence of long time series depicting the past ecological state of the marine cave habitat in several Mediterranean regions (e.g. eastern and southern sections) is a major impediment to the monitoring and evaluation of potential impacts and changes in their ecological status (Gerovasileiou et al. 2016b, 2017a, Sempere-Valverde et al. 2019).

Conservation value and current threats

Conservation value

Marine caves are acknowledged as 'biodiversity reservoirs' and 'refuge habitats' of great conservation value, as they harbour a rich biodiversity (32–71% of the Mediterranean sponge, anthozoan, bryozoan, tardigrade and brachiopod species) that includes a considerable number of rare, cave-exclusive, endangered, protected, and deep-sea species (Harmelin et al. 1985, Gerovasileiou & Voultsiadou 2012, 2014, Gerovasileiou et al. 2015a, Rosso & Di Martino 2016, Ouerghi et al. 2019). Among the most emblematic and charismatic species inhabiting marine caves are the Mediterranean monk seal *Monachus monachus* (Figure 31A) and the red coral *Corallium rubrum* (Figure 31B), both listed as endangered (EN) in the IUCN Red List of Threatened Species.

The survival of important monk seal populations in the north-eastern Mediterranean, especially in the Aegean Sea, is linked to the availability of high numbers of suitable cave habitats across the coasts and insular locations of the region (Voultsiadou et al. 2013) coupled with the extensive coastline of the insular locations, which provide protection from human disturbance and prevailing winds. Considering that the species has a very prolonged lactation period (Pastor & Aguilar 2003), marine caves represent a habitat of high conservation value for its survival.

The red coral has been traditionally considered a typical species of the semidark cave biocoenosis, where it can form dense facies (Pérès & Picard 1964). Recent studies have suggested that the cave habitat provides natural protection from possible human-induced disturbances, as shown by the finding of abundant and healthy populations in caves of Marseille region and Corsica (Garrabou et al. 2001, 2017).

Figure 31 Two of the most charismatic protected species in Mediterranean marine caves: (A) a group of Mediterranean monk seals, *Monachus monachus*, resting in a marine cave in the Aegean Sea, Greece (on the left an adult female with her two-month-old pup); (B) the red coral *Corallium rubrum* on the ceiling at the entrance of the Marcante cave, Portofino, Italy. Photos by P. Dendrinos (A) and C.N. Bianchi (B).

Several other protected species listed in Annexes II (list of endangered or threatened species) and III (list of species whose exploitation is regulated) of the Bern Convention and the SPA/BD Protocol of the Barcelona Convention are commonly found in caves, such as the orange coral *Astroides calycularis*, the gastropods *Naria spurca* (Figure 5I) and *Luria lurida*, the date mussel *Lithophaga lithophaga*, the hatpin urchin *Centrostephanus longispinus*, the slipper lobster *Scyllarides latus* (Figure 11E) and the brown meagre *Sciaena umbra*. In addition, all protected sponges are also found in caves, including the deep-water species *Lycopodina hypogea*, first described from the famous 3PP Cave of Marseille region (Vacelet & Boury-Esnault 1996), and typical cave-dwelling species, such as the relict calcareous sponge *Petrobiona massiliana* (Figure 5B) and the demosponge *Aplysina cavernicola*. The four Mediterranean bath sponges, listed in Annex III of the Bern and Barcelona Conventions, which were recently classified as endangered at the regional level of the Aegean Sea (Gerovasileiou et al. 2018), have been reported from numerous marine caves (Gerovasileiou & Voultsiadou 2012, Manconi et al. 2013, Padiglia et al. 2018).

Several benthic taxa are considered, so far, exclusive to this key habitat. Most of these are recorded from a small number or only from a single marine cave (Gerovasileiou & Voultsiadou 2012), even though future research might show that some could be also distributed in other cryptic or deep-sea habitats. Thus, marine caves have been considered as ‘natural laboratories’ or ‘deep-sea mesocosms’ in the littoral zone because they provide direct human access to bathyal-like conditions within reach of scuba divers (Harmelin & Vacelet 1997). In addition to the cave-exclusive and deep-sea faunal elements, marine caves harbour a considerable percentage of the total Mediterranean endemic fauna (e.g. 41% of the Mediterranean endemic sponges; Gerovasileiou & Voultsiadou 2012). This concerns not only sessile taxa, but also motile fauna, such as the rare gobids *Corcyrogobius liechtensteini*, *Didogobius splechtnai*, *Gammogobius steinitzi* and *Speleogobius trigloides*, which live in marine caves and other cryptic habitats (Bussotti et al. 2015 and references therein, Ragkousis et al. 2021).

The presence of caves in rocky coasts may provide additional resources for fishes (e.g. refuge against predators, sand patches within a rocky matrix) compared to rocky reefs without caves, thus affecting local species richness and distribution patterns (Bussotti & Guidetti 2009, Bussotti et al. 2015). Several fishes and crustaceans that shelter in marine caves (e.g. during cold seasons) or use them occasionally as nursery habitats are of commercial interest (Gerovasileiou et al. 2015a). Furthermore, recent studies have raised biotechnological interest in cave biota (e.g. sessile taxa and microbial mats) as potential sources of bioactive substances (Uriz et al. 1991, Martí et al. 2005, Turon et al. 2009, Audoin et al. 2013) and for bioenergy and bioremediation (Polymenakou et al. 2018).

The high and unique biodiversity of marine caves, coupled with their geomorphological complexity and high aesthetic value, make them popular locations for marine-based recreational activities (Rovere et al. 2011, Salomidi et al. 2012), such as boat tours, snorkelling and scuba diving throughout the Mediterranean Sea. In addition, some marine caves are interesting from paleontological, archeological and paleo-climatological perspectives (e.g. Antonioli et al. 2001, Poulakakis et al. 2002, Collina-Girard 2004, Galanidou et al. 2020). Notable examples include the famous Grotte Cosquer in the Marseille region and the Elephant’s Cave in Crete.

The examination of a biostalactite collected in the ‘lu Lampiùne’ marine cave in Italy (Apulia) showed that its accretion started ca. 6000 years ago with a rapid growth of large-sized serpulids (*Protula*), and then decreased ca. 3000–4000 years ago, reflecting a shift in main bioconstructors, probably caused by environmental changes (Belmonte et al. 2020, Rosso et al. 2021 and references therein). Other examples of unique bioconstructions include large sponge masses of the lithistid *Neophrissospongia endoumensis* recently found in marine caves of Crete (Greece) by Pisera & Gerovasileiou (2021) that could be approximately 769–909 years old in the case of the largest specimen observed (about 100 cm across). The occurrence of such slow-growing formations highlights the urgent need for appropriate management and conservation actions.

For all the foregoing reasons, marine caves are listed for protection by the EU Habitats Directive (92/43/EEC – habitat code 8330 ‘Submerged or partially submerged sea caves’) and, at the Mediterranean level, under the ‘Action Plan for the conservation of the coralligenous and other calcareous bio-concretions’, which also integrates semidark cave communities (Ballesteros et al. 2008), and the ‘Dark Habitats Action Plan’ for the conservation of habitats and species associated with seamounts, underwater caves and canyons, aphotic hard beds and chemo-synthetic phenomena in the Mediterranean Sea of the Barcelona Convention (Pergent et al. 2015).

The number of marine caves included in marine protected areas (MPAs) is unknown, although the habitat is represented in 33 Mediterranean MPAs (Abdulla et al. 2008). Despite designations and conservation action plans, according to a preliminary comparison of different protocols for marine cave visitation worldwide, in most countries no specific regulations or management plans are implemented (Petricioli et al. 2015). Surprisingly, few MPAs have set specific limitations regarding the maximum number of divers or have required permits for visiting caves. The large number of marine caves in coastal areas with extensive rocky outcrops, coupled with the lack of detailed mapping and monitoring initiatives, hinders the effective conservation and management of these unique ecosystems and the evaluation of potential impacts on cave biota. Therefore, marine caves are currently exposed to numerous threats and impacts.

Threats and impacts

Marine caves are fragile ecosystems, vulnerable to both natural and human disturbances (Giakoumi et al. 2013, Rastorgueff et al. 2015a). Severe storm waves can occasionally reach the innermost parts of caves, bringing in sediment and detritus and abrading walls and ceilings, thus causing mortality of the cave-dwelling organisms. Marine heat waves, which cannot be considered as a natural disturbance, the present seawater warming being mostly of anthropogenic origin (Bianchi 2007), cause important changes to both the motile and sessile components of cave communities (Chevaldonné & Lejeusne 2003, Parravicini et al. 2010, Costa et al. 2018, Sempere-Valverde et al. 2019).

Despite difficult access to caves, when compared to open sea habitats, there is increasing evidence of local impacts caused by human activities, such as illegal red coral harvesting, spearfishing (e.g. of *Sciaena umbra* and *Phycis phycis*), urbanization and building of coastal structures, waste outflows, littering (Figure 8D), and multiple unregulated visits by tourist boats and divers (Di Franco et al. 2010, Guarnieri et al. 2012, Giakoumi et al. 2013, Rastorgueff et al. 2015a, Nepote et al. 2017, Mačić et al. 2018, Sempere-Valverde et al. 2019). Sessile benthic communities in marine caves have low recovery potential, since the development of communities in a 'mature' state could take more than a decade (Harmelin 1980, Harmelin et al. 1985, Rastorgueff et al. 2015a). Several sessile invertebrates with erect morphologies, as well as their bioconstructions, are slow-growing, fragile, and thus highly vulnerable to mechanical damage caused by divers colliding unintentionally with them, which is more likely to happen inside caves and beneath overhangs than elsewhere. Typical examples are the anthozoans *Astroides calycularis*, *Leptopsammia pruvoti*, *Parazoanthus axinellae* and *Corallium rubrum*, and the erect and fragile bryozoans *Myriapora truncata* and *Reteporella* spp. (Figure 32)

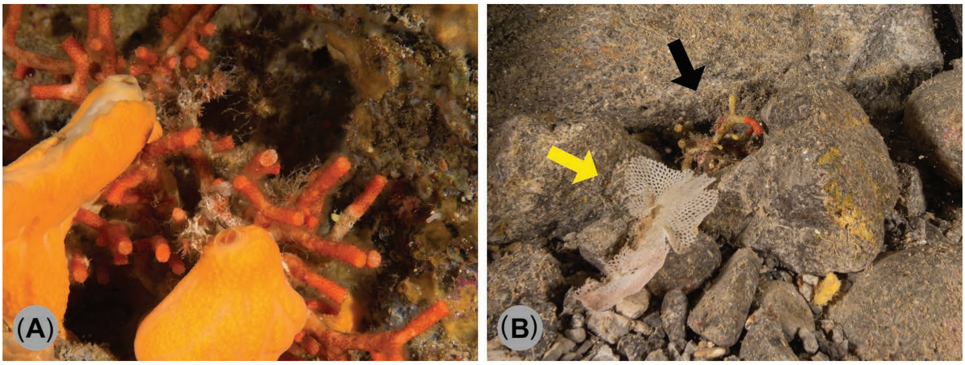

Figure 32 Erect bryozoans are fragile and vulnerable to mechanical damages: (A) the 'false coral' *Myriapora truncata* is a typical dweller of cave walls and ceilings; (B) fallen fragments of the branching species *M. truncata* (black arrow) and *Reteporella* sp. (yellow arrow) on a rocky cave floor, detached from the walls and ceilings either naturally or due to contact with divers. Photos by T. Dailianis.

(Milazzo et al. 2002). The comparison of benthic assemblages of three marine caves from the MPA of Capo Caccia (Sardinia, Italy), characterized by different intensities of diving tourism, showed that organisms with erect calcareous skeletons are the most vulnerable to diving activities and that the quantity of skeletons and skeletal fragments in cave bottom sediments is a good indicator of the level of diving impact (Scinto et al. 2010). Di Franco et al. (2009) evaluated diver behaviour in seven types of subtidal habitats in Capo Gallo-Isola delle Femmine MPA in Sicily and found that the highest rates of total and unintentional contacts occurred in caves (in particular by divers with higher certification levels). The anthozoans *Eunicella singularis* and *Astroides calycularis* were the species most frequently damaged by divers. Guarnieri et al. (2012) examined the effect of recreational diving on four marine caves in MPA of Capo Caccia-Isola Piana (Sardinia, Italy) where diving activities are regulated and found that organisms with vertical growth and rigid body structure (e.g. *Lithophyllum stictiforme*, *Reteporella grimaldii* and *Idmidronea triforis*) were significantly more abundant and homogeneously distributed in a fully protected cave than in the visited ones. Sediment resuspension and accumulation of exhaled air bubbles at the cave ceiling can also have detrimental effects on sessile suspension-feeders (Milazzo et al. 2002, Lloret et al. 2006, Di Franco et al. 2010, Burgués et al. 2016). Coastal structures (e.g. jetties, breakwaters, groynes) alter sediment transport and may cause increased sediment deposition in the innermost parts of caves (Figure 8C), with consequent smothering of the encrusting fauna (Nepote et al. 2017, Montefalcone et al. 2018).

An additional potential threat to Mediterranean marine cave communities is related to the continuous spread of non-indigenous species, especially in the eastern and southern regions. A total of 56 non-indigenous species (NIS) and cryptogenic taxa have been reported so far from approximately 50 marine caves and tunnels of the Mediterranean (Gerovasileiou et al. 2016b), including molluscs (15), cnidarians (9), bryozoans (7), polychaetes (6), crustaceans (6), macroalgae (3), fish (3) and tunicates (2). Most of these taxa (66%) were found in caves of the south-eastern Levantine Sea (mainly in Lebanon: Zenetos et al. 2015), with shipping and Lessepsian migration through Suez Canal being their main pathways of introduction (Figure 33). These taxa were mostly reported from the entrance and semidark zones of shallow and semi-submerged caves and tunnels. The impacts of these taxa on native cave dwellers have not been investigated to date. Nevertheless, their presence in most marine caves of the Levantine and southern Aegean seas, and the population explosion of non-indigenous fishes, for instance *Pempheris rhomboidea* (Figure 34A), *Pterois miles* (Figure 34B) and *Sargocentron rubrum*, in marine caves of this regions should be further studied and monitored (Gerovasileiou et al. 2016b, and unpublished data by both authors).

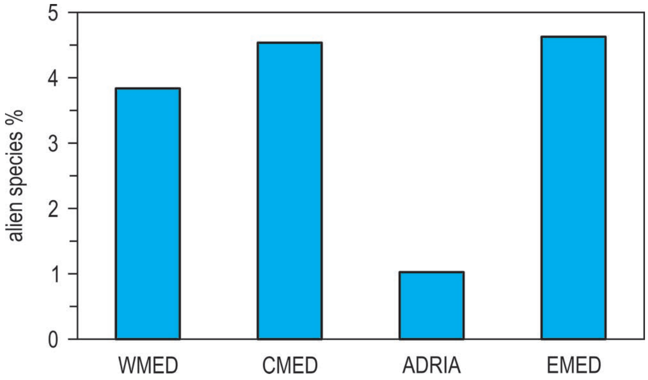

Figure 33 Occurrence of alien species in marine caves expressed as percentage of the total number of alien species known in the corresponding Mediterranean ecoregion. WMED: western Mediterranean: CMED: central Mediterranean; ADRIA: Adriatic Sea; EMED: eastern Mediterranean. Based on data from Gerovasileiou et al. (2016b).

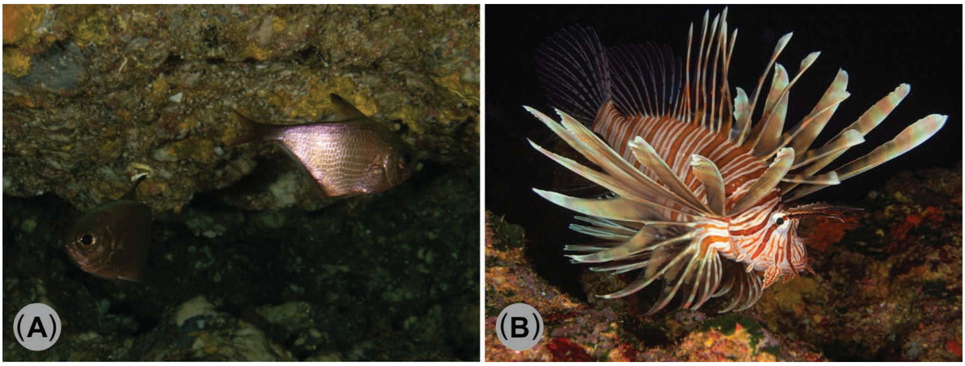

Figure 34 Several non-indigenous species of Indo-Pacific origin have invaded marine caves of the eastern Mediterranean Sea: (A) the sweeper *Pempheris rhomboidea* can form large schools in caves and crevices; (B) the highly invasive lion fish *Pterois miles* is common in marine caves of the Levantine, south Aegean and Ionian seas. Photos by T. Dailianis.

Conservation priorities and suggestions

Marine cave communities are characterized by high levels of 'individuality', generated by cave-specific topographical features (Bussotti et al. 2006, Gerovasileiou et al. 2013), but also by large-scale biogeographic heterogeneity, with several cave-exclusive and rare taxa recorded only from a few or a single marine cave (Gerovasileiou & Voultsiadou 2012). This points to the need for protecting marine caves of different morphological types in different biogeographic regions, in order to address small- and large-scale heterogeneity, thus safeguarding maximum representation of diversity aspects (Gerovasileiou & Voultsiadou 2012, Giakoumi et al. 2013). Special priority should be given to

- Particular cave types or caves with geomorphological features and microhabitats that could support unique communities (e.g. anchialine caves, marine caves with sulphur or internal freshwater springs, those having a descending profile or vertical pits, caves with bioconstructions)
- Caves harbouring cave-exclusive, relict and rare species (e.g. steno-endemics)
- Caves harbouring protected, threatened and commercial species
- Caves with high species richness and functional diversity.

In addition, given that cave ecosystems largely depend on external trophic inputs and larval supply from nearby environments (Harmelin et al. 1985, Fichez 1990b, Benedetti-Cecchi et al. 1997, Jimenez et al. 2019), it is important to safeguard good ecological status and maintain connectivity with nearby habitats (e.g. rocky reefs and *Posidonia* meadows) in conservation planning.

Gaps in scientific knowledge and future research directions

Despite the fact that marine caves of the Mediterranean Sea have been studied more intensively than those in any other region of the world ocean (Gerovasileiou & Voultsiadou 2016), there are still important gaps in our knowledge regarding their distribution, biodiversity, ecosystem structure and functioning, dynamics, ecological status, impact and management potential.

Previous overviews on Mediterranean marine caves (Bianchi et al. 1996, Cicogna et al. 2003, Gerovasileiou & Voultsiadou 2012, 2014, Gerovasileiou et al. 2015a) highlighted that information on their distribution and biodiversity remained highly scattered and fragmented. In addition, several gaps and limitations came up, such as (1) lack of geographic coordinates and geomorphological information (e.g. water depth of the entrance and cave type) about numerous marine caves; (2) several caves having the same names (e.g. 'Blue Cave'); (3) lack of ecological information (e.g. cave zone and depth) about several taxa recorded from caves; and (4) taxonomic inconsistencies (e.g. synonymies and possible misidentifications). The recent development of online open access biodiversity information systems, such as the World Register for marine Cave Species (WoRCS) thematic database (Gerovasileiou et al. 2016a, 2020) and synergies between parallel initiatives, regional (sub) registers and infrastructures, provide the platforms and tools in order to catalogue, quality control and eventually mobilize datasets (e.g. georeferenced, taxonomically updated species lists accompanied by relevant metadata). In addition, citizen science initiatives could significantly contribute to increase data availability on the distribution and biodiversity of marine caves, and possibly their monitoring, especially in understudied regions.

Based on the gaps identified during the present and previous reviews, it is recommended that future marine cave research should focus on

- Filling regional knowledge gaps, e.g. baseline studies and inventories in understudied southern and eastern Mediterranean regions, such as the north African, Aegean and Levantine coasts.
- Filling thematic gaps regarding particular groups of biota (e.g. microbial diversity and meiofaunal taxa), cave assemblages and formations (e.g. sediment infauna and bioconstructions), deeper caves (in the circalittoral zone and in deep waters) and peculiar cave types (e.g. anchialine caves and caves with hydrothermal activity or freshwater springs).
- Understanding and monitoring ecosystem structure and functioning (e.g. biotic interactions) and revisiting previously studied caves in order to assess potential changes and impacts caused by different drivers (e.g. water temperature rise, non-indigenous species, human visitation).
- Investing in multidisciplinary, integrated approaches and capacity building in order to better understand abiotic–biotic interactions, impacts or even to investigate potential applications in the framework of the Blue Growth sectors (e.g. biotechnology).
- Investigating and applying management (including monitoring) and restoration options/protocols, at different spatial scales in order to achieve future conservation targets.

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‘A CLOSE AND FRIENDLY ALLIANCE’: BIOLOGY, GEOLOGY AND THE GREAT BARRIER REEF EXPEDITION OF 1928–1929

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Abstract The 1928–1929 Great Barrier Reef Expedition marks an important milestone in the evolution of modern coral reef science, from its nineteenth-century theoretical and deductive foundation – so clearly exemplified in Darwin’s coral reef theory – to the twentieth-century focus on empirical and analytical studies. Here, we consider the anatomy of the expedition, its antecedents, its immediate scientific achievements and its longer-term legacy. This truly interdisciplinary expedition differed from its ship-borne or short-stay reef reconnaissance predecessors, being housed on a single reef and sand cay (Low Isles, northern Great Barrier Reef) for a period of 13 months. Its intensive, rather than extensive, investigations involved meticulous microscopic work and painstaking laboratory and field observation, measurement and experimentation, cataloguing linkages between reef habitats, tidal processes and physical and chemical properties of water, as well as a quantitative inventory of reef-flat and reef-front biota spatially grounded in accurate transect surveys and planimetric controls. Results were published in the Expedition’s exhaustive Scientific Reports over the next three decades, as well as in a host of other scientific journals.

We assess the Expedition’s major achievements: highlighting the importance of the carnivorous diet of corals; describing a natural coral bleaching event and mechanisms of algal loss; determining how corals survive submerged within variably oxygenated and turbid waters; estimating adult and juvenile coral growth rates and the effects of transplanting corals; understanding relationships between lunar periodicity and mass spawning of corals; and recognizing the commonalities and differences in reeftop sediments and landforms and their indicative role of past storms and sea levels and contemporary morpho-dynamic changes. Finally, we argue that these and many other topics explored during the expedition continue to be relevant in modern reef science, not least in providing an exceptional set of ecological and geomorphological benchmarks against which it has been possible both to measure one hundred years of ecological and morphological change and to provide a dynamical environmental envelope against which to assess potential future changes.

Keywords: Coral Physiology; Coral Growth; Coral Bleaching; Reef Flat Ecology; Low Wooded Islands; Reef Island Mapping

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Introduction

'but the time has come when a close and friendly alliance between workers in all sciences concerned with coral reefs is not only desirable but necessary' J.A. Steers (1930, 2) in A Geographical Introduction to the Biological Reports, Scientific Reports of the Great Barrier Reef Expedition 1928–1929, Volume III.

'*results were pooled and compared, so that the surveyor was forced to understand that a reef is a living organism and the biologist was made to realise that he must measure his environment. Each group kept the other in mind'*. Comments by Michael Spender in answer to questions during discussion at the Royal Geographical Society (RGS) following publication of 'The Coral Islands and Associated Features of the Great Barrier Reefs': Discussion' by Balfour et al. (1937, 141).

Almost 100 years ago, in 1922, steps were taken to initiate the 1928–1929 Anglo-Australian Great Barrier Reef Expedition (Brown 2007a). As this centenary, and that of the expedition itself approaches, it is worth re-examining the role that this interdisciplinary research effort played in defining a new era of reef science and its relevance to coral reef studies today. Stoddart (1969, 433–434) noted 'that the work of the Great Barrier Reef Expedition of 1928–1929 emphasized for the first time the relationships between reef growth and environment and the critical importance for their study in the field' while Mather (2002, 459) viewed the expedition as having 'a profound effect on coral science for the next 45 years'. The continued significance of this expedition is marked by the numerous recent citations of this pioneering research over 90 years since its first execution (Edmunds and Gates 2003, Holmes 2008, Todd 2008, Downs et al. 2009, Goodkin et al. 2011, Wijgerde et al. 2011, Hoegh-Guldberg et al. 2017, Coles et al. 2018, Nelson & Altieri 2019). In this chapter, we revisit and emphasize previously unacknowledged important findings of the Expedition and contextualize their significance and legacy, with both a retrospective awareness of subsequent Australian and international research pertaining to coral reefs and for those discovering these achievements for the first time.

Background

The 1928–1929 Expedition marks an important step in the evolution of modern coral reef science, from nineteenth-century concerns with theorizing and deductive reasoning, based on generalized mapping and the interpretation of hydrographic charts, to a twentieth-century focus on empirical studies with a strong emphasis on field observation, measurement and experimentation. The drivers for this shift came from the widening geographical exploration of reef systems, the growth of seasonal and then permanent field stations, and the move from largely individual inquiry and exploration to programmes of research framed by national and international scientific agendas set by Academies of Science and their Committees (although often driven by committed scientific visionaries) (Spencer et al. 2008).

The long sequence of events that led to the Expedition's arrival at Low Isles on the northern Great Barrier Reef in July 1928 has been set out by Hopley et al. (2007), Brown (2007a) and, in some detail, by Hill (1984) and Bowen & Bowen (2002). These authors identify a set of key milestones: Charles Hedley's paper on biological field stations at the Pan-Pacific Union in Honolulu in August 1920; Henry Richards' presentation on the 'Problems of the Great Barrier Reef' to the Queensland Branch of the Royal Geographical Society of Australasia in April 1921; the formation of the Society's Great Barrier Reef Committee in September 1922; and Richards' paper on 'The Great Barrier Reef of Australia' at the Second Pan Pacific Science Congress, held in Melbourne and Sydney in August 1923. These signal events need to be seen, however, in the context of not only the loosening of the old colonial ties (albeit with the maintenance of the historical linkages to the major London institutions for science and exploration), the parallel scientific engagement with emerging US interests in the Pacific (exemplified in a coral reef context by the roles taken by W.M. Davis, T. Wayland Vaughan and A.G. Mayor) but also both scientifically and politically, through the 'emerging self-image of science in Australia' (MacLeod & Rehbock 2000, 209).

Much of the stimulus for a renewed interest in Pacific coral reef research at the beginning of the twentieth century came from the leading geomorphologist of the day, William Morris Davis. Davis wrote his first paper on coral reefs in 1913, to celebrate the centenary of the birth of James Dana, geologist and mineralogist on the United States Exploring Expedition (1838–1842) (Davis 1913); it was Dana's highly popular *On Coral Reefs and Islands* (1872) that established coral reefs as a legitimate object of scientific inquiry in North America (Appleman 1985). This was a field of research that then consumed Davis for the next 15 years,[1] culminating, at the age of 78, in his major publication, *The Coral Reef Problem* (Davis 1928). Like many of the theorists before him, Davis' physical engagement with the Great Barrier Reef was remarkably slight. Following the British Association for the Advancement of Science 'imperial meeting' in Melbourne and Sydney in August 1914, he spent one night on Green Island, near Cairns (Figure 1), 'an entertaining experience' but 'entirely fruitless as far as the origin of the reef is concerned' (Davis 1928, 347). However, when he returned to the USA, he proposed that more extensive coral reef work should be organized by all interested Pacific nations; this was taken up by the American Association for the Advancement of Science and folded into the plans for a congress of the newly formed Pan-Pacific Union. The Congress took place in Honolulu from 2 to 20 August 1920, with Davis present. The Australian attendees included

Figure 1 Great Barrier Reef between 14 and 17°S, with locations mentioned in the text.

Ernest Clayton Andrews, senior geologist of the New South Wales Geological Survey (from 1899; and its Director (1920–1930)) (Walsh 1979) who had accompanied Davis to New Caledonia and the New Hebrides ahead of the 1914 meeting; Charles Hedley, conchologist and (then) Acting Director of the Australian Museum, Sydney (Fairfax 1983); and Henry Caselli Richards, the recently appointed (1919) Professor of Geology at the University of Queensland (Hill 1988). Following the 1920 meeting, one of the prime organizers of the conference, the Yale geologist and then Director of the Bishop Museum, Herbert E. Gregory, established a group to determine the location of the next meeting. This group included Andrews and the American geologist Thomas Wayland Vaughan who had entered Harvard University as a graduate student in 1892, two years after Davis' promotion to Professor of Physical Geography (Thompson 1958). In 1919, Gregory had been appointed to chair the newly formed US National Research Council's Committee on Pacific Investigations of which Vaughan became vice-chair. Given the backgrounds of Gregory, Vaughan and Andrews, it is perhaps not surprising that the intellectual rationale for the next gathering – the Pan-Pacific Congress of 1923 – was emphatically geological (MacLeod & Rehbock 2000). This was particularly strongly articulated by Andrews: 'To appreciate the possibility of this community of scientific interests it is necessary to understand the underlying geographical and structural unity of the area, which is shown in the peculiar and symmetrical arrangements of its ocean depths, its volcanoes, its earthquake zones, its mountain ranges, its islands, and its coral reefs. The simplest explanation of this remarkable unity is that the floor of the Pacific Ocean has sagged slightly as a whole, and that the bordering continents have been drawn to it in the form of earth waves, undulations, or crinkles'.[2] And writing to Vaughan a year later, he ventured to suggest 'The more I consider the case for the 'Geographical Unity of the Pacific['] and the attempt to co-ordinate the present state of knowledge of the structure of the continents, the more it seems to me that the sub-oceanic mass of the Pacific appears to exercise a great control on the surrounding continents. It has occurred to me that this work might be undertaken some time by somebody – perhaps myself – who could coordinate all the main facts of structure within the Pacific Region'.[3]

While the determination, and political networking skills, of Henry Richards were critical in general terms in promoting scientific research on the Great Barrier Reef, his energies were strongly directed towards geological problems. Is the Great Barrier Reef 'in a static condition or one of elevation or of subsidence'? Richards asked (1922, 51), highlighting the debates around 'the coral reef problem' that had been circulating since the mid-nineteenth century and which had drawn the Great Barrier Reef's structure and history into their orbit. The theoretical framework for explaining the large-scale structure and distribution of coral reefs had been set by the Darwinian revolution of the 1830s and 1840s yet neither Darwin himself, nor one of his greatest supporters, Dana, ever set foot on any of the reefs of the Great Barrier Reef (Mozley 1964); it was left to Joseph Beete Jukes, geologist on the survey vessel H.M.S *Fly*, to apply the Darwinian model to the Reef (Jukes 1847, Vol 1, 333). Jukes had met Darwin before leaving England in April 1842, sailed with a copy of *The Structure and Distribution of Coral Reefs*, and once in Sydney discussed Darwin's theory with W.B. Clarke (Mozley, 1969), like Darwin and Jukes, a former pupil of Adam Sedgwick, Woodwardian Professor of Geology at the University of Cambridge. It was Clarke who made Jukes aware of Dana's support for the subsidence theory (Stoddart 1988). Jukes' argument was not unproblematic: as elsewhere, the application of Darwin's theory was wholly inferential, the subsidence process being too slow to be demonstrated by observation and the critical test of the presence of great thicknesses of shallow water limestones not amenable to mid-nineteenth century drilling technologies (Stoddart 1989). It was not difficult therefore for Alexander Agassiz, on the basis of minimal fieldwork during the 1896 cruise of the steamer *Croydon*, and with 'free indulgence in speculative interpretation' (Stoddart 2018, 167), to propose an equally untested, and diametrically opposed, history for the Reef. Agassiz argued that the Great Barrier Reef was the product of the 'mere action of erosion and denudation' (Agassiz 1898, 127) leading to 'a comparatively thin veneer of coral rock overlying the denuded land' (Agassiz 1913, 320). When coral boring did become feasible, this was undertaken in an oceanic setting at Funafuti Atoll, 3500 km east of the Great Barrier Reef, over three expeditions between 1896 and 1898. While the first of these expeditions was very much an initiative of the Royal Society of London, the second and third expeditions, a rejection of the old system of imperial dominance (Macleod 1987), were led from Sydney by the charismatic T.W. Edgeworth David and, under Edgeworth David's direction, A.E. Finckh respectively. Drilling across the three campaigns achieved progressively greater depths until terminated, before reaching reef basement, at 340 m (Royal Society 1904). This strong, yet inconclusive, test of Darwin's theory (and the subsequent drilling attempt by Alfred G. Mayor and technician John Mills at Pago Pago, Samoa (Stephens & Calder 2006)) helped underpin the early arguments about where scientific effort on the Great Barrier Reef needed to be focused. Following the establishment of the Great Barrier Reef Committee – 'instituted to investigate the origin, growth and natural resources of the Great Barrier Reef of Australia' (Thomson & Hedley 1925, ix) – in Brisbane on 12 September 1922, Richards moved swiftly to promote geological investigations. He reported on a five-week survey between Cairns and the Torres Strait in June–July 1923 which he had undertaken with Hedley to claim 'submergence on a grand scale has gone on' (Richards & Hedley 1923, 1) and 'the idea of a thick coral mass' (Richards & Hedley 1922–1923, 109). By November 1924, Richards and Hedley (who was by now the Scientific Director of the Great Barrier Reef Committee) began to raise the possibility of a drilling programme both on the outer edge of the Reef and at a series of mid-shelf locations and to draw Vaughan (whom Richards had visited in La Jolla, California in January 1925) and J. Stanley Gardiner, of the Zoological Laboratory at the University of Cambridge and who had been a member of the first of the Funafuti Expeditions (Brown 2007a), into the discussions on possible boring sites. Richards' preference for a boring on the far north of the Great Barrier Reef, at Raine Island,[4] did not meet with Vaughan's approval; conversely, he was 'heartily in favor of one of the Bunker or Capricorn Group'[5] at the southern end of the Reef. And for Gardiner, speaking after the presentation of a paper on the Great Barrier Reef to the Royal Geographical Society (RGS), London, on 23 February 1925 by his close colleague Gerald Lenox-Conyngham (who had sent greetings from the British government, the Royal Society of London and Cambridge University (where he was Reader in the new subject of Geodesy) at the opening of the 1923 Congress and had visited the Great Barrier Reef after the meeting), 'the proper place for the first boring is not at the edge of a reef, but rather halfway across, then there would be less difficulty and more certainty of reaching the underlying rocks, which it is all-important to determine' (Douglas & Gardiner 1925, 332). By 1926, mounting costs had restricted an ambitious drilling programme to just one location, and Oyster Cay, Michaelmas Reef (Figure 1), which could be serviced from Cairns, became the chosen drill site. Drilling began in May 1926, under the supervision of Charles Hedley, who had experience of coral drilling from the first Funafuti Expedition. The stratigraphy of the borehole was, however, confusing, with alternating coral sands and muds, and the operation was abandoned, with funds exhausted, in August at a depth of 183 m without reaching a clear reef basement. Uncharitably, Vaughan told Richards 'I do not feel so much surprise as you and your associates appear to have experienced'.[6] Little of immediate scientific value could be extracted from the exercise; indeed, the full analysis of the core materials was not published until 1942 (Richards & Hill 1942). Drilling was not resumed on the Great Barrier Reef until the Heron Island bore of May 1937, again somewhat inconclusively to a depth of 223 m (Hill 1984, 10).[7] Following these activities in 1926, there was then a serious shift from wholly geological to more broadly biological problems; we now discuss this shift below.

At the beginning of the twentieth century, an 'initial interest in coral morphology and taxonomy extended to embrace more dynamic aspects covering function and ecology' (Yonge 1980, 445). In this regard, Yonge identified Wayland Vaughan, as reef biologist rather than geologist, and Mayor as significant pioneers, through their leadership (1908–1915) of the Florida program from the U.S. Geological Survey and the Carnegie Institution of Washington, respectively. Vaughan carried out pioneering experiments on coral growth rate and observations on the effects of light, and salinity on corals in addition to establishing their food sources and larval biology in southern Florida

(Vaughan 1912). The most thorough set of Vaughan's early measurements were made on corals in the Dry Tortugas. Increments in colony height, diameter and, at times, weight were made for the major reef framework-building corals and other species on the reef. These careful studies revealed considerable variability in growth rates, for both individual colonies over time and between colonies of the same species (Vaughan 1915a, 1915b, 1916). Work by Mayor on Samoa also included research on coral growth (Mayor 1918, 1924), involving transplantation of a variety of corals in the field to assess growth rates, as well as performing experiments on Caribbean coral feeding responses at different temperatures and coral survivorship at extreme temperatures (Mayer 1918b).[8] Mayor had been with Agassiz on the cruise of the *Croydon* and inspired by the high-resolution chromolithographic and photographic plates of emergent reef flats depicted in William Saville-Kent's (1893) *The Great Barrier Reef of Australia*, established a summer field station in October 1913 on the Maer (Mer) reefs of the isolated Murray Island group in the Torres Strait. By monitoring water levels, air and water temperatures, substrate characteristics and sedimentation and the distribution and morphology of coral colonies in squares (measuring approximately 15 m × 15 m) staked out at 60 m intervals along a 500 m long transect – in what might be seen as the first example of modern coral reef ecology – Mayor was able to establish the critical limits to the duration of subaerial exposure and sediment loading that might be tolerated by corals (Mayer 1918a).

Nothing remotely comparable had been undertaken on the Great Barrier Reef up to this time. Charles Hedley had, like Gardiner, accompanied the first of the Funafuti Expeditions; his observations and voluminous collections were published in a series of memoirs of the Australian Museum (Hedley, 1896, 1899a,b,c,d; the first resulting in considerable friction over publication rights with the Royal Society [Rodgers & Cantrell 1988]). On the second Funafuti Expedition, Edgeworth David's second-in-command, the Melbourne geologist George Sweet, compiled maps of all 30 of the islands on Funafuti's reef rim, together with almost 100 geological cross sections identifying 20 different geological units, with notes on unit ages and environment of deposition (Royal Society 1904, Spencer et al. 2008). The observations at Funafuti by Hedley and Gardiner, and these remarkable maps of atoll motus, began to set a very different, yet complementary, agenda to that of the reef theorists. However, none of this work translated into a proper programme of coral reef research on the Great Barrier Reef. In 1901, Hedley and Andrews made descriptions of the continental shelf between 20 and 21°S, revisiting some of the evidence for uplift previously described by Jukes (Andrews 1902); in 1904, Hedley visited Masthead Island in the Bunker-Capricorn Group (Hedley 1906); and in 1906, in what has been described as the first paper by Australians on Australian reefs (rather than reef biota) (Stoddart 1989), Hedley and T. Griffith Taylor, another protégé of Edgeworth David, provided the first reef transects from Hope Island and Cairns Reef, northern Great Barrier Reef, detailing wave-driven transport of carbonates across reef platforms (Hedley and Taylor 1907, Taylor 1958) and made 'a valuable contribution to the scleractinian fauna of the Great Barrier Reef' (Veron & Pichon 1976, 1). But these were merely isolated, brief field visits.

In December 1921, Henry Richards wrote to Sir Matthew Nathan, Governor of Queensland and President of the Queensland branch of the Royal Geographical Society of Australia, to urge 'we should do here what Mayor and Vaughan are doing in the Gulf of Mexico'.[9] Early in 1922, Nathan put out some feelers to the Royal Geographical Society (RGS) in London, writing to the President, Sir Francis Younghusband, 'we should like very much to know that we have the sympathy of the parent Society'.[10] Subsequently, immediately following the formation of the Great Barrier Reef Committee, in October 1922, Nathan wrote a letter to Sir Sidney Harmer, The Director of the British Museum (Natural History) and also to Arthur Hinks, the Secretary to the RGS seeking both interest and cooperation and appending a proof copy of Richards' paper on the 'Problems of the Great Barrier Reef' (Richards 1922). In December, Hinks replied to say 'The Society is in cordial sympathy with your proposal',[11] and in February 1923, Harmer replied to also confirm interest in the project and to list suggestions of additional topics for study[12]; a similarly extensive reply was received from Hinks in the same month.[13] These dialogues, alongside those undertaken with universities, scientific institutions and societies in Australia, fed into Richards' presentation to the Second Pan Pacific Science Congress in August 1923. Entitled 'The Great Barrier Reef of Australia', the presentation outlined a revised plan of research (Richards 1923). Bowen & Bowen (2002, 240) claim that in this paper, Richards 'simply reiterated his plea for more geological research into the still unresolved issue of the formation of the Reef', but careful scrutiny reveals a much broader remit. The research outline covered physiographical, oceanographic, geological, botanical and zoological proposals. Particular reference was paid to detailed topographical and oceanographic surveys of the Great Barrier Reef (including chemical and physical characteristics of seawater); the quantitative study of plankton; the biology of invertebrates of economic importance; and 'pure research' on aspects of the coral reef. In the latter category, the following research concerns were addressed 'the systematic, morphological and embryological study of inadequately known groups, ecological studies – including that of the reef as a living entity, coral charting and observation of growth of the same and different species of coral under varying conditions and the collection and preservation of specimens and the establishment of aquaria' (Richards 1923, 5).

Clearly, the revised programme was ambitious, involving long-term research proposals which would be costly and labour-intensive; the realities could not meet the ambition. Internationally, the impetus for reef ecological studies had waned with the death, from drowning, of Mayor in 1922 and the move of Vaughan from the US east to west coast in 1924 to become the Director of the Scripps Institution, where his focus became directed towards establishing the new science of oceanography. Although Vaughan had been asked after the Third Pan-Pacific Science Congress (Tokyo, October – November 1926) to chair a Committee on Coral Reefs, he only began to get around to this task in July 1927, having first concentrated on establishing the International Committee on the Oceanography of the Pacific.[14] These difficulties were compounded in Australia itself. The Great Barrier Reef Committee was seriously weakened by the loss of both its chair, Sir Matthew Nathan, who had retired as Governor of Queensland in September 1925 and returned to England, and its Scientific Director, Charles Hedley, who died suddenly from a heart attack in September 1926. There continued to be a lack of trained marine biologists from Australia's young universities.

Conversely, in England, the drive to undertake research other than simply reef borings continued to be strongly promoted by Stanley Gardiner. In January 1925, Gardiner wrote to Richards to say 'three-quarters of the value of any boring may well be lost in the Barrier Reef region without a concurrent physical and biological survey of an area of the region much more thorough and comprehensive than was undertaken at Funafuti'.[15] And trenchantly to Hinks 'I'm against boring *without* proper detailed survey *at the same time*, this to be both biological+topographical, both to be *very* thorough'.[16] Representing the University of Queensland, Nathan attended the Third Congress of the Universities of the Empire in Cambridge, England, in July 1926 and there met with Gardiner to discuss suitably trained individuals who could spend a significant period of time, perhaps up to one year, on the Reef. Gardiner proposed his Cambridge colleague, Frank Armitage Potts. Potts had been with Mayor in the Torres Strait in 1913 (and in Fiji and Samoa in 1920) and had described observations and findings from the 1913 expedition in a lecture at the RGS in February 1925, published as Part II of a Great Barrier Reef paper with Lenox-Conyngham (Lenox-Conyngham & Potts, 1925). In the ensuing discussion, Gardiner remarked 'tonight Mr. Potts has shown us how the corals live; how they form the reef; at what rate they grow; what affects their growth; and, finally, what binds them together into a solid rock' (Douglas & Gardiner 1925, 331). Not surprisingly, therefore, the minutes of the meeting of the Great Barrier Reef Committee on 9 September 1926 record that a proposal had been received from Mr. F.A Potts of Cambridge University, England, to carry out a biological expedition to the Great Barrier Reef.[17] The precise brief was 'to study the ecology of a coral cay for a period from July 1927 to July 1928'. The Great Barrier Reef Committee decided that such an expedition would be valuable and proposed that Low Isles on the northern Great Barrier Reef was a suitable location for the investigation. In the Great Barrier Reef Committee, minutes of 23 February 1927 the members of Pott's expedition are listed – they included Dr. H. Graham

Cannon, Professor of Zoology at the University of Sheffield; Mr. F.S. Russell, an assistant naturalist at the Marine Biological Association, Plymouth; and Mr. E.B. Worthington from Gonville and Caius College, Cambridge.[18]

The stakes had been raised, however, by a resolution from the Third Pan-Pacific Science Congress, held in Tokyo, October–November 1926. The Congress was attended not only by Vaughan but also by William Setchell, the Yale botanist who had been appointed to the chair in Botany at UC Berkeley in 1895. An expert in marine algae, he had broadened his interests into coralline algae from accompanying Mayor to Fiji and Samoa in 1920, travelling widely through Polynesia thereafter (Campbell 1945). It was Setchell who framed the seventh resolution at the Congress, calling for the formation of a Committee of biologists, oceanographers and geologists to investigate the coral reefs of the Pacific Ocean because 'coral reefs are symbiotic entities whose origin and growth relations have received too little attention' and where 'methods of investigation are complicated and costly' (Setchell 1928, 153). Bowen & Bowen (2002) argue that this resolution, with its implications for the likely international scrutiny of the expedition that would necessarily take place at the next Pan-Pacific Congress, planned for Java in 1929, caused Gardiner to re-consider whether the proposed expedition was sufficiently well planned with its current leader and personnel. However, a great deal of momentum had been developed for an expedition by this time with the establishment of a British Barrier Reef Committee (with Nathan acting as its Chairman) in January 1927. This Committee subsequently became the Great Barrier Reef Committee of the British Association at their Leeds meeting in September 1927 (Nathan 1927); Yonge (1930a) details its full 25-person strong membership. In addition, the Balfour Trustees in the Department of Zoology at Cambridge, guided by Gardiner (see Morton, 1992 for the full story), offered a Balfour studentship to Dr. C. Maurice Yonge in April 1927, then researching feeding and digestion in the British oyster, *Ostrea edulis*, at the Plymouth Laboratory of the Marine Biological Association, in the anticipation that he would accompany the Potts' expedition. However, following the failed launch of this expedition Gardiner made it clear to Yonge (in a letter of 3 May 1927) that he could follow his marine biological interests in laboratories as far afield as Naples, Woods Hole or Bermuda if he so desired.[19] In July, Gardiner wrote, rather disingenuously, to Vaughan to inform him 'unfortunately Potts who married last year cannot go but I hope we shall be able to find somebody, if not with equal knowledge of coral reefs, quite thoroughly efficient'.[20] But it is clear that Gardiner had already found that 'quite thoroughly efficient' person, appending to the letter a project outline that identified Yonge as 'the leader of the expedition and a comparative physiologist'. By 10 August 1927, Richards wrote to Vaughan 'now I hear from Potts that he will be unable to come next year, but that Dr Bidder [George Bidder, marine biologist who lectured in Cambridge 1920–1927] and Dr Stanley Gardiner were hoping to get away an expedition next year under a marine biologist named Yonge of whom I know very little'.[21] In reply, Vaughan assured Richards that all was well: 'Stanley Gardiner is one of my really old friends. We have known each other personally since January 1898'. He went on to say 'Gardiner's program will be just about as fine as it is at present possible to make it' and 'highly valuable results are assured'.[22] Following the Leeds meeting, and discussions among Nathan, Edgeworth David, Potts and Yonge,[23] a new proposal to send an expedition to the Great Barrier Reef was explored. The programme was formalized in a letter to Sir Matthew Nathan from Gardiner on 24 September 1927.[24] In this letter, the key elements of the proposed research were:

> To examine a sector of the Great Barrier Reef from shore to ocean off Cairns, chart it accurately, survey associations of plants and animals on its surface both qualitatively and quantitatively, study the food and power of lime formation in the same and all other matters as concern the formation and growth of that part of the Reef. In detail it was proposed to undertake an investigation extending through 12 calendar months; this enabling a proper knowledge of the seasonal problems concerning the physical and chemical conditions, the rate of growth, seasonal reproduction of animals and plants and other food organisms, etc. etc. as well as giving time for the necessary work connected with a thorough scientific

> survey of the area. The members of the expedition would be housed in the camp of the Australian Barrier Reef Committee on Low Islands, about 20 miles north of Cairns and it is anticipated that a power boat would be obtained for the purposes of this expedition.

But this was not all. At the meeting of the British Great Barrier Reef Committee on 4 October 1927, 'Mr. Debenham' asked for information as to the extent to which geographical investigations were to be undertaken; in response, the Committee asked him to prepare a memorandum to form the basis of an appeal to the RGS for funds.[25] Frank Debenham had just been promoted from University Lecturer to Reader and Head of the Department of Geography at Cambridge, having been from 1919 RGS Lecturer in Surveying and Cartography, a post previously held (1908–1913) by Arthur Hinks before he moved to the RGS to become Assistant Secretary, and then Secretary and Editor of *The Geographical Journal*, a post he held for 30 years until his death in 1945. Debenham, an Australian, had been trained in petrology at Sydney University by Edgeworth David and had participated in Scott's fateful *Terra Nova* Expedition in 1910–1913, along with Griffith Taylor (Speak, 2008). While in Cambridge, Hinks wrote two influential books, *Map Projections* (1912) and *Maps and Survey* (1913), and Debenham promoted plane table mapping, the use of a mounted drawing board as a solid level surface on which landform positions are plotted in the field. This was, and still is, an efficient approach for rapid field surveys, as captured in Debenham's highly successful handbook, *Map Making* (1936). It is not surprising, therefore, that both Hinks and Debenham were interested in the high-resolution measurement of position and 'changes of level'.[26] But with the biological party in place by the start of 1928, far less progress had been made with the 'geographical investigations'. Gardiner sent a hurry up to Hinks in January 1928 'There remains a Chemist and a Geographer… personally I'm very very keen to have one. Is there any possibility of your providing us such a person?' and '… you know more than I do on what is wanted and clearly Davis, Daly [Professor of Physical Geography at Harvard who had replaced WM Davis in 1912] and Vaughan agree with me in stressing this side and consider that there is real scope'.[27] Hinks shifted the problem away from the RGS onto Debenham who throughout January struggled to come up with a name. But then in February, he wrote to Hinks to put forward the name of J. Alfred Steers who had been appointed to a University Lectureship in Geography the previous year.[28] Debenham extolled the virtues of his young recruit: 'He is extremely adaptable, and has improved in width of outlook, technique etc., tremendously in the last two or three years, but he does need a good long trip, such as this [the Great Barrier Reef Expedition], to make him of first-class value to my department. Of course Steers has never seen a coral reef, but he has the greatest interest in coast lines, and has lectured in considerable detail on the formation of coral reefs. He is also a man who would get up the subject very thoroughly en route to the work. Altogether I rather like the idea'.[29] And so at the Meeting of the British Great Barrier Reef Committee on 23 February 1928, 'Mr Debenham announced that his assistant, Mr Steers, Fellow of St. Catharine's College, Cambridge, desired to accompany the expedition and that he could be spared from his duties from June to December'.[30] At much the same time, a final year undergraduate in Engineering from the University of Oxford, Michael Spender, having seen the notice on the Expedition in the journal *Nature* for 11 February, wrote immediately to Hinks to see if there were 'any junior posts yet to be filled', mentioning, music no doubt to Hinks' ears, that he had 'taken the survey course of the school; which includes a month in the field with the usual instruments and a good deal of work in the drawing office'.[31] References were obtained from the Professor of Engineering at Oxford, Frewin Jenkin, and Spender met with both Hinks and Gardiner. All were impressed; Debenham less so: 'Spender is full of ideas, and active, but I am afraid he has a lot more to learn than he thinks, and must drop some of his Oxford manner when in Australia. Steers should provide a good calming influence'[32] (for insights into the highly complex individual that was Michael Spender see Shipton (1945)). The other member of the Section, for a six-week period, was E. C. Marchant, from St. John's College, Cambridge, who had read Part I of the Geographical Tripos.[33] All that was left was for a programme of 'geographical investigations' to be established. This was provided by Debenham on 14 March 1928 in a Memorandum on work to be carried out by the RGS members of the Barrier Reef Expedition:

> The time seems opportune for beginning a more exact type of investigation, in which the surface changes already suspected in connection with coral reefs shall be the subject of careful measurement. The results and deductions of such measurements will not be available for a period of years, but when available they should be quite conclusive on such subjects as emergence and subsidence, growing and wasting of coral banks, scouring and filling of lagoons.[34]

Debenham went on to outline in detail the types of measurements required, including the determination of mean sea level from a recording tide gauge; establishment of a network of bench marks; depth sounding and collection of bottom sediment samples; and observations on coral growth, marine erosion, solution and storm deposits, with across-reef transects mapped by plane table, theodolite and compass-and-chain.

And so, after a faltering start, the Expedition was finally underway. The leader, Maurice Yonge, and some of his team set off from London on the RMSA ORMONDE bound for Australia on 26 May 1928. The group arrived at Brisbane on 9 July and finally at Low Isles, their headquarters for the next 12 months, on the 16 July 1928. Low Isles is situated at 16°23′S, 145°34′E on the inner shelf, 65 km north-northeast of Cairns and 15 km northeast of Port Douglas on the Queensland coast. The outer barrier of the Great Barrier Reef lies 40 km to the east (Figure 1). A modern image of Low isles is shown in Figure 2; it comprises a small sand cay (0.02–0.03 km^2) and a larger mangrove forest (0.17 km^2 in 1928, 0.46 km^2 in 2017) on top of a horse-shoe-shaped reef platform occupying an area of 1.77 km^2 and typically 2 km in width. The Expedition was housed in six huts, prefabricated

Figure 2 Aerial photograph of Low Isles taken at an oblique angle from the south east on 5 October 2007. Woody Island, the mangrove stand on the exposed side of the reef, can be seen in the foreground, while the smaller, vegetated sand cay where the Expedition was based can be seen in the background (reproduced under licence #2011071, photo credit: David Wall © davidwallphoto.com).

off site and then assembled *in situ* on the sand cay, ready for the arrival of the field party (Figure 3); the laboratory hut had been used on Oyster Reef for the drilling operations there in 1926. This was a meticulously planned and extremely well-equipped expedition: details of the laboratory spaces, aquaria, library facilities, met. station, field equipment and boat support are detailed by Yonge (1930a, 1931a).

Figure 3 (A) The sand cay at Low Isles at the time of the Expedition (1928–1929) from Tripneustes Spit looking west across the Anchorage; (B) the expedition huts on the Low Isles sand cay (both images by kind permission of the Royal Geographical Society).

Table 1 Personnel of the Great Barrier Reef Expedition at Low Isles, 16 July 1928 to 28 July 1929 (after Yonge, 1930a)

Name	Position	Nature of work	Time on expedition (months)
CM Yonge	Expedition Leader	Physiologist	12.5
FS Russell	Deputy Leader Leader, Boat Party	Zooplankton worker	5
JA Steers	Leader Geographical Section	Geographer	4
TA Stephenson	Leader, Shore Party	Zoologist	11.5
AP Orr		Chemist and hydrographer	12.5
SM Marshall		Phytoplankton worker	12.5
FW Moorhouse		Economic zoologist	12.5
AG Nicholls	Assistant to Leader		12.5
GW Otter		Zoologist	11
G Russell	Assistant to Mr. Russell		5
A Stephenson		Honorary zoologist	11.5
G Tandy		Botanist	5
MJ Yonge	Assistant to Leader	Medical officer	12.5
JS Colman		Zooplankton worker	10.5
EA Fraser		Zoologist	4
SM Manton		Zoologist	4
CE Marchant		Geographer	3
MA Spender		Geographer	11

The Expedition's personnel are detailed in Table 1 and the wider party in November 1928 shown in Figure 4. The advance party consisted of Dr. C. M. Yonge, leader of the Expedition and physiologist, together with his wife, Mrs. M. J. Yonge; Mr. F. S. Russell, second in command and in charge of the Boat Party and a zooplankton worker, also with his wife Mrs. G. Russell; Dr T. A. Stephenson, zoologist and leader of the Shore Party with his wife Mrs. A. Stephenson; Miss S. M. Marshall, a phytoplankton worker; Mr. A.P. Orr, chemist and hydrographer; Mr. G.W. Otter, zoologist; and Mr. G Tandy, botanist. They were accompanied to Low Isles by Mr. F.W Moorhouse of Brisbane described as an 'economic zoologist' and then joined two days later by Mr. A. G. Nicholls, as assistant to the leader, from Perth. Other personnel came out from England during the course of the Expedition while others left; the arrivals included Mr. J.S. Colman, zooplankton worker; Miss E. A. Fraser, zoologist; and Miss S.M. Manton also a zoologist (Yonge 1930a, 1931a). For Manton, arriving at the end of March 1929, 'The amount they've done and the bright and intelligent things they're at is astonishing, and a little overpowering at first when you plunge into the middle of it armed with abysmal ignorance. They work jolly hard too…' (Clifford & Clifford 2020, 57). For four to six weeks in the latter part of 1928, the Expedition was joined by five members of the Australian Museum; one of these members, the conchologist Mr. T. Iredale, was also involved in the Expedition's 1929 fieldwork at Three Isles (Figure 1). There were also some 15 occasional visitors with scientific interests, including Henry Richards and, perhaps the first example of a journalist embedded within an expedition to the reef seas, Charles Barrett of the *Melbourne Herald* (McCalman 2014). For the Geographical Section, Steers and Spender arrived in Townsville in August and were then joined by Marchant at Cooktown in mid-October. Steers left to return to Cambridge in early November 1928 but Spender stayed on to the end of the Expedition, the camp being evacuated on 28 July 1929. The huts were locked up with a plan to maintain them as a permanent field station; unfortunately, that dream ended with the destruction of the buildings in the cyclone of 3 March 1934 and the resignation of Moorhouse, as the Queensland Government's marine biologist and site manager, a year later.

Figure 4 Party at Low Isles, 3 November 1928. From left to right, back row, standing: H.C. Vigden, F.A. McNeill, J.A. Steers (largely obscured), A.P. Orr, H.S. Mort, H.A. Longman, E.O. Marks, M.A. Spender, J.S. Colman, G. Tandy, C.E. Marchant, A.A. Livingstone, T. Iredale; front row, seated: F.W. Moorhouse, A.C. Wishart, Miss S.M. Marshall, F.S. Russell, Mrs. Russell, Professor H.C. Richards, Mrs. Yonge, C.M. Yonge, Mrs. Stephenson, T.A. Stephenson, A.G. Nicholls; seated on ground: Master Iredale, G.W. Otter (photo credit: M.J. Yonge) (by kind permission of the Royal Geographical Society).

While the Expedition was based at Low Isles throughout, there were a series of short visits by smaller groups to the outer barrier and islands inside the barrier for plankton, hydrographic and dredging operations, as far north as 14°30′S (Figure 1) (the activities of the Geographical Section are considered in further detail below). The longest of these visits was the two-week ecological and topographic survey of Three Isles in May 1929 and a similar length visit to Lizard Island and the neighbouring outer barrier (Figure 1) in the following month. In March 1929, A.P. Orr and G.W. Otter used the visit of Commonwealth Lighthouse Service's SS CAPE LEEUWIN to Willis Island in the Coral Sea, 450 km east of Cairns, to undertake open ocean oceanographic sampling and in the period April to May 1929, the Yonges, Nicholls and Moorhouse made an extended visit to Thursday Island and the Murray Group in the Torres Strait. Furthermore, the entire team spent some time on the Atherton Tableland, inland from Cairns, as a respite from the summer heat and there were frequent Sunday excursions to the mainland coast.

Novel aspects of the 1928–1929 Expedition

The Great Barrier Reef Expedition of 1928–1929 was ground breaking in several respects. First, the interdisciplinary nature of the Expedition was a clearly articulated philosophy, from the planning stages right through to publications. Gardiner writing to Hinks in February 1928 set out the necessary interactions: 'fix the places to be so surveyed the biologists must tell us precisely what is the life complex on each – and the exact position (on the geographers survey) of any peculiar complexes or striking groups of corals should be noted. I think that the geographer should make an independent estimation of the wash of the sea (tide, currents waves etc. but not necessarily with extreme accuracy as the use of terms such as tide etc. imply) on each survey reef because the biologist will have 80% of his mind on his organism & the geographer 80% of his on physical conditions'.[35] This was followed up by Debenham, writing to Hinks in March 1928: 'the biologists made a definite request, which I thoroughly agree with, that during the later part of the time, that is when Spender is based at headquarters [i.e. Low Isles] he should, in addition to carrying out such work as is in the memorandum [see above and source no. 33], make a survey of the guiding marks and beacons which the biologists will set up when taking their dredgings and soundings, etc.'.[32] Although the intention of setting up what would have been the first long-term record of water level variations on a coral reef was stymied by a shipping strike, which delayed the arrival of the tide gauge at Low Isles until February 1929, thereafter, after some difficulties in establishing a stable measurement platform, a near continuous water level record was obtained for the period from 8 February to 24 July 1929; subsequent analysis of the tide gauge record by the Liverpool Tidal Institute started to make sense of the water level variations that the Expedition found 'capricious and unreasonable' and 'consistently baffling' (Spender 1932, 203–204). It was possible to relate the different morphological components of the Low Isles reef system to tidal levels and, for example, to study the distribution of coral cover down to 5.5 m, with maximum coral cover being found at ~0.6 m below datum (Spender 1930; Figure 5).

As Steers' time on the Expedition was coming to an end in October 1928, there were discussions between Richards, Debenham, Hinks, Steers and Yonge about how Spender's time might be most usefully deployed. After the fact, and when Steers had been back in England for three months, Yonge wrote to Steers: 'The question of Spender's programme has been difficult…. I want Spender to do all he possibly can to help you but Richards, Stephenson, Spender and myself are in complete agreement that it is far better to do the one job of surveying the island really properly than that scrappy work should be done on a series of surveys and borings none of which could give any satisfactory result'.[36] In purely practical terms, once Marchant left in early January 1929, Anne Stephenson was deployed as 'staff man' for Spender's surveys and 'Spender is learning the animals and plants so that they can do biological survey also'.[37] By April, Spender told Hinks: 'I am still confident that this piece of work will be importantly useful in all these problems – the general coral reef problem, the problem of these unique (?) Low wooded Islands, and the biological problem of this reef. No ecological work comparable has ever been done in coral reef work'.[38] Progress improved significantly once daytime low tides allowed access to the reef flats and in the 'statement of position' on 28 May Spender was able to say 'the mapping of Low Islands is very nearly complete. Several level traverses have been made across the flat, along the ramparts and over the strip sections being ecologically surveyed by Dr Fraser and Miss Manton',[39] summarizing by mid-June 'Geographical work obviously interlocks with the Shore Party work; we have in fact, worked together the whole way through. When Davies [surely a mis-spelling of WM Davis] denies any significance in the biological aspect of the reef, he cannot be anything but exaggerating'.[40] By the time of the publication of the Expedition Reports, Gardiner was able to say 'on the bio-logical side we can now zone the areas downwards & ecology becomes a matter of physiological reactions in waters; this is what interests U.S.A.'[41] (although he was rather more circumspect subsequently[42]).

Second, unlike earlier expeditions on coral reefs, it brought scientists together at a single research site for long-term *in situ* observations and experimentation over a period of nearly 13 months. The chosen location of the Expedition at Low Isles on the northern Great Barrier Reef was a key factor and much was made in early deliberations of selecting a site which satisfied the requirements of using a reef as a natural laboratory (and which could also be sustained by servicing on a regular basis from Port Douglas; Figure 1). Thus, the British Great Barrier Reef Committee reported at the BAAS meeting in Glasgow in 1928 that the 'work of the expedition consists of research on the growth, feeding and reproduction of organisms around the camping island, to a large degree the sea forming a substitute for laboratory tanks'.[43] In this shallow water environment which Yonge also later referred to as 'a natural aquarium' (Morton 1992, 391), a range of scientific activities were carried out that included an assessment of the role of zooxanthellae in sustaining corals; oxygen exchange between corals and surrounding water; sediment cleansing by corals; estimates of coral

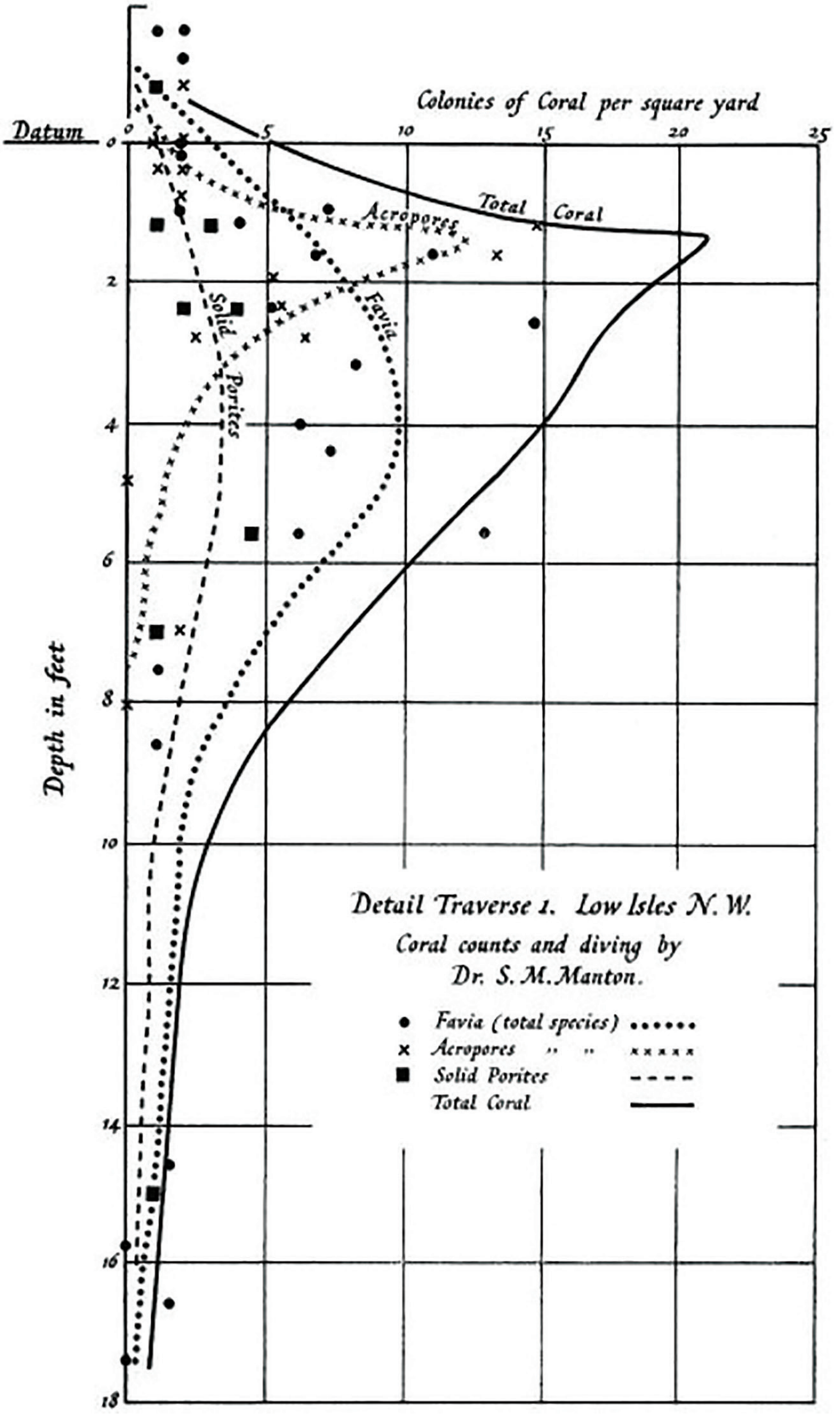

Figure 5 Graph showing relation between abundance of coral growth and depth, seaward of the boulder-zone, Transect I (see Figure 12 for location, Figure 14 for transect bathymetry) (reproduced from Spender, M. 1930. Island-reefs of the Queensland Coast. *The Geographical Journal* **76**, 193–214, 273–293 (Figure 4), by kind permission of the Royal Geographical Society).

growth rates; the effects of transplantation of corals from one site to another; and coral reproduction and development of juvenile corals from planula larvae.

A third novel feature of the Expedition was the introduction of relatively sophisticated (for the time and area of study) experimentation into the scientific programme with Gardiner describing the Expedition members as 'experimentalists' (Brown 2007a) (Figure 6). As we have detailed above, the Expedition was not the first to engage in experimental studies. But the prolonged stay at the Low

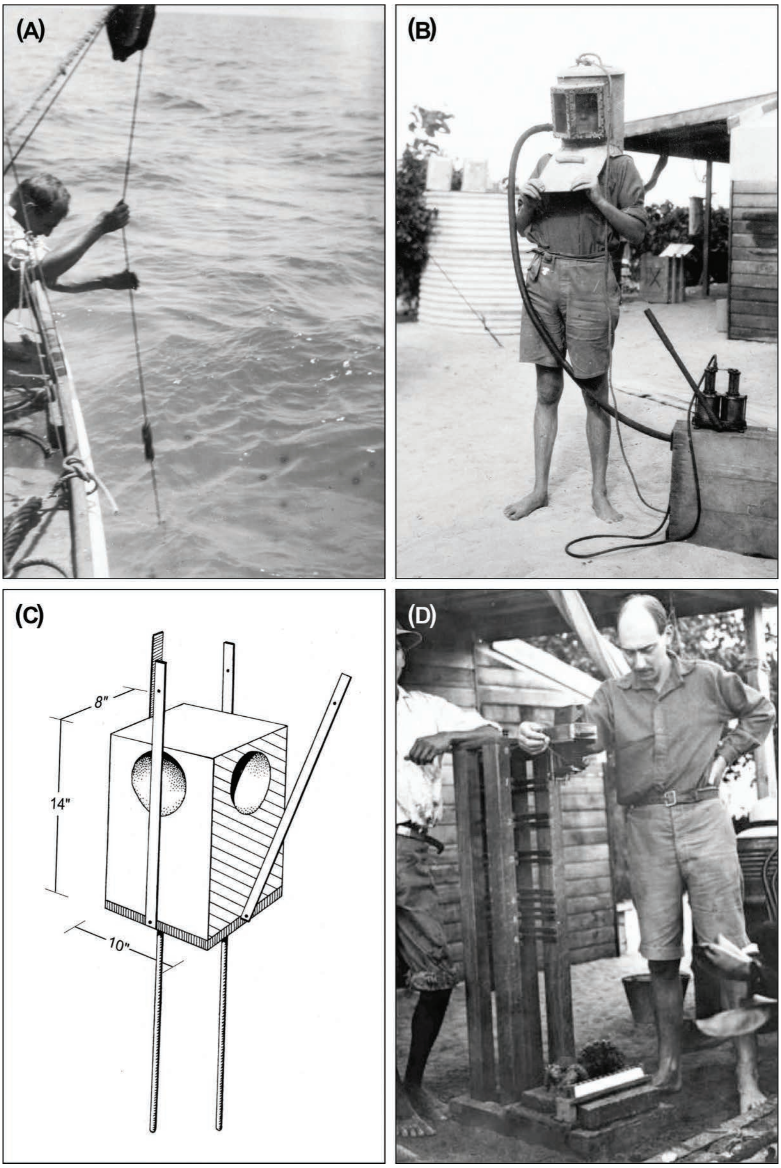

Figure 6 Methods used by the Expedition. (A) hydrographic survey: Freddie Russell sending messengers down the wire to the water sampler (by kind permission of the Royal Geographical Society); (B) demonstrating the Expedition's diving helmet (by kind permission of the Royal Geographical Society); (C) the 'clock-tower' – a structure devised by Alan Stephenson to rear coral planulae on the reef. Re-drawn from Stephenson (1931); (D) Alan Stephenson and apparatus for photographing coral colonies (ANL archives, PIC/11204/349 LOC ALBUM 1115/4, with kind permission of the National Library of Australia).

Isles base and the person power and expertise available meant that experimentation could be taken to a different level and a whole range of physiological experiments were performed in both the field and laboratory, many using the observations of Mayor and Vaughan as their starting point. Indeed, good use was also made of the diving hood developed by Mayor for underwater observations and the 'light- proof live-car' of Vaughan (described by Yonge & Nicholls [1931a] as a 'coffin-shaped box') to test the effects of darkness on selected corals and their zooxanthellae.

The Expedition also took the major innovative step of checking ground observations at Low Isles against aerial photography flown on 24 September 1928 (Figure 7) by the Royal Australian Air Force (RAAF)[44] (Stephenson et al. 1931). This was well ahead of its time: the widespread potential of aerial photography for detailed reef mapping was not realized until towards the end of WWII (Steers 1945, Hamylton 2017). Fittingly, one important case study site at the time of this renewed interest was Low Isles. The reef was overflown by the RAAF on 21 January 1945, with photography and subsequent ground referencing by Rhodes Fairbridge and Curt Teichert[45]; the timing allowed assessment of the impacts of the tropical cyclone of 1934 (Fairbridge & Teichert 1948 [and see also Moorhouse 1936]). By 1968, it was possible for W. G. H. Maxwell to develop an elaborate taxonomy of reef types and to link these types together in an inferred, multistrand evolutionary sequence from the remarkable aerial photography archive of the Great Barrier Reef, funded from 1964 by the Australian Commonwealth Government (Maxwell 1968). In 1982, the Great Barrier Reef Marine Park Authority commissioned the first full inventory of the GBR Marine Park that identified 2904 discrete reefs based on a combination of Landsat satellite imagery and aerial photographs (Hopley et al., 2007). The resulting gazetteer was used for management zoning, and the later re-zoning under the Representative Areas Program, of the Great Barrier Reef Marine Park (Day, 2019). The reef classification scheme at the heart of the gazetteer was based on the evolutionary model proposed

Figure 7 Expedition members and support staff meet the aircrew and inspect the aircraft at The Anchorage, Low Isles during the aerial survey of 24 September 1928 (source: James Cook University Library Special Collections, Sir Charles Maurice Yonge Collection, Great Barrier Reef Expedition Photo Album 2, Creators: Frederick Stratten Russell and Gweneth Kate Moy Russell (1928). Reproduced with kind permission of the James Cook University Library, Australia).

by Hopley (1982). This Holocene model of reef development proposed initial vertical reef growth upward from antecedent reef platforms in juvenile stages, transitioning to horizontal, lateral outward growth once the upper reef surface had reached sea level in later stages. This was followed by sediment infill and the development of reef-top sedimentary landforms. This arrangement of reefs into a temporal sequence of morphological evolution therefore placed a longer-term geomorphic perspective of reef development at the centre of Great Barrier Reef Marine Park management.

Not all the intended technical innovations were successful. Debenham and Hinks' 'armchair plans'[46] of mapping from stereo pairs of photographs obtained by photo-theodolite failed at the first attempt, at Orpheus Island in August 1928. Here, Spender and Steers were unable to establish sight lines in thick vegetation, found moving the heavy instrumentation across steep terrain difficult and 'sand and ants prevail everywhere'.[47] In retrospect, the methodology was never going to work on a low relief, sea level reef system, unlike the spectacular success that Spender was subsequently to have with the technique in the extensive mapping of the mountainous terrain of the southeast coast of Greenland in 1932–1933 (Norlund & Spender 1935) and on the north face of Mt. Everest in 1935 (Spender 1936).

Fourth, the Expedition incorporated strong collaboration between Australian and English scientists with some Australians spending a full 12½ months at Low Isles while others visited for periods between four and six weeks. The Expedition was also noteworthy for the participation of a number of female scientists – Mrs. M. Yonge, Mrs. G Russell and Mrs. A Stephenson were wives of the Expedition leader, his deputy and leader of the shore party, respectively, but all had active parts to play in research activities with Anne Stephenson working on the ecology and zonation of reefs, growth and asexual reproduction in corals and breeding patterns of other reef invertebrates and, towards the end of the Expedition, assisted with ground survey measurements (Figure 8). Mattie Yonge assisted in both laboratory assays and environmental measurements. Other women scientists, such as Miss S. M. Marshall, Miss S. M. Manton and Miss E. A. Fraser had specific zoological roles. Sheina Marshall specialized in phytoplankton production but also studied the breeding of reef corals and the effects of sediments on corals. Sidnie Manton participated in the ecological and quantitative surveys of coral reefs and detailed study of *Pocillopora* growth, while Elizabeth Fraser specialized in the life-history of hydroids on the reef. While not without precedent – as Caroline (Cara) David (née Mallett)[48] (Cantrell 1993) had accompanied T.W. Edgeworth David on the second drilling expedition to Funafuti in 1897 – the inclusion of women in the research party, widely commented upon in newspaper and other popularist accounts at the time (McCalman 2014), served as a catalyst for greater involvement of women in Australian science.

It is also worth pointing out that none of the British biologists had ever visited a coral reef before but many were classically trained zoologists equipped with powerful observational skills and a sound understanding of invertebrate structure and function. Similarly, almost half a century later, Steers reflected 'when Spender and I began work on the reefs we had no definite idea of what there was to do, and how we were to do it! Discussions with geographers were optimistic rather than helpful, because no one interested in geomorphology had visited the Barrier . . . We had to find our problems as we sailed along the coast' (Steers 1978, 161–162). Taking his cue from Debenham, Steers was always a strong advocate of the primacy of field measurements; in later life, he wrote 'I am convinced that physiographers should travel, and observe intelligently, as much as possible' (Steers 1960, 9) and that 'wide reading, field excursions, personal field work are all vital in the training of a physiographer' (Steers 1960, 13).[49] There is no doubt that he brought these observational skills into play on the Great Barrier Reef, not least in setting the studies at Low Isles into the broader regional context, initially visiting the Capricorn and Bunker Group (23°S) and then establishing, through the cruise of the *Tivoli*, the variability in both reef and mainland shoreline types between the Whitsunday Islands (20°S) and Cape Melville (14°S), a distance of almost 1500 km. Steers was the first scientist to extensively study the reef islands of the Great Barrier Reef, separating out the often highly dissected high or rocky continental islands with their fringing reefs, distinguishing

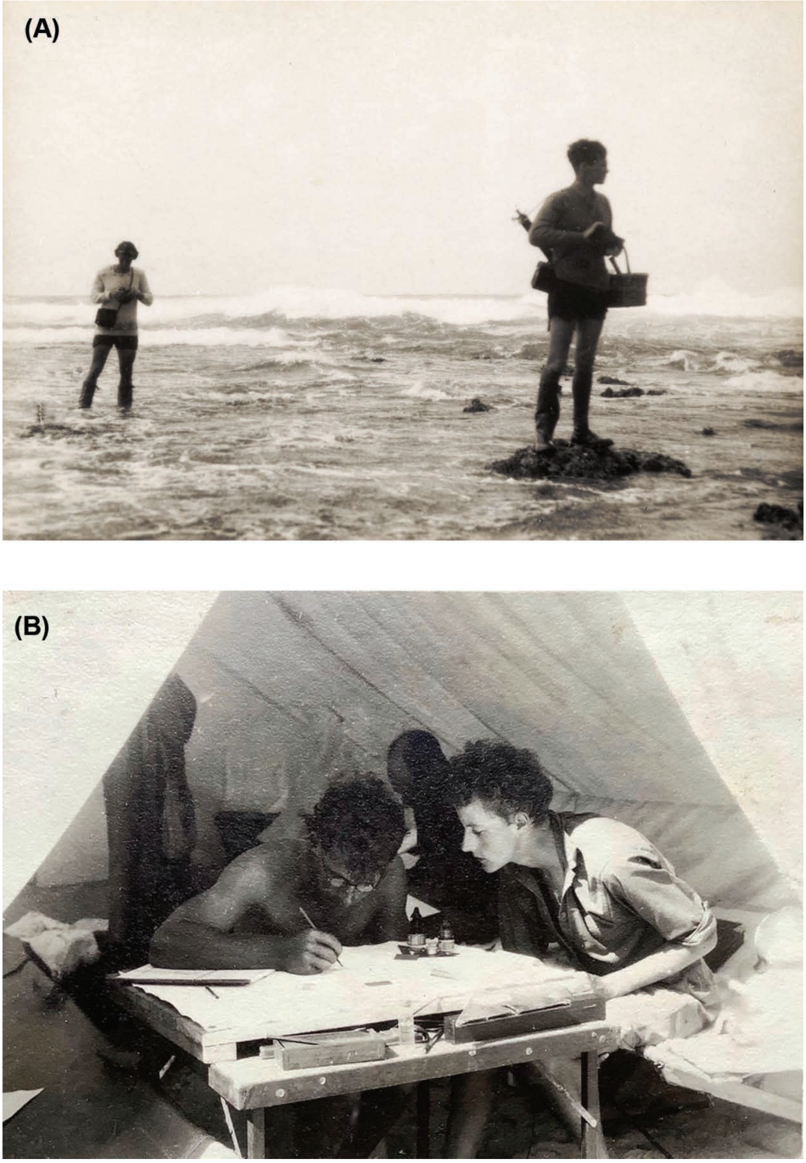

Figure 8 (A) Sidnie Manton (left) and Anne Stephenson mapping on the outer barrier reef. Stephenson carries 'pail, hammer, chisel, "chicken run" and numerous things tied about for mapping' (Clifford & Clifford 2020, 100) (reproduced by kind permission of the Royal Geographical Society); (B) drawing up from field mapping, (from left to right: Michael Spender, Alan Stephenson, Anne Stephenson) (photo credit: S. Manton, with kind permission from the family's archives). These images relate to the Expedition's excursion to Lizard Island and the reefs of the neighbouring outer barrier, 31 May to 13 June 1929.

between sand cays and shingle cays and providing the descriptive term 'low wooded island' for the complex reef systems of the inner shelf north of 16°S. The other main member of the Geographical Section, Michael Spender, was a supremely talented surveyor who, at Low Isles and Three Isles, took reef surface mapping to a completely new level, as recognized by Yonge when writing to Steers in April 1929; 'Spender is making a beautiful job of the map and when it is finished you will have the finest survey of this type of island ever accomplished'.[50]

Significance of the scientific findings from the Expedition

Five areas of particular significance to coral reef biology and geology/geomorphology are identified below. We do not review the collection and preservation of marine specimens which was an important remit for the Expedition; ultimately, three of the six volumes of Scientific Reports were devoted to descriptions and identifications of marine invertebrates and fish, culminating in 29 papers by various taxonomic experts. The coral collection, of 174 species divided among 54 genera, was eventually described by Cyril Crossland (1952) where Veron & Pichon (1976, 1) were of the view that 'this study is of particular value because of the care with which the collections were made at Low Isles, and also because Crossland had had extensive experience of coral reefs. His approach to coral taxonomy is therefore quite different from that of Vaughan, basically a geologist and palaeontologist'. Nor do we review the Expedition's activities in the field of 'economic zoology', led by Frank Moorhouse, studying bêche de mer and sponges and the cultivation of pearl oysters and trochus in specially constructed reef flat pens (Moorhouse 1932).

Yonge's work on coral physiology

C. M. Yonge's research remit on the Expedition relied strongly on his PhD and postdoctoral investigations of the comparative physiology of digestion in marine invertebrates, particularly the bivalve molluscs (Yonge 1928). Specifically, he agreed to make a thorough study of feeding mechanisms in corals by investigating their food, mode of digestion and assimilation as well as assessing the function and significance of their symbiotic algae.

The background literature available to Yonge was very limited, but even in 1928, there was considerable controversy over the role of zooxanthellae in the nutrition of corals. Gardiner (1931), Gravier (1908) and Boschma (1926) all considered that zooxanthellae contributed to at least part of the coral's diet while Murray (1889), Duerden (1906), Carpenter (1910), Vaughan (1912) and Mayor (1918) believed that corals fed exclusively on zooplankton. The most significant findings arising from the Expedition's experimental work were that corals were carnivores with highly specialized feeding mechanisms (Yonge 1930b) and that they could live perfectly well without zooxanthellae (Yonge & Nicholls 1931a). However, Yonge (1930b) admitted that the artificial nature of the experimental setup used at Low Isles would favour a greater carnivorous tendency than that observed in a natural setting. The conclusion that zooxanthellae did not contribute to the diet of corals resulted from experiments in outdoor aquaria near the laboratory base (Yonge & Nicholls 1931b) and also from experiments in a large light-tight box on the reef flat (Figure 9) (Yonge & Nicholls 1931a) where massive corals survived highly shaded conditions for 152 days although practically all their zooxanthellae were killed or ejected. Yonge & Nicholls (1931a) found no evidence for digestion of zooxanthellae by corals but noted disintegration of algae within host tissues, a common finding in cnidarians subsequently studied by other workers (Muscatine 1973, Trench et al. 1981, Suharsono et al. 1993, Brown et al. 1995, Titlyanov et al. 1998, Dunn et al. 2004, Ainsworth & Hoegh-Guldberg 2008). Yonge & Nicholls (1931b) also concluded that there was no evidence for transference of material from the zooxanthellae to the host, a fact that was later refuted by the elegant experiments of Muscatine & Hand (1958) using novel radio-autographic ^{14}C techniques and the anemone *Anthopleura elegantissima*.

Yonge et al. (1932) also ran an extensive set of experiments on conditions affecting the production of oxygen by coral zooxanthellae as a result of photosynthesis and the consumption of oxygen by coral respiration. These experiments were carried out both 'in nature' using light and dark crates on the reef and also in outdoor aquaria. The relevance of these studies today is reflected in a recent comprehensive review on the significance of oxygen in the functioning of coral reefs (Nelson & Altieri 2019) where the work of the Great Barrier Reef Expedition is highly cited. These modern-day authors recognize the work of Yonge et al. (1932) as the first to quantify oxygen consumption

Figure 9 Aubrey Nicholls (left) and Maurice Yonge demonstrate the ‘coffin-shaped box’ used to test the effects of darkness on selected corals and their zooxanthellae (by kind permission of the Royal Geographical Society).

over a range of oxygen partial pressures and the Expedition’s resulting conclusion that ‘reef building corals are exceptionally well fitted for survival in water of very variable oxygen content’ (Yonge et al. 1932, 244) is one that is repeated throughout the studies that followed over 50 years later.

Results of other experiments with zooxanthellate corals and the azooxanthellate coral *Dendrophyllia nigra* in dark and light conditions also provided important findings on the role of zooxanthellae in excretion of waste products (Yonge & Nicholls 1931b). While *Dendrophyllia* excreted large amounts of phosphorus, the zooxanthellate corals did not. In contrast, they frequently removed phosphate from the surrounding water, even when this had been greatly increased by the addition of phosphate. Yonge (1931b, 309) noted that ‘zooxanthellae are thus capable of utilising much more phosphorus than is normally produced by the catabolic processes of the corals in which they live. The same is probably true of nitrogen and possibly sulphur’. The role of zooxanthellae in removal of waste products of the animal host was seen by Yonge (1931b) as a critical element of the symbiotic association and an important factor in the overall success of reef corals.

One aspect of the Expedition’s work that is seldom referred to in the now extensive modern literature is that concerning coral bleaching. Interestingly, the expedition scientists published the first account of thermally induced whitening or ‘bleaching’ in the field in 1929 (Yonge & Nicholls 1931a) although Mayer (1914) had described corals being ‘injured’ by high seawater temperature in the Caribbean as early as 1911. On 29 February 1929, the Expedition scientists noticed widespread coral bleaching on the reef flats surrounding Low Isles, with seawater temperatures of 35.1°C in coral pools during a particularly calm spell of weather. Yonge & Nicholls (1931a) report that many corals were killed during this period. These authors made little of their observations in the field (Figure 10) and included no photographs of the bleached reefs in their extensively illustrated reports although they followed up these observations with temperature experiments, histological descriptions of possible bleaching mechanisms and notes on the coral recovery which occurred three months later.

Figure 10 Mattie Yonge sitting on the aerially exposed reef flat at Low Isles during February 1929 at the time of a very low tide and surrounded by corals bleached white by unusually high seawater temperatures (with kind permission from Maurice Yonge Collection, the Natural History Museum, London.© The Natural History Museum, London).

It is clear that Yonge considered the 1929 bleaching as a natural event that might regularly occur during the warmer summer months (Yonge & Nicholls 1931a). Indeed, attempts were made by the Expedition scientists to quantitatively measure zooxanthellae densities of corals in the field on a monthly basis throughout their 13-month stay on Low Isles, but these were abandoned because of the difficulty of obtaining adequate numerical accuracy.[51] Had they succeeded they would have predated by 67 years the observation of a natural seasonal pattern of coral bleaching noted first by Stimson (1997) and soon after by others from reefs all around the world (Brown et al. 1999, Fagoonee et al. 1999, Fitt et al. 2000).

Adult and juvenile coral growth, coral reproduction and effects of sedimentation on reef corals

(Thomas) Alan Stephenson, leader of the Expedition shore party, was responsible for much of the work on the growth and reproduction of corals, working alongside Sheina Marshall and Sidnie Manton and ably assisted by his wife, Anne Stephenson. Again, results from this research significantly expanded earlier work by Vaughan (1923) and Mayor (1924) and provided a foundation for future studies, which in the case of coral reproduction did not develop until the 1980s (Harrison & Wallace 1990, Guest et al. 2005). Like Yonge, Stephenson made full use of the 'aquarium-like' surroundings of Low Isles. He devised ingenious schemes to maintain corals – at all life stages – in the natural environment to monitor reproduction, settlement and growth, with the minimum of human interference. To this end, he used the diving helmet (Figure 6B) to collect and observe marked corals underwater at depths of 4 to almost 9 m. In another example, he created 'clock-towers' for the rearing of planulae in the wild – these structures were solid concrete blocks with four hollow faces, each inset with four finger bowls that could be easily removed (Stephenson 1931). Planulae collected from corals in the laboratory aquaria were settled in these bowls and placed out on the reef to grow, the whole 'clock-tower' structure being set upon iron legs that were planted into the reef. The finger bowls were kept in place by four wooden laths attached to the outside of the block and which could be swivelled to one side for retrieval of the finger bowls (Figure 6C). This methodology proved highly successful and resulted in rapid growth of the settled planulae under natural conditions. His innovative approach for measuring growth in adult corals is best summed up in his own words in the Expedition report of 14 November 1928 (and see Figures 6D and 11):

'The work which has occupied most of my time during the last three months has been the setting up of and experiment on the growth rate of corals. One hundred square blocks of concrete have been made, and upon each one of these has been affixed one or more living corals, belonging to a varied selection of genera. The blocks have been placed in the sea in two specifically constructed pens and fastened down with iron spikes. One of the pens is situated in a shallow lagoon, the other in more open water in the anchorage. Each block with its attached corals has been photographed by the aid of an apparatus which ensures that the same block can be photographed subsequently from exactly the same angle and distance. By the inclusion of an accurate scale in each photograph, measurements can be made from the negatives. Ten further blocks have been provided with the halves of divided colonies, the two halves of each colony being planted out in different habitats so that any differences in mode of growth due to environment may be noted'.[51]

Stephenson (1931) and Stephenson & Stephenson (1933)'s work on coral growth was wide-ranging and included experiments on the development and formation of colonies of *Pocillopora bulbosa* (now *Pocillopora damicornis*) and *Porites haddoni* (now *Porites stephensoni*) following settlement; measurement of growth in 169 corals of various species over a six-month period;

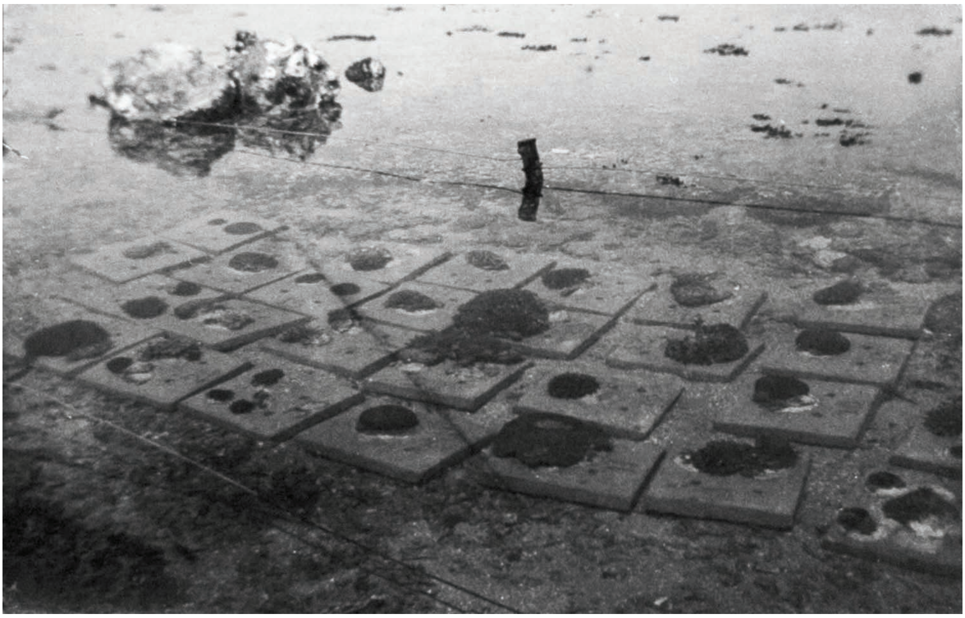

Figure 11 Translocated coral colonies on cement blocks used for measurements of skeletal growth between September 1928 and May 1929 by Alan Stephenson (source: James Cook University Library Special Collections, Sir Charles Maurice Yonge Collection, Great Barrier Reef Expedition Photo Album 3, Creators: Frederick Stratten Russell and Gweneth Kate Moy Russell (1928). Reproduced with kind permission of the James Cook University Library, Australia).

observations of intra-tentacular and extra-tentacular budding patterns in *Favia* and *Lobophyllia*; and descriptions of regeneration in broken branches of *Acropora* and notes on the effect of habitat on colony form in a number of species. Apart from quantitative accounts of growth rate differences between massive and branching corals, the authors highlight the marked within and between variations in growth rate of colonies of the same species. They also note the extreme intraspecific variation in growth forms between colonies living in different environments, a feature that was subsequently described as 'ecomorph' variation by later authors (Veron & Pichon 1976).

The bulk of the work on reproduction of corals was carried out by Sheina Marshall and Alan Stephenson (Marshall & Stephenson 1933) although other members of the Expedition were credited for their collaboration in collections and Sidnie Manton for her examination of fresh gonads. A key aim of this aspect of the Expedition was to evaluate whether sexual reproduction in corals took place all year round or whether the majority of corals reproduced at a particular time of year – a theme that has since been extensively developed for locations worldwide (see reviews by Harrison & Wallace 1990, Harrison 2011). Marshall & Stephenson (1933) attempted to examine 10 species of corals on a monthly basis for over 13 months. Three genera, namely *Favia* (now *Dipsastraea*), *Symphyllia* and *Lobophyllia*, were subject to gonad analysis (using fresh material and histological analysis of preserved samples) while others *Montipora ramosa* (now *Montipora digitata*), *Acropora hebes* (now *Acropora aspera*), *Psammocora gonagra* (now *Psammocora contigua*), *Goniastrea pectinata*, *Porites stephensoni* and *Pocillopora damicornis* were examined for planula production. At the time of the Expedition it was believed that the majority of corals were viviparous and brooders of planulae larvae. However, it should be noted that the authors admit that they only witnessed planulae production in two of their selected species – *Pocillopora damicornis* and *Porites stephensoni*. It is now recognized, since work in the early 1980s, that at least 157 coral species broadcast spawn gametes, 50 species brood planulae and another 10 species display both modes of development (Harrison & Wallace 1990, Harrison 2011).

Nevertheless, Marshall & Stephenson (1933) were the first to note the lunar periodicity of planula production in *Pocillopora damicornis* – this species planulating on the new moon between December–April and with the full moon during July and August – a finding that has since been supported by Harriott (1983) for the same species at Lizard Island on the Great Barrier Reef. Explaining this transition, Marshall & Stephenson (1933) noted a coincidence with tidal pattern, but it has since been shown that lunar periodicity of *Pocillopora damicornis* planula release is a geographically variable phenomenon (Harriott 1983). The drivers are still unclear but with factors such as dynamic light processes, sea temperature, tidal cycles and other biological effects, such as endogenous rhythms and hormones, all potentially playing a role in lunar periodicity of mass spawning species (Boch et al. 2011).

In the preface to their paper, Marshall & Stephenson (1933) recognized the shortcomings of their work, emphasizing that theirs was very much a preliminary study. The small sample sizes and sometimes irregular sampling limited their conclusions, and they stated that after their studies, 'The next workers to take the matter up, however should now be in a position to carry it rapidly to a more advanced stage' (Marshall & Stephenson 1933, 219). It was, however, not until ~55 years later that major advances were made into our understanding of coral reproduction through the comprehensive study of mass spawning on the Great Barrier Reef (Babcock et al. 1986).

As well as investigating important aspects of coral physiology, the 1928–1929 Expedition also monitored sediment production and its effects upon corals at Low Isles. This work was carried out by Sheina Marshall and her colleague A.P. Orr and involved comprehensive deployment of sediment traps across the reef (Figures 12 and 13A) over a seven-month period, with sediments being collected weekly and subsequently, dried, weighed and graded according to particle size. This work showed the role of hydrodynamic processes (waves and tides) in sorting different sediment size populations on the reef flat, pre-figuring the development of environmental sedimentology in the 1950s and 1960s (e.g. Folk and Robles 1964); shallow coring of reef flat surfaces (Figures 12 and 13A) and

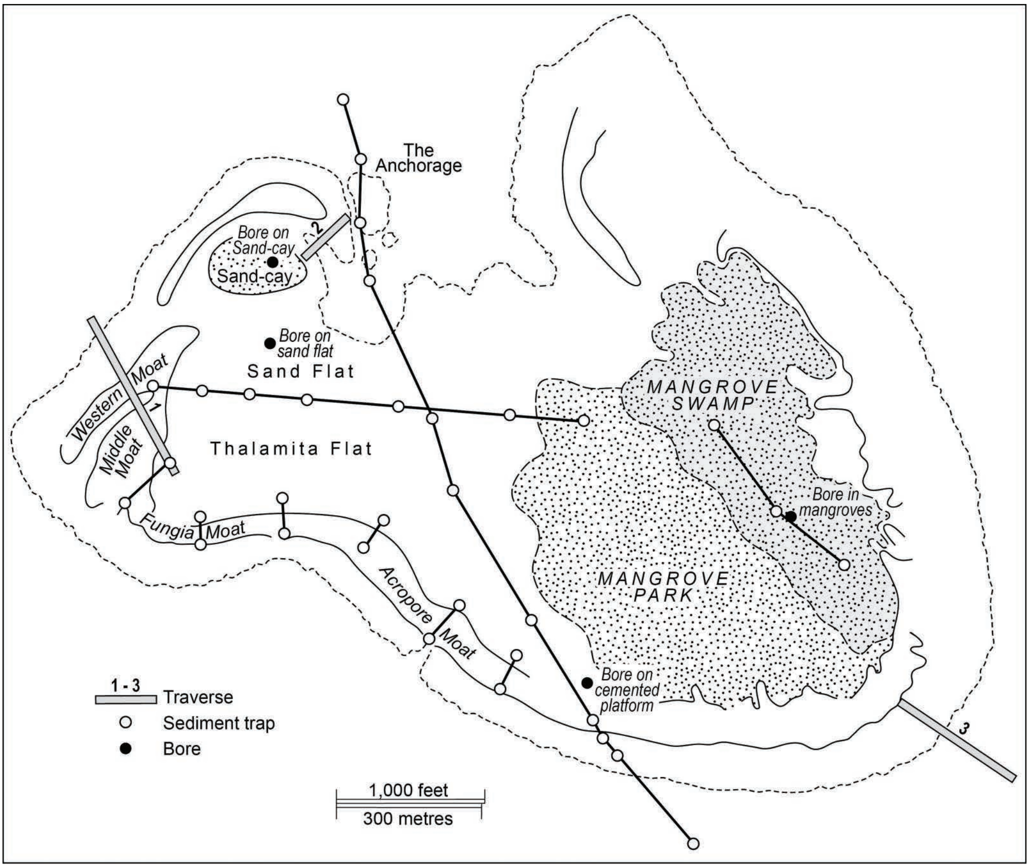

Figure 12 Location of sediment trap transects and shallow bores on Spender's basemap (re-drawn from Marshall & Orr 1931) and positions of three surveyed traverses (taken from Manton & Stephenson 1935).

the sand cay (to 5 m); chemical analysis of sediments; and experiments on sediment shedding by corals (Marshall & Orr 1931). As a result of this work, these authors very quickly realized that the common perception that corals grow well in only clear, sediment free waters was quite false. They comment that 'corals can and do live in slightly turbid waters and for a limited period can withstand large quantities of sediment falling from above. Water movements and ciliary action of the corals themselves are the effective agents of removing sediments' (Marshall & Orr 1931, 131).

Interestingly, even as late as 2012, authors still discussed whether turbid environments should be considered sub-optimal for 'healthy' coral reef growth (Browne et al. 2012). As the 1928–1929 Expedition discovered, turbid reef environments can support a healthy and diverse assemblage of corals, a finding echoed elsewhere on the inner Great Barrier Reef (Browne et al. 2012; Perry et al. 2013), in the Kimberley region of western Australia (Richards et al. 2015); the Andaman Sea (Brown 2007b), Singapore (Guest et al. 2016) and Java (Tomascik et al. 1997).

Marshall & Orr (1931) were the first to experimentally measure the sediment shedding ability of a variety of corals although Wood-Jones (1912) had already observed the efficient removal of sediment by *Fungia*. The Expedition scientists worked with eight coral genera in sediment shedding experiments in the field (*Pocillopora*, *Galaxea*, *Dipsastraea*, *Symphyllia*, *Fungia*, *Psammocora*, *Acropora* and *Porites*) and with four genera in aquaria (*Dipsastraea*, *Porites*, *Fungia* and *Psammocora*). In aquarium-based experiments, they used three types of sediment – muds, fine sand and coarse sand – and concluded that almost all corals were able to readily cleanse themselves of

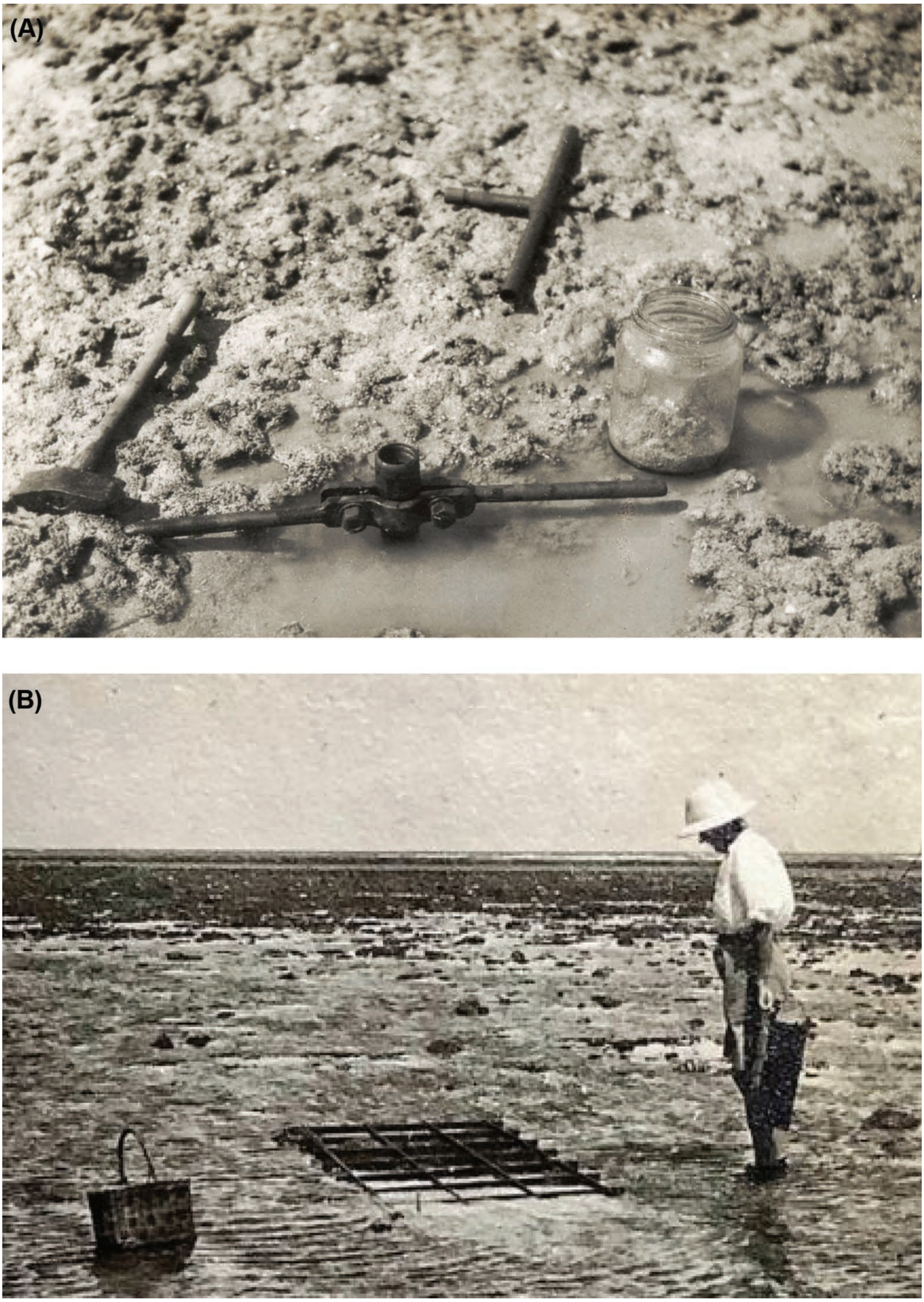

Figure 13 (A) The bore in the cemented platform on the Low Isles reef flat (see Figure 12 for location) and sediment trap sampling jar. Hand boring revealed a surficial layer of cemented ‘honeycomb rock’ (that required a crowbar, hammer and chisel to penetrate) overlying a soft grey mud with little sand (photo credit: M.A. Spender, by kind permission of the Royal Geographical Society); (B) Mattie Yonge inspects the sampling frame on the Low Isles reef flat (photo credit: S. Manton, with kind permission from the family’s archives).

applied sediments with *Porites* being the least efficient. They also noted that sediment removal was most effective in the field where wind-driven currents, tidal water movement and the coral's ciliary currents, described by Yonge when studying coral feeding mechanisms during the Expedition (Yonge 1930b), ridded the sediment load within 24 hours in many species. While the Expedition focussed on sediment shedding, it is now realized that fine sediments may be an important food source of corals living in turbid waters. Such waters contain bacteria, microbial exudates, interstitial invertebrates and adsorbed and detrital organic matter (Houlbreque & Ferrier-Pages 2009) with heterotrophic feeding being potentially significant for corals living on inshore reefs, such as Low Isles (Anthony 2000).

Coral quantification and ecological surveillance

Echoing Mayor (1918, 1924), three traverses (T1, T2 and T3) were established on Low Isles, two on the leeward side of the reef with quantification of corals along their length and a third on the windward edge of the reef where quantification was not possible because of time constraints and lack of suitable weather conditions (Manton & Stephenson 1935). The traverses spanned approximately 100–400 m in length (Figure 12). In the case of T1 and T2, a 0.9 m wide strip of reef alongside the traverse was examined using a rectangular wooden frame measuring 0.9 m × 1.8 m, cross-partitioned into sub-units of 0.09 m^2 (Figure 13B). Describing her first 'marvellous' day diving with the helmet on Traverse 1 in a letter to her family on 24 May 1929, Manton writes 'Yesterday I fixed a rope at low tide to an iron stake 4 ft long 140 yards out on the rich coral rock area, jumped out into space from the coral edge with anchor and rope in hand and swam out with it dropping it in position – I quite forgot that booted and gaitered and carrying the anchor swimming would not be so easy, and I only just kept my nose out! Today we found the place and I went down, bucket and frame in hand and pencils tied about me' (Clifford & Clifford 2020, 91). Counts of coral colonies and dominant algae were made in every sub-unit of the frame along the entire 0.9 m wide strip along traverses T1 and T2. In addition, notes were made of the sizes of coral colonies within the frame by measuring their largest diameters.

Traverse T1 spanned the reef flat, the moat, the boulder tract and the seaward slope to a depth of approximately 5.6 m below chart datum, where datum refers to water level at the lowest low tide. Moving away from the shore traverse T2 comprised beach sand, beach sand-rock, the inshore reef and seaward slope to a depth of approximately 1.5 m below chart datum while traverse T3 covered the outer rampart and windward reef slope where the occurrence of organisms on four successive 30 m long strips was recorded to a depth of approximately 20 m (Figure 12). While the reef slopes of T1 and T2 were accessed by means of the diving helmet, used by Sidnie Manton down to a depth of ~ 5 m (Figures 5 and 6B), observations on the steeper, windward slope of T3 were made from a boat. Figure 14 shows the reef profile, the distribution of algae and corals and the total number of coral colonies recorded along traverse T1. In addition to these measurements, large-scale maps of small portions of the traverses were made in different habitats so that comparisons could be made of different reef areas (Figure 15). Manton was in no doubt as to the value of this work, writing on 23 June 1929 'The sections are truly handsome- nobody has ever made a section of a reef edge before let alone examine its fauna with anything but a dredge' (Clifford & Clifford 2020, 103).

The interdisciplinary philosophy of the Expedition, referred to earlier in this paper, was probably no better exemplified than in the ecological survey of the reefs around Low Isles. A general description of the reefs and other habitats at Low Isles and a selection of reefs in other locations was provided by Stephenson et al. (1931) with quantification of corals at Low Isles addressed by Manton and Fraser while Tandy monitored abundance of algal cover (Manton & Stephenson 1935). The traverses were accurately mapped and tidal levels established by Spender (1931) while Orr sampled physical and chemical variables (salinity, temperature, pH, turbidity, oxygen saturation

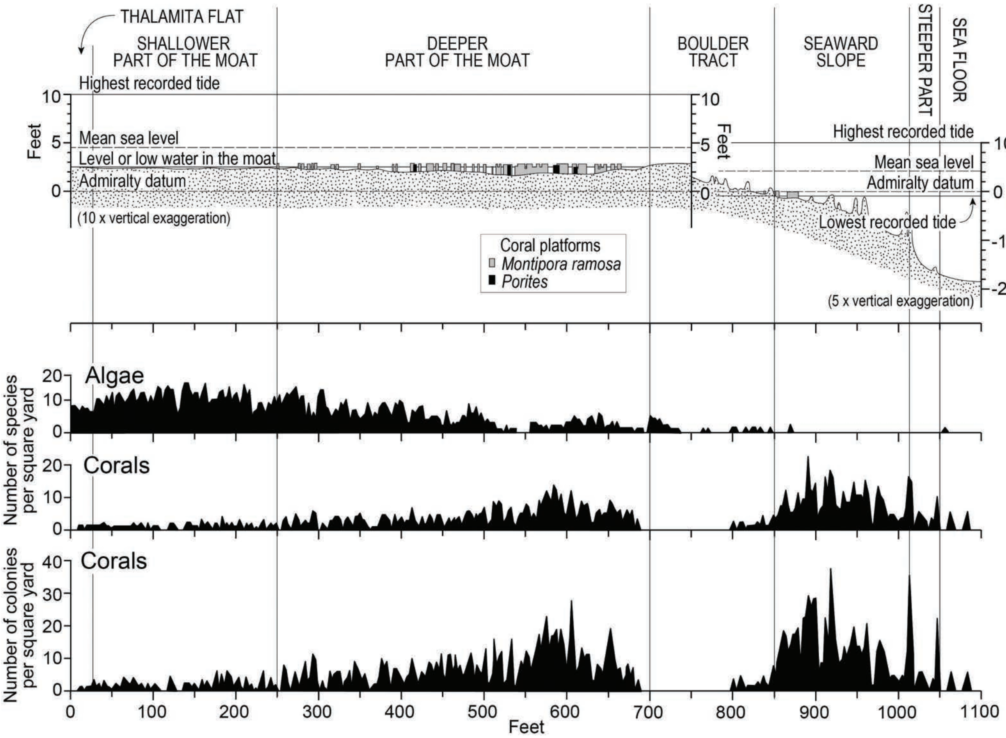

Figure 14 Bathymetry, number of different species of algae and corals and total number of coral colonies, Traverse I (for location see Figure 12). Re-drawn from Manton & Stephenson (1935).

and phosphate concentration) on a diurnal basis at specific points on the traverse (Orr 1933, Orr & Moorhouse 1933). In addition, plankton hauls were carried out over the reef flat and beyond the edge of the reef during the day and night by Russell & Colman (1931) with the aim of determining availability of food for the reef corals (Figure 6A).

The detail of these surveys and importantly their accurate mapping has provided an exceptional baseline for further studies. Subsequent work on the islands was carried out by Moorhouse (1933, 1936), Fairbridge & Teichert (1947, 1948), Stephenson et al. (1958), Stoddart et al. (1978a), Bell & Elmetri (1995), Frank & Jell (2006), Schueth & Frank (2008) and Hamylton et al. (2019). The Australian Institute of Marine Science have been running manta tow (since 1986) and permanent transect surveys (since 1992) on the reef perimeter at Low Isles (AIMS 2015) and the most recent paper (Fine et al. 2019), drawing data from 2004, 2015 and 2019, actually repeated surveys of the traverses described by the 1928–1929 Expedition, highlighting the value of the highly accurate mapping and ecological surveillance contained in this early work. This latest study showed a long-term decline in coral and invertebrate richness at Low Isles since 1928–1929, likely resulting from repeated cyclone and coral bleaching damage and increasing eutrophication, the latter either from regional mainland agricultural activity (Bell & Elmetri 1995) and/or with increased local nutrient inputs from the expansion of the mangrove forest (Frank & Jell 2006) in the intervening years. These findings echoed the observations of Yonge himself: 'When we there in 28/29 the reef flat when exposed at low tide was literally an aquarium. I was briefly there again for some hours in 1965 and over it again in 1975 in a light aeroplane. But I really saw it properly again in 1978 (50 years on) when I was working at AIMS south of Townsville. All that exposed reef was covered with sediments with only holothurians in their element and flourishing. The sediment had come from the mouth of the Daintree River some 10 miles away. This is the result of replacing the rain forest by sugar

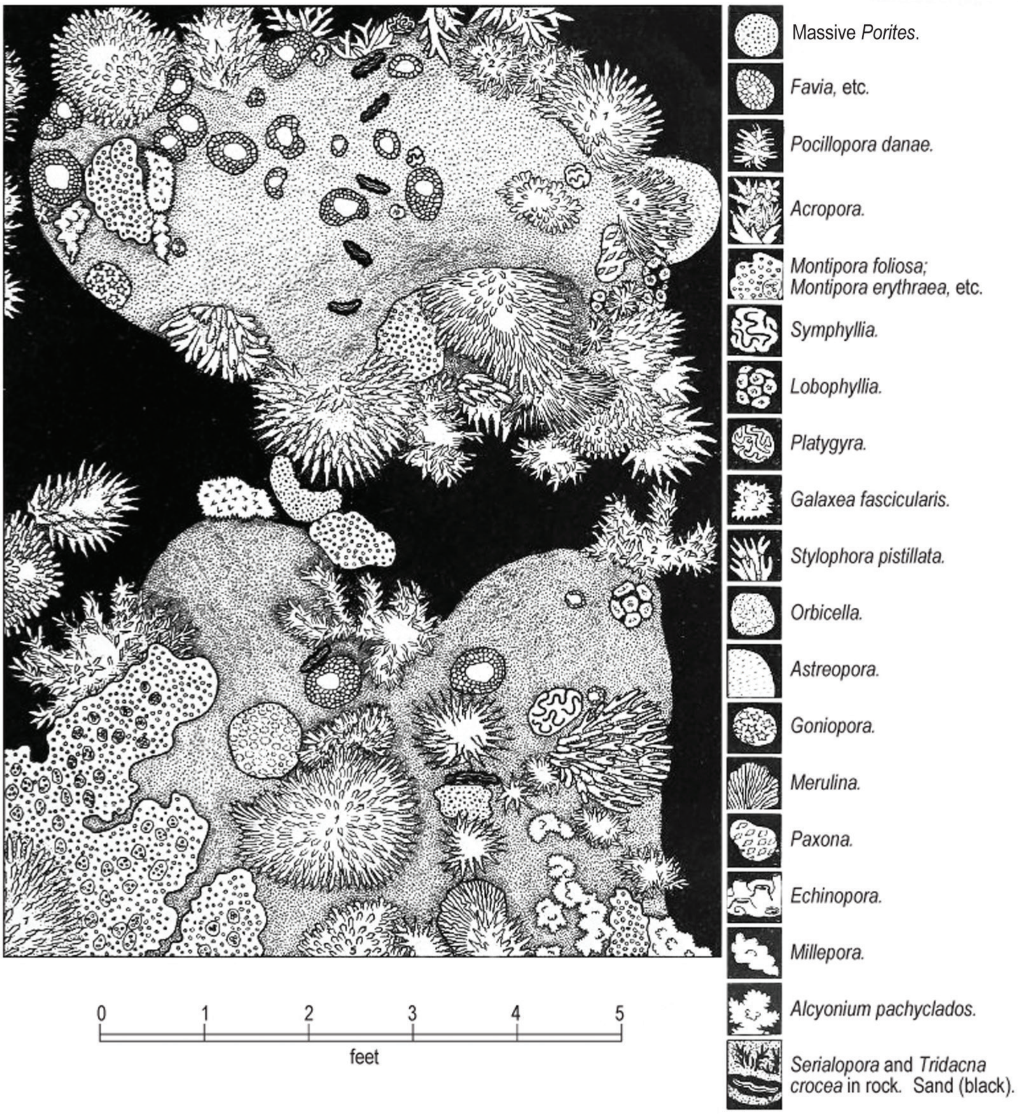

Figure 15 Detail of large-scale map of the area of maximum coral growth on the seaward slope of Traverse I. Rock substrate, in grey, with individual coral colonies (see key to species alongside) and sandy floor in black. Re-drawn from Manton and Stephenson (1935).

cane fields'[52] (and see Morton, 2004). Despite these sombre results (and see Hughes et al. 2011), the value of the ecological surveys carried out by the 1928–1929 Expedition should not be understated, providing as it does the basis for one of the longest (91 years) coral reef surveys published to date.

Regional variability in reef and island types and sea level change along the northern Great Barrier Reef

In establishing the regional variability in both reef and shoreline types between the Whitsunday Islands (20°S) and Cape Melville (14°S) (Figure 1), Steers was the first since Jukes to thoroughly consider the possible evolutionary linkages between offshore reefs and the mainland coast. Furthermore, the 1928 cruise was a precursor to a second expedition to the Great Barrier Reef, in May–August 1936 with FE Kemp of Selwyn College, Cambridge, which ranged even more widely, from Brisbane to Cape Direction (12°50′S) and back to Bundaberg (24°51′S), a track of over 4800 km (Steers & Kemp 1937, Steers 1938). In reviewing the literature on the structural geology of the shelf after the 1928–1929 Expedition, Steers contrasted those who saw the reef as a thin veneer (with some limited submergence) with those who invoked subsidence in the Darwinian sense. Steers found 'himself on the side of those favouring subsidence on a fairly extensive scale, though not necessarily of equal amount in all parts of the Barrier'… 'the subsidence as having been due partly to simple warping and partly to faulting' (Steers 1929, 239, Steers 1933). These ideas ultimately stimulated techniques of reef drilling, seismic surveys and radiometric dating of reefal materials and intellectual debates on eustatic and hydro-isostatic controls on sea level change along and across the continental shelf which were documented in the region during the 1973 northern Great Barrier Reef Expedition (Stoddart 1978, Thom et al. 1978) and later followed up by John Chappell and others (Chappell et al. 1982).

In the 1929 paper (and again in 1938), Steers also pointed out the widespread prevalence of benching on the high islands, particularly at + 30–60 cm above the 'oyster level', which he thought was recent but not contemporary, and a less common level at + 2.4 m, and speculated on the connections between these levels and both the beach rock and conglomerate platforms on the low wooded islands of the inner shelf and the alluvial plains on the mainland coast. The 1973 Expedition also established that northern Queensland experienced a higher sea level at ca. 6000 years BP, peaking in the 4000–3000-year BP period before falling thereafter to its present level. Many recent studies on the Great Barrier Reef have confirmed the generality of this sea level picture using a range of physical and biological indicators (Kench et al. 2012, Lewis et al. 2013), including fossil 'oyster levels' (Lewis et al. 2015). Despite broad agreement on these paleo-sea level trends, two contentious issues remain. One relates to the precise elevation, timing, duration and geographic extent of the mid-late Holocene sea level high stand (Yu & Zhao 2010, Smithers et al. 2018) and the other to whether sea level fell smoothly (Chappell 1983, Beaman et al. 1994, Lambeck et al. 2010) or oscillated during its fall to present position (Baker and Haworth 2000, Lewis et al. 2008, Leonard et al. 2016). It is also evident that reef island development was not only influenced by sea level but also by high wave energy levels and enhanced sediment transport around 5000–4000 years BP (Stoddart et al. 1978b; Kench et al. 2012; Perry et al. 2013).

Reef island mapping and quantitative survey of reef environments

Hamylton (2017) reproduces six maps made of Low Isles, by different methods and to varying degrees of resolution, between 1928 and 2014, to which now can be added Hamylton et al.'s (2019) own drone- and ground-survey-based map of 2017. The earliest map is EC Marchant's plane-table 'physiographical sketch map', reproduced as Figure 5 in Steers (1929).[53] But this was soon superseded by Michael Spender's iconic maps from 1929 (Spender 1930, Plate 1; although not to universal acclaim[54]). Spender's maps were subsequently revised in the Great Barrier Reef Reports by including additions from the 1928 aerial photography (Stephenson et al. 1931), annotated by Moorhouse following the storms of 1931 and 1934 (Moorhouse 1933, 1936) and then substantially revised from repeat aerial photography in January 1945 and a follow-up visit 30 January–4 February 1945 (Fairbridge & Teichert 1947, 1948) (Figure 16). Following the cyclone of 1950, the Great Barrier Reef Committee Expedition of 12–26 August 1954 also noted changes (Stephenson et al. 1958). However, the most detailed re-survey before the application of modern aerial surveys was the detailed compass and measuring tape survey, with complimentary levelling transects, carried out over the period 24–29 August during the 1973 Royal Society and Universities of Queensland Expedition to the northern Great Barrier Reef (Stoddart et al. 1978a).

The Low Isles complex, as described by Spender (1930), includes two laterally extensive, asymmetric shingle ridges on the windward side of a patch reef; a small sand cay with beachrock on

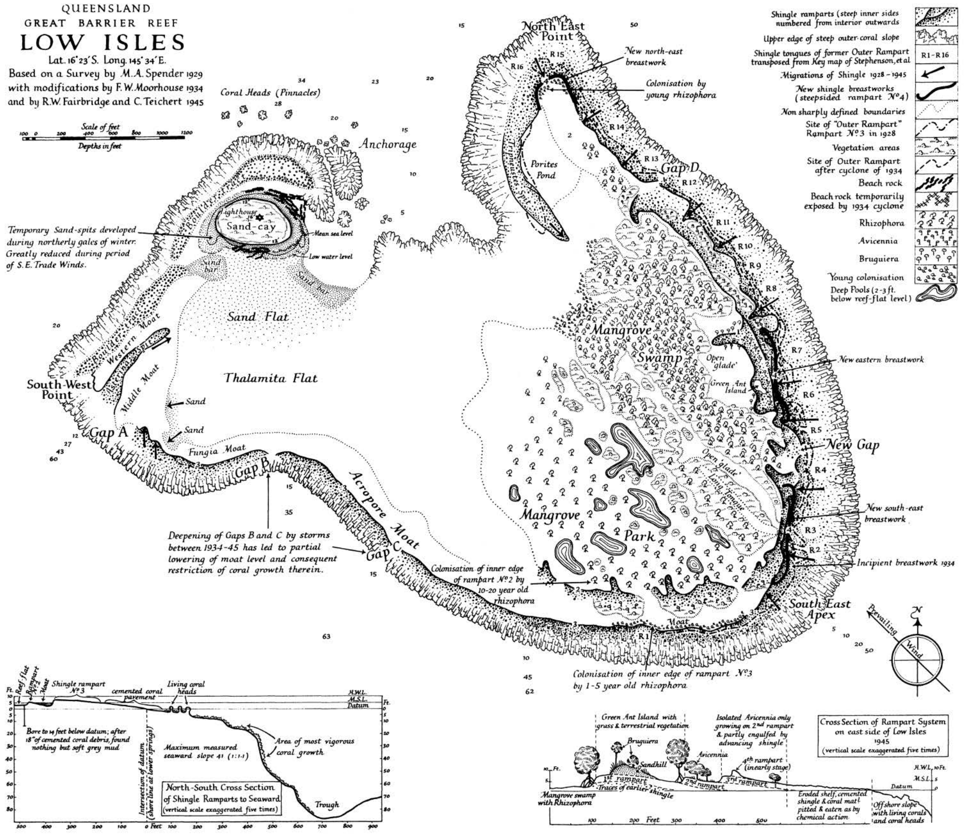

Figure 16 Fairbridge and Teichert's map of Low Isles (1948). The investigation was carried out under the auspices of the Royal Australian Air Force, the object being to improve the accuracy of photo-interpretation of coral reefs during WWII by correlating ground features with their appearance on aerial photographs. Fieldwork on Low Isles in January–February 1945 involved taking the air photographs, Spender's 1929 map and Moorhouse's 1934 post-cyclone map to carefully check every feature on the ground. The detail and commentary on the three panels in this figure illustrate the result of this methodology including changes over the 17 years since the 1928–1929 Expedition (Fairbridge, R.W. & Teichert, C. 1948. The Low Isles of the Great Barrier Reef: A new analysis. *The Geographical Journal* **111**, 67–88 (facing p. 74), by kind permission of the Royal Geographical Society).

the leeward side of the reef, and an extensive reef-top flat, part of which is occupied by mangroves (Figure 2). Stephenson et al. (1931) divided this latter element into two components: a 'mangrove swamp' of *Rhizophora* woodland up to 20 m tall and a 'mangrove park' adjacent to the swamp, formed by outlying *Rhizophora* patches and seedlings in a *Thalassia* seagrass meadow.

In particular, this long record of the changing distribution of reef-top landforms and habitats at Low Isles, and at the other low wooded islands of the Great Barrier Reef, has allowed the evaluation of changes to reef-top landforms including sand cays and mangrove forests (Hamylton et al., 2019). The 90-year evaluation represents a considerable timespan within the global record, exceeded only by the 118-year record provided by the maps of the islands on Funafuti surveyed during the Royal Society of London Expeditions in 1896–1898 (David and Sweet 1904, Kench et al. 2015). Beyond providing an accurate record of the previous location of landforms to provide a baseline against which changes can be estimated, such historic records also allow greater consideration of the fundamental processes determining the nature of such changes. In the case of Low Isles, the 1929 maps reveal insights into two different models of reef responses to environmental forcing. Spender (1930, 290) preferring the term 'island reef' to 'low wooded island', favoured a model of dynamic equilibrium: 'The relics of previous movements seen in the sand-rock, conglomerates, and occasional dead or dying mangroves, the limits of the mangrove-swamp, and also the historical evidence, all suggest that the islands have existed long enough to find an equilibrium of the elements on the reef, about which distribution alternate growth and destruction make small oscillations…. Each [island] has reached for the given form of the reef and weather conditions a comparatively stable and balanced finality'. The alternative model, as expressed by Steers (1937), was an evolutionary one whereby once a reef top has stabilized behind a protective rim, or 'bassett edge', mangrove spreads across the platform surface from the windward margin towards the leeward sand cay, ultimately at the final stage of evolution completely filling the reef-top accommodation space. Matters came to a head in the Discussion that followed Steers paper to the RGS on 7 December 1936. Opening the proceedings, Spender began 'In both of Mr. Steers' papers [published as Steers 1929 and Steers 1937] he describes the cays as "unstable". This is a misleading description. To a scientist "unstable" means that the cay, given a slight displacement, would vanish. Nothing of the sort happens. When the cyclone came to Low Isles in I934, even that enormously displacing factor failed to prevent the cay from being rebuilt as soon as it had passed. A cay is, in fact, a perfect equilibrium structure due to the drift over the reef flat, the wave system of the lee of the reef and the height of the flat. For that reason, cays tell nothing of the past history of the reef but only of the actual momentary level of the reef'. He went on: 'The habit of physiographers to use terms like "less" and "more advanced" stages of development implies an evolutionary idea in this case to which I object. I have already expressed the opinion that the extent to which the mangroves cover the reef is conditioned by the momentary distribution of shingle on the reef. There is no reason to suppose that an island covered with dense mangroves is a "mature" form, because if the platform which protects them is, as Mr. Steers states, being eroded, the sea will eventually eliminate it and strip numbers of mangroves off the reef. As a matter of fact I am prepared to argue that that might have happened at Low Isles and has happened at Three Isles' (Spender in Balfour et al. 1937, 141–142). In reply, Steers only backed down to a degree: 'The use of the word "unstable" need not give rise to any difficulty. I used the word as meaning "apt to change or alter", or "not stationary", and Mr. Spender seems to me to make rather a finical comment' and 'The extent to which mangroves cover a reef is not, I think, fundamental. I have suggested that their spread must depend on many incalculable factors. I would however suggest that the size of the shingle island, or the number and size of the various ridges, does measure a stage in the development of low wooded islands' (Steers in Balfour et al. 1937, 144, 145). And there the matter was left.[55] The 1973 re-survey at Low Isles did not resolve these arguments; rather, it revealed the complex feedback loops between hydrodynamic processes, carbonate sedimentation, mangrove colonization and spread, and the episodic formation and destruction of encircling marginal ramparts under cyclone impacts (Stoddart et al. 1978a). However, following a review of mangrove coverage on 21 reefs on the northern Great Barrier Reef, Stoddart (1980, 282) was able to conclude: 'Depending on the time perspective adopted, one can agree with either Steers's view of an evolutionary progression in low wooded island form, calibrated by development of mangrove, or Spender's of a series of equilibrium states. In the short term, as the comparative surveys of Low Isles and other reefs have shown, mangroves are patterned opportunistically in terms of substrate topography in the manner that Thom (1967) suggested for certain geomorphically active continental coasts. In the longer term, however, there is no doubt that mangrove cover extends to cover the reef-top. The evidence suggests that once mangrove growth is made possible by the protection of the reef-top afforded by construction of shingle ramparts, such extension is variable in rate but can be very rapid. The extent and history of mangrove cover is therefore governed by factors peculiar to individual reefs, and mangrove development per se cannot be used to correlate development sequences between individual reefs'. These arguments, however, sit within the argument for a dynamic environment but one within a recorded range of historical environmental variability. Thus, Hamylton et al. (2019) raise the question as to how these dynamics seen over the last 90 years at Low Isles will be impacted by increased frequencies of coral bleaching consequent upon ocean warming and a rising trend in ocean acidification, pointing out that the short-term impacts of changing water temperature and chemistry on the 'carbonate factory' (Kench et al. 2009) are likely to take time to propagate through geomorphic pathways and thus find expression in changing reef island morphologies.

The legacy – how the Expedition and its results came to be viewed by the rest of the world, its impact on subsequent science and development of international links in reef science

On a broad international scale, the Expedition stimulated such interest in reef processes that, following the Fourth Pan-Pacific Congress in Batavia-Batong in 1930, the International Committee on the Coral Reefs of the Pacific (chaired by Vaughan) suggested building an international institute of marine biological science in the Pacific (Konishi 2004). As a result, Dr. Sinkisi Hatai, from the Tohoku Imperial University, Japan proposed the building of the Palao Tropical Biological Station to the Japanese Society for Promotion of Science and a small laboratory was built in 1935 at Koror Island, Palau (Omori 2012). Yonge (1940) describes the early work of Japanese scientists at the laboratory which followed a programme of research very similar to that carried out by the 1928–1929 Expedition. These early studies were published in the Palao Tropical Biological Station Studies in 1937 (Fautin 2002) and work continued at the laboratory until 1943 when the station was taken over by the Japanese Navy prior to capture by American forces. Research on Pacific coral reefs then resumed after the end of WWII in earnest with projects that included geological (Ladd et al. 1953) and biological work (Goreau & Austin 1947, Odum & Odum 1955) in the Marshall Islands. By 1969, coral reef science came of age with the holding of the First International Coral Reef Symposium at Mandapan Camp, India, with delegates participating from twelve countries. The Proceedings of that meeting boasted 37 papers and included one by Yonge, leader of the 1928–1929 Expedition.

Threaded through these latter developments in reef science were individuals who were influenced either by interactions with members of the 1928–1929 Expedition or by the extension of research themes developed during work on Low Isles and surrounding reefs. Three individuals, in particular, stand out because of their significant contribution to galvanizing reef scientists and influencing reef research in the twentieth century and whose legacy continues to the present.

The first individual whose research was influenced by findings from the 1928–1929 Expedition was Len Muscatine (1932–2007) (Hoegh-Guldberg et al. 2007). Muscatine played a key role himself in development of the science on algal-invertebrate symbioses and his research students (and their research students) and postdoctoral researchers made, and continue to make, outstanding contributions in coral physiology, zooxanthellae diversity, coral bleaching responses and the evolutionary ecology of coral-dinoflagellate associations. Muscatine's PhD supervisor was the invertebrate zoologist Cadet Hand, based at the University of California at Berkeley. Following the work by Odum & Odum (1955) on the trophic structure and productivity of a Pacific reef, Hand (1956) questioned their assumption that corals were herbivores in the light of the most recent evidence from the 1928–1929 Expedition that corals were carnivores (Yonge 1930b). Hand's paper was entitled 'Are corals really herbivores?' (Hand 1956). His collaboration with Muscatine, who suggested the use of radioisotopes to investigate the role of algae in nutrition, provided the first direct experimental evidence of a nutritional role for symbiotic algae in a sea anemone (Muscatine & Hand 1958; and see Muscatine 1967, Muscatine & Cernichiari 1969). Friendly correspondence between Muscatine and Yonge in 1972[56] reveals their shared interest in transfer of photosynthetic products between zooxanthellae and their animal hosts, the exchange of publications and also their admiration[57] of a second individual, Tom F. Goreau (1924–1970), who explored research themes first developed by Yonge on the Expedition.

An assistant oceanographer during the summer of 1947 at Bikini Atoll,[58] Goreau enrolled as a graduate student at Yale under Evelyn Hutchinson, completing a PhD on the biology and histology of corals in 1956. He subsequently established the Discovery Bay Marine Laboratory on the North coast of Jamaica in 1965, in association with the New York Zoological Society's 'Coral Reef Project – Jamaica'.[59] It was here that Yonge joined Goreau to follow up the work on the significance of zooxanthellae to both corals and clams (Goreau et al. 1965, Goreau et al. 1971). Goreau & Goreau (1960) and Muscatine & Cernichiari (1969) demonstrated that ^{14}C could be translocated from the zooxanthellae to coral tissues and in 1971 Yonge, acknowledging the latest research, published with Tom and Nora Goreau (Goreau et al. 1971) a paper entitled ' Reef corals: autotrophs or heterotrophs?' Yonge became a close friend of the Goreau family through his research collaborations and wrote movingly in a tribute to Goreau following his death as follows: 'It remains for the writer to add that six years of scientific collaboration with Tom Goreau starting and ending at Jamaica but ranging from Europe across the Pacific to Australia in the years between, and with continually increasing friendship, were deeply memorable. The difference between our ages seemed to disappear while our interests were entirely complementary. Tom's name will endure indefinitely as amongst the greatest of workers on coral reefs- in all aspects of their wide diversity – and the memory of him will persist throughout the lifetimes of all who knew him as that of a striking personality and a most lovable man' (Yonge 1971a, xxxii–xxxiii).

Today, there is still debate about the relative importance of autotrophy and heterotrophy to reef corals. Scientists have since concluded that corals should be considered as polytrophic, relying on both ingested and translocated carbon (from zooxanthellae) as energy sources, there being considerable variation in their dependence on heterotrophy with species, depth, plankton availability and bleaching status (Houlbreque & Ferrier Pages 2009).

The third person is David Stoddart (1937–2014) whose PhD, on three atolls on the Belize Barrier Reef in the Caribbean, was supervised by Alfred Steers and examined by Maurice Yonge.[60] Both men continued to be an influence on Stoddart who was subsequently based as a young lecturer in Steer's Department of Geography at Cambridge.[61] Stoddart later described his PhD viva as an important factor in reviving the interests of both Steers and Yonge in coral reefs (Stoddart, 1987); Yonge was subsequently a close ally of Stoddart throughout his career, and together, they collaborated in organizing a significant number of international meetings on coral reefs (e.g. Yonge 1971b, Stoddart 1972). Steers visited Brisbane and Townsville in 1967, and later talked to Yonge about further research; on 27 December 1967, they wrote jointly to the Executive Secretary of the Royal Society about the possibility of sending an expedition to the Great Barrier Reef, suggesting possible personnel but noting that the staffing should be 'essentially Australian'.[62] With the full support of the Royal Society and the University of Queensland,[63] planning meetings in Brisbane, Townsville and the UK in 1969, 1971 and 1972, orchestrated by the UK (Steers, Stoddart and Yonge) and Australian (G.R. Orme) principals,[64] ultimately led to a complex, three-phase expedition led by Stoddart from mid-July to mid-November 1973, extending from Cairns to the remote northern Great Barrier Reef (to the latitude of Cape Grafton at 11°30′S) with 24 scientists (the majority Australian), the use of four vessels and collaboration with the Royal Australian Navy (Stoddart 1978). The results were presented at a Discussion Meeting at the Royal Society in London on 28–29 January 1976, the published papers coming to over 350 printed pages (Yonge 1978).

Following the inaugural meeting in 1969, which he had co-convened with Yonge, Stoddart continued to be actively engaged in the organization of regular International Coral Reef Symposia through working with the International Association for Biological Oceanography (IABO). In particular, along with R. Endean, P. Mather and G.R. Orme of the Great Barrier Reef Committee, he organized the Second International Coral Reef Symposium. The meeting immediately preceded the 1973 Expedition, cruising the waters of the Great Barrier Reef between Brisbane and Lizard Island aboard the M.V. Marco Polo. The Symposium was attended by both Yonge and Steers, and there was an opportunity to revisit Low Isles (Figure 17). Furthermore, the Symposium 'provided a chance to let other reef researchers see the Lizard site and discuss a possible research station there. Along with Frank [Talbot], Don McMichael and Pat Hutchings from the Museum, a number of overseas researchers looked at a site on the eastern site of the island. The international group were strongly supportive of the idea… So Lizard Island was chosen...The future of Lizard Island Research Station was set'.[65] Straight after the Symposium (2–10 July 1973), the Coral Reef Working Group of the Scientific Committee on Oceanic Research (SCOR), chaired by Stoddart and with active collaboration from members of the Great Barrier Reef Committee, met at the research station on Heron Island to discuss the standardization of coral reef research techniques,

Figure 17 Alfred Steers (far left), Richard Orme (second left), David Stoddart (back to camera) and other symposium participants discussing the shingle rampart features at Low Isles on a field excursion during the Second International Coral Reef Symposium, 22 June to 2 July 1973 (photo credit: David Hopley, with kind permission of the originator).

to aid comparative studies between different reef areas. This effort represented a revision of the Handbook for Atoll Research, developed by the Pacific Science Board for its coral atoll expeditions of the 1950s (Fosberg & Sachet 1953). In particular, the revision took account of recent advances in the study of functional coral reef ecology, including methods being piloted on the southern Great Barrier Reef (e.g. Kinsey 1972). Draft methodologies were reviewed, with testing of methods both at Heron Island and at the Australian Museum field station on One Tree Island. The ultimate outcome was the publication of the UNESCO Handbook on *Coral Reefs: Research Methods* (Stoddart & Johannes 1978).

Stoddart was the prime founder of the International Society for Reef Studies in 1980 (now renamed the International Coral Reef Society) and key to the establishment of the Society-related journal *Coral Reefs* in 1982. In his first editorial to the latter (Stoddart 1982, 1), he highlighted the changing face of coral reef studies in the twentieth century and the need to improve coordination of reef research and efficient flow of information between scientists:

'For many years, reef studies were carried out during occasional expeditions to remote areas, and their aim was primarily the recording of topographic and biotic diversity. This inventory approach is now largely completed, and the focus of activity has moved from expeditionary work to more detailed and longer-term studies, carried out at research stations, by universities, and on research vessels in the tropical seas. The numbers of research students has increased greatly, especially in the last 15 years, and the doctoral thesis on reef topics –once a rarity– is now an expected means of entry to the field'.

Conclusions

The varied contemporary agenda of the Australian coral reef science community continues to bear the hallmarks of experimental field research that was undertaken during the Expedition, while some of the early observations made, and records established, have paved the way for future comparative work. Key themes that have been carried forward include the work on coral physiology, particularly aspects of coral growth that have informed later reef restoration efforts and, as the influence of environmental change has increasingly been felt on the world's reefs, the causes and implications of coral bleaching on the Great Barrier Reef. In the fullness of time, Frank Debenham's pre-Expedition comments on the value of early, accurate measurement of reef surface features to act as a benchmark against which the movement of coral banks and reef flat sediments could be elucidated would prove to be particularly pertinent. On the 45th and 90th anniversaries of its production, Spender's map of the reef flat has served as a comparative record for studies of landform evolution, which have yielded insights into the dynamic nature of sand cays and mangrove forests on the low wooded islands of the Great Barrier Reef.

As the Expedition was preparing to leave Low Isles (Figure 18), Michael Spender wrote to Arthur Hinks at the Royal Geographical Society to say 'the results of the work will, I am hoping, justify themselves. They cut new ground, so far as I know: but it is difficult and dangerous this navigation among coral reef problems, and the wrecks of many worthy scientists are there as an awful example'.[66]

But surely, Spender was being unduly pessimistic. And it seems apposite to close with an opening. At the First International Coral Reef Symposium at Mandapan Camp, India in 1969, which Stoddart and Yonge co-convened, Stoddart (1972, 17) noted in his opening remarks to the meeting 'The Symposium is timely for three main reasons. First it is being held, in 1969, on the fortieth anniversary of the Great Barrier Reef Expedition of 1928–1929. It implies no reflection on the work of Gardiner and Sewell, Vaughan, Mayor and many others, to suggest that this Expedition set new standards and defined new goals in reef studies. This was true not only of C.M. Yonge's work on coral physiology, but of Stephenson's ecological and Steers'

Figure 18 Getting ready to leave: the end of the Expedition in July 1929 (by kind permission of the Royal Geographical Society).

geomorphological studies too. This co-operative work represented the first major advance on the predominately theoretical and deductive mode of work which had long dominated discussions of the "coral reef problem"'.

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Notes

1. Between 1913 and the publication of *The Coral Reef Problem* in 1928, Davis published 42 academic papers, abstracts and conference proceedings on coral reefs, amounting to over 650 pages of published material; the book itself was 596 pages in length (Chorley et al. 1973).
2. Andrews to Vaughan, 13 May 1922; File FR:IC, Archives, National Academy of Sciences, Washington D.C.
3. Andrews to Vaughan, 26 November 1924; Smithsonian Institution Archives, Accession 99–124, Thomas Wayland Vaughan Papers, Series 1, Box 2, folder Great Barrier Reef Expedition.
4. Richards to Vaughan, 17 November 1924; Smithsonian Institution Archives, Accession 99–124, Thomas Wayland Vaughan Papers, Series 1, Box 2, folder Great Barrier Reef Expedition.
5. Vaughan to Richards, 22 December 1924; Smithsonian Institution Archives, Accession 99–124, Thomas Wayland Vaughan Papers, Series 1, Box 2, folder Great Barrier Reef Expedition.
6. Vaughan to Richards, 8 July 1927; Smithsonian Institution Archives, Accession 99–124, Thomas Wayland Vaughan Papers, Series 1, Box 2, folder Great Barrier Reef Expedition.
7. By way of further explanation of the apparently baffling Michaelmas Reef and Heron Island records: ‘As all the fossils in the bores appeared similar to present day forms it was suggested that there was no firm evidence of any sediment older than Recent (deposited within the past 20,000 years). As all the fossils appeared to be shallow-water forms it was concluded that subsidence of perhaps 200 m had occurred. Although the Darwinian hypothesis of reef growth on a subsiding basement received support, the sub-reef material was unconsolidated sand and not volcanics, as required by Darwin’s theory. These two findings confused reef researchers for almost 40 years… It was not until the early 1970s that a major breakthrough in the interpretation of the drilling results occurred, when researchers demonstrated that several major solution unconformities or erosion surfaces could be recognized in the drill-cores. These features were identified as zones of calcite, formed by recrystallization of the pre-existing aragonitic skeletal material due to exposure to freshwater during subaerial exposure of the limestone. Subsequent studies of the microfossil content of the bores supported the suggestion of a much older age for the Reef. The time of commencement of reef growth has been established at the Heron Island drill site as being late Pliocene (prior to about 2 million years before present)’ (Chivas et al. 1990, 13–15). Interestingly, it was at the Second Coral Reef Symposium, just prior to the 1973 Northern Great Barrier Reef Expedition, that Peter Davies described the solutional unconformities in the Heron Island core and, by comparison with similar horizons identified by Schlanger (1963) at Eniwetok and Bikini Atolls, Central Pacific Ocean, speculated that the Great Barrier Reef cores comprised mainly pre-Holocene sediments (Davies 1974). Subsequently, Searle and Harvey (1982) identified the Holocene/Pre-Holocene boundary at a depth of 8–12 m in the Michaelmas Reef bore (and see also Webster and Davies [2003]).
8. Alfred Goldsborough Mayor was born Alfred Goldsborough Mayer. During WWI, in 1918, he changed his surname to Mayor to dissociate himself from his Germanic ancestry. He is referred to in the text as Mayor throughout, but individual references refer to the surname used in the authorship of the paper.
9. Richards to Nathan, 7 December 1921; University of Queensland archives, S0226/3, quoted in Bowen and Bowen (2002, 233).
10. Nathan to Younghusband, 4 July 1922; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1.
11. Hinks to Nathan, 4 December 1922; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1.
12. Harmer to Nathan, 5 February 1923; Zoology Catalogue DF 214/1, British Museum (Natural History) (BMNH), London.
13. Hinks to Nathan, 27 February 1923; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1.
14. Vaughan to Richards, 8 July 1927; Smithsonian Institution Archives, Accession 99–124, Thomas Wayland Vaughan Papers, Series 1, Box 2, folder Great Barrier Reef Expedition.
15. Gardiner to Richards, 9 January 1925; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1.
16. Gardiner to Hinks, 17 January 1925; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1.

17. Reference contained in the Minutes of the Great Barrier Reef Committee 9 September 1926 (No. 33), filed in Zoology Catalogue DF 214/1, British Museum (Natural History) (BMNH), London.
18. Reference contained in the Minutes of the Great Barrier Reef Committee 23 February 1927 (No. 36), filed in Zoology Catalogue DF 214/1, British Museum (Natural History) (BMNH), London.
19. Gardiner to Yonge, 3 May 1927; Yonge collection of Great Barrier Reef correspondence, reference E48 (3), British Museum (Natural History) (BMNH), London.
20. Gardiner to Vaughan, 28 July 1927; Smithsonian Institution Archives, Accession 99–124, Thomas Wayland Vaughan Papers, Series 1, Box 2, folder Great Barrier Reef Expedition.
21. Richards to Vaughan, 10 August 1927; Smithsonian Institution Archives, Accession 99–124, Thomas Wayland Vaughan Papers, Series 1, Box 2, folder Great Barrier Reef Expedition.
22. Vaughan to Richards, 27 September 1927; Smithsonian Institution Archives, Accession 99–124, Thomas Wayland Vaughan Papers, Series 1, Box 2, folder Great Barrier Reef Expedition.
23. British Association for the Advancement of Science, Report on the Ninety-Fifth Meeting, Leeds-1927, August 31–September 7, Sectional Transactions, 333.
24. Gardiner to Nathan, 24 September 1927, Zoology Catalogue DF 214/6, British Museum (Natural History) (BMNH), London.
25. Minutes of the meeting of the British Great Barrier Reef Committee, 4 October 1927; filed in Zoology Catalogue DF 214/8, British Museum (Natural History) (BMNH), London.
26. Hinks, of course, had already responded to Richards' 'Problems of the Great Barrier Reef', sending a series of notes to Colonel Sir Charles Close, the Director General of the Ordnance Survey (the national mapping agency of the UK) (Hinks to Close, 28 November 1922; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1). In response to Hinks' questions, Close felt that a long tidegauge record would answer the question of subsidence, that mean sea level should certainly be determined but that a 'full geodetic standard may be too much to expect' (Close to Hinks, 10 December 1922; CB9 1921–1930, Great Barrier Reef Expedition, Box 1). A year later, he was still at it: 'what I am of course interested in principally is survey and fixing mean sea level, bench marks etc…' (Hinks to Nathan, 21 December 1923; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1).
27. Gardiner to Hinks, 16 January 1928; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1, file 2.
28. Steers took Part I of the Diploma in Geography at Cambridge in 1917 and was in the first cohort of the BA degree in Geography (Part II of the Geographical Tripos) in 1921, obtaining the highest classification, a starred First. He was appointed to a Departmental Demonstrator in 1922 and a University Demonstrator in 1926, before promotion to a University Lectureship the following year.
29. Debenham to Hinks, 14 February 1928; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1, file 2.
30. Minutes of the meeting of the British Great Barrier Reef Committee, 23 February 1928; filed in Zoology Catalogue DF 214/8, British Museum (Natural History) (BMNH), London.
31. Spender to Hinks, 12 February 1928; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1, file 2.
32. Debenham to Hinks, 15 March 1928; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1, file 2.
33. On Marchant, Spender wrote in mid-expedition (7 January 1929) to Hinks 'I am a little alarmed about men without qualifications since Marchant has been here. I don't mean that he hasn't been exceedingly willing but it is awkward for a young man to have to deal with an older man who knows little of the principles of survey and has not even the mathematics to be able to check one's calculations'. (Royal Geographical Society CB9 1921–30, Great Barrier Reef Expedition, Box 1, file 2).
34. Memorandum on work to be carried out by the R.G.S. members of the Barrier Reef Expedition by F. Debenham, 14 March 1928; filed in Royal Geographical Society CB9 1921–30, Great Barrier Reef Expedition, Box 1, file 2.
35. Gardiner to Hinks, 29 February 1928; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1, file 2.
36. Yonge to Steers, 4 April 1929; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1.

37. TA Stephenson to Tandy 18 March 1929; Zoology catalogue DF421/1, British Museum (Natural History) (BMNH), London. The feeling was clearly mutual: 'I find this a most interesting combination of work and feel sure that you will assent to your geographer's time being spent in this way' Spender to Hinks, 7 January 1929; Royal Geographical Society CB9 1921–30, Great Barrier Reef Expedition, Box 1.
38. Spender to Hinks from Low Isles, 8 April 1929; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1.
39. Statement of Position, 28 May 1929; filed in Zoology Catalogue DF 214/8, British Museum (Natural History) (BMNH), London.
40. Spender to Hinks from Low Isles, 15 June 1929; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1.
41. Gardiner to Hinks, 19 May 1938; Royal Geographical Society CB10 1931–1940, Gardiner file.
42. Gardiner to Hinks, 19 November 1938; in discussing problems associated with publishing the Expedition's reports: 'on Yonge I fear he may have failed altogether in visualising the great geographical problems of these and all reefs'. On 20 November, Hinks replied to say 'If Yonge failed to visualise the geographical problems of the Reef we shall have to fall back on Spender, who has been visualising a great deal'; filed in Royal Geographical Society CB9 1921–1930, Gardiner file.
43. British Association for the Advancement of Science, Report on the Ninety-Sixth Meeting, Glasgow-1928, September 5–12, Reports on the State of Science, 395–396.
44. A9-4 was one of six Seagull Mk. III aircraft ordered by the Australian Government from the Supermarine Aviation works, Southampton, England, in April 1925. On 1 July 1926, RAAF No. 101 (Fleet Cooperation) Flight was formed to work with HMAS PORT MORESBY on the Great Barrier Reef Survey; Low Isles was flown, from a base at St Bees Island near Mackay, in phase 2 of the Survey (May–December 1928). A9-4 continued to operate until 19 March 1930 when it crashed into the sea, with one fatality, off the Tasmanian coast and could not be recovered intact (McGuiness, 2020).
45. with Fairbridge and Teichert taking it in turns to hang out of the aircraft door with the camera (Crick and Stanley 1997)
46. Debenham to Hinks, 23 October 1928; 'I have also heard from Steers and he has told me that he was endeavouring to explain to you the difficulties they were up against in carrying out our armchair plans' (Royal Geographical Society CB 1921–1930, Great Barrier Reef Expedition, file 3).
47. Spender to Hinks, from Orpheus Island, 4 September 1928; Royal Geographical Society Great Barrier Reef CB 1921–1930, file 2.
48. Cara Mallett chronicled her three months on Funafuti in a book of over 300 pages, providing 'an unscientific account of a scientific expedition'. Following Victorian sensibilities, she dedicated her book 'To the Leader of the Expedition' (her husband) and authored it as Mrs. Edgeworth David (David 1899).
49. Physiography is a rather elusive term, subject to multiple definitions and usages since its appearance in the late eighteenth century (Stoddart, 1975). Steers himself compared the terms 'geomorphology' and 'physiography': 'geomorphology does not exclude a consideration of, e.g., the plant cover, but it does not of itself include it, although it is much concerned with its effects on weathering. Physiography seems to me to be the more comprehensive word, and in my own field work I have been constantly aware of the importance of tree and plant growth, of climate, and other factors in the development of land forms, so that the wider term appeals to me far more' (Steers 1960, 1–2). For the application of the 'Cambridge physiographic tradition' to the low islands of the Great Barrier Reef, see the detailed analysis of Woodroffe (2018).
50. Yonge to Steers, 4 April 1929; Royal Geographical Society CB9 1921–1930, Great Barrier Reef Expedition, Box 1.
51. Yonge Archives at Natural History Museum UK DF214/7 Expedition Progress Report November 14 1928.
52. Yonge to Brown, 14 September 1983; E75, correspondence files, Maurice Yonge Collection, Natural History Museum UK.
53. An abstracted version of Steers' paper on 'The Queensland coast and the Great Barrier reefs' (Steers, 1929) was read by the author at the Royal Geographical Society on 4 February 1929, and at that stage, Spender's map had not even begun to take shape. On 1 December 1929, Steers wrote to Hinks 'I have not yet seen his [i.e. Spender's] maps, but I gather they are good' (Royal Geographical Society CP9 1921–1930 Spender file); they were not revealed until the Royal Geographical Society meeting of 16 December 1929.

54. Hinks to Spender, 29 May 1929: ‘I confess that I did not anticipate that you would spend so long a time on Low Island making a map on so large a scale as 200 feet to the inch which may no doubt be very useful to ecologists but which is hardly in my mind a geographical scale. You will have to be prepared to defend’ (Royal Geographical Society CB 1921–1930, Great Barrier Reef Expedition, file 3).
55. The importance of personal field observations did on occasion bring Steers into conflict with Spender. He was clearly irritated by Spender’s discussion, on 7 December 1936, of the formation of reef platforms on the Great Barrier Reef: ‘I doubt if there is much significance in Mr. Spender’s remarks on Beanley Island, on which I do not think he has ever set foot . . . Much more detailed work is necessary to solve the problem, but I would ask him to visualize the whole problem of benches and platforms on the Queensland coast and reefs before he comes to a definite conclusion’ (Steers in Balfour et al. 1937, 145). The day after the discussion of his paper, Steers wrote privately to Hinks, to ask to see Spender’s written comments before returning his own, noting that ‘Spender does not advance the matters at all by merely putting forward his ideas which do not take in the cumulative facts. Spender weakened some of his arguments by talking of places he had not visited’ (Steers to Hinks, 8 December 1936; Royal Geographical Society CB10 1931).
56. There is evidence of correspondence between Muscatine and Yonge (C.M. Yonge correspondence files Natural History Museum 1972 E36) regarding Yonge’s work with the then late Goreau and papers relating to the translocation of photosynthetic product from zooxanthellae by the giant clam *Tridacna maxima* (Goreau et al. 1973).
57. Yonge to Muscatine, 11 July 1972; ‘I am glad you liked my appreciation of Tom – It came very much from the heart’. E36, correspondence files, Maurice Yonge Collection, Natural History Museum, UK.
58. As a diver and a chemist, Goreau collected radioactive specimens from the Bikini lagoon. It seems highly likely that he received lethal radiation exposure from this work and that this lies behind his early death from cancer at the age of 45.
59. Goreau initially trained in medicine and was appointed lecturer in physiology in what was then the University College of the West Indies in Kingston, Jamaica, in 1951. He continued to teach medical physiology until his appointment as Professor of Marine Science in 1967. The Coral Reef Project was formally started by Goreau in 1956, but the paper by Goreau and Goreau (1973) refers to field observations from 1955 and unpublished field notes from the north coast of Jamaica from 1952 onwards. This paper contains remarkable fish eye photographs of the deep reef front. Perhaps, Tom Goreau developed this interest and skill from his father, Fritz Goro, who was a photographer for *Life* magazine and *Scientific American*, specializing in macrophotography.
60. The PhD viva was the first time that Stoddart met Yonge in person. In the course of the viva, Yonge disputed that there were such things as solitary, rolling corals. Stoddart went back to his office, picked one up, returned to the viva and rolled it back across the table to Yonge (Stoddart, pers. comm. to Spencer, Rarotonga, Cook Islands, February 1983).
61. ‘I was in Belize in 1962 when I had a postcard from Alfred [Steers] in a hotel on the Isle of Wight. “My dear David, would you like a job in Cambridge? Yours ever, Alfred”. No nonsense about curriculum vitae, referees’ reports, appointments committees: simply straightforward patronage. In the Cambridge context of the time, it worked. Unless one did something quite dreadful, it meant a job for life. My response was instantaneous “Dear Professor Steers . . .” (i.e., what a good idea)’ (Stoddart 2001, 246).
62. Steers and Yonge to the Executive Secretary, Royal Society, 27 December 1967; Committee minute books of the Royal Society, CMB/179b/8.
63. Sir Fred Schonell, Vice Chancellor, University of Queensland to Steers, 10 May 1968; Committee minute books of the Royal Society, CMB/179b/9.
64. Minutes of the Royal Society’s Southern Zone Research Committee: 6th Meeting, 13 August 1968 (Committee minute books of the Royal Society, CMB/174/34); 7th Meeting, 2 July 1969 (Committee minute books of the Royal Society, CMB/174/37); 8th Meeting, 16 June 1970 (Committee minute books of the Royal Society, CMB/174/41); 21 February 1972 (Committee minute books of the Royal Society, CMB/179/1); 18 September 1973 (Committee minute books of the Royal Society, CMB/179/4). For an Australian perspective, see Hill (1985).
65. Letter from former Director of the Australian Museum, Frank Talbot, to the Australian Coral Reef Society (S Hamylton (President) and P Hutchings), 5 November 2019.
66. Spender to Hinks, from Low Isles, 20 July 1929; Royal Geographical Society Great Barrier Reef CB 1921–1930, file 2.

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PHYLOGEOGRAPHY OF SOUTHERN HEMISPHERE BLUE MUSSELS OF THE GENUS *MYTILUS*: EVOLUTION, BIOSECURITY, AQUACULTURE AND FOOD LABELLING

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Abstract Smooth-shelled blue mussels of the genus *Mytilus* have long been a major focus of research because such mussels have an interesting global (antitropical or bipolar) distribution, have a complex phylogeographic history, are ecosystem engineers, are economically important as an aquaculture product, are very successful as bioinvaders, hybridise readily both naturally and after accidental introduction, and have a complex and still incompletely resolved taxonomy. Historically, most research has been focussed on Northern hemisphere mussels, and investigation has spanned a range of different methodological approaches that have set the foundation for our current understanding of the global situation. However, research into native blue mussels in the Southern hemisphere has tended to lag behind that in the Northern hemisphere. The result has been that native Southern hemisphere mussels have often been viewed only in the perspective of their Northern hemisphere congeners. Recently, however, the application of new molecular markers – single nucleotide polymorphisms, SNPs – has substantially improved our understanding of the taxonomy of Southern hemisphere blue mussels, their biogeography and indirectly their evolutionary histories. Based largely on new SNP surveys of native and non-native blue mussels from all major Southern hemisphere regions, we highlight the need for recognition of distinct species that are consistent with a large body of evidence, both SNP-based and other, and can be understood in the context of Southern hemisphere oceanography. We also highlight with the new SNPs-based data the ongoing difficulty of agreeing on what constitutes a distinct species by emphasising different interpretations of the data, and discussing how the use of species delimitation models may remove some of the qualitative assessment that is so often applied to the problem. The recognition of new species has implications for management, including the identification of bioinvasive mussels, the conservation of native genetic diversity, aquaculture production statistics, food labelling and traceability.

Keywords: Blue Mussels; *Mytilus*; Southern Hemisphere; Phylogeography; Taxonomy and Systematics; Hybridisation and Introgression; Bioinvasions; Aquaculture; Food Labelling and Traceability.

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The global distribution of smooth-shelled mussels of the genus *Mytilus*

The first scientific description of mussels of the genus *Mytilus* dates to 1758 and is attributable to the great Swedish biologist, Carl Linnaeus (Linnaeus 1758). He described *M. edulis* from the European coast of the North Atlantic Ocean and the Baltic Sea (the exact location does not seem to have been recorded), and subsequently, the great French naturalist Jean-Baptiste Lamarck described *M. galloprovincialis* from the Mediterranean Sea (Lamarck 1819). During an unprecedented period of exploration and collecting, from approximately 1750 to 1850, a substantial number of biological samples were collected from many regions of the world, both Northern hemisphere and Southern hemisphere (the genus is found naturally on all continents except Antarctica). Many of these blue mussel samples were returned to European museums, where they were catalogued and often given new names (reviewed by Lamy 1936, Soot-Ryen 1955). What soon became apparent is that the genus, like many other marine taxa, has an antitropical distribution, sometimes also referred to as a bipolar distribution (Ekman 1953, Briggs 1974, Santelices 1980, Lindberg 1991, Hilbish et al. 2000). Attempting to explain this distribution and the evolutionary relationships between Northern and Southern hemisphere mussels has been a challenge for biologists, and has been aided and hindered by the tangle of taxonomy that developed from the earliest days.

For blue mussels, which are very variable in their shell phenotypes (Figure 1), it was often the case that even only limited morphometric difference was viewed as being enough to erect a new species or subspecies or variety. For example, the World Registry of Marine Species (WoRMS Editorial Board 2020) lists 21 synonymised names for *M. edulis*, 25 synonymised names for *M. galloprovincialis*, and eight synonymised names for *M. trossulus* (Gould, 1850). As subsequent large spatial scale studies of shell trait and shell shape variation have demonstrated (e.g., McDonald et al. 1991, Gardner & Thompson 2009), many of the shell characters (traits and shape) do have genuine taxonomic resolving power, which means that disentangling the complexities of the old nomenclature against today's thinking has, at times, been fraught (e.g., as discussed by Larraín et al. 2018).

The decade of the mid-1980s to the mid-1990s saw an incredible explosion of new knowledge that changed the way researchers thought about the taxonomy and biogeography of smooth-shelled blue mussels of what was and still is called the *Mytilus edulis* species complex, and laid the foundation for much of today's interpretation of the taxonomy and systematics of the genus (Koehn et al. 1984, McDonald & Koehn 1988, Varvio et al. 1988, McDonald et al. 1991 and references therein). While most of this body of work was carried out using allozymes (protein variation), a lot of it was supported by increasingly sophisticated analyses of shells, including trait and shape variation. In addition, this research was being conducted at a time when newly developed molecular methods such as the analyses of mtDNA (mitochondrial DNA) RFLPs (restriction fragment length polymorphisms) were being developed and applied, and at a time when much attention in biological sciences was focussed on the challenge of defining a species (reviewed by Cracraft 1983, 1989, Mishler & Brandon 1987, Templeton 1989, Avise & Ball 1990, Wallace & Willis 1994, Mallet 1995, Zink & McKitrick 1995).

The application of new molecular markers such as single nucleotide polymorphisms (SNPs) and the development of new analytical approaches have significantly advanced our understanding in many areas of biology, forensics, medicine and agricultural production. While the taxonomy, evolutionary origins and genetic diversity of blue mussels in the Northern hemisphere are now reasonably well understood, this is not the case for the Southern hemisphere mussels. However, recent analysis of native blue mussels from the Southern hemisphere using SNPs (usually involving a panel of reference Northern hemisphere mussels) has profoundly improved our understanding of the global situation. Because SNPs are high-definition markers (i.e., they are easy to interpret and generally provide higher species-level and population-level differentiation than other marker types), they are co-dominantly inherited and they can be found throughout the genome in very high numbers; they provide a new level of detail about regional genetic differentiation, hybridisation and introgression,

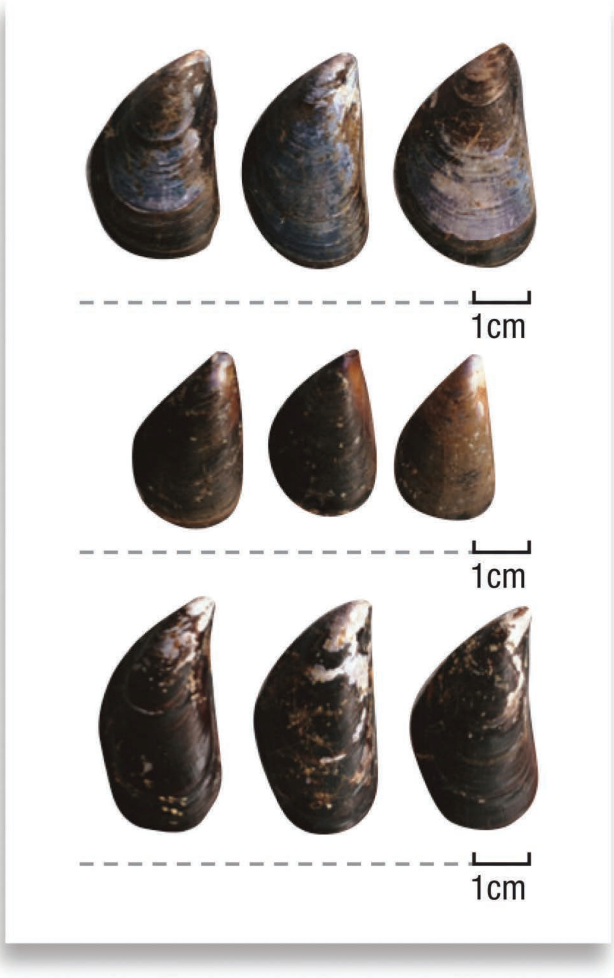

Figure 1 Examples of *Mytilus edulis* Linneaus, 1758 (top panel) collected from Magdalen Island, Quebec, Canada, of *M. galloprovincialis* Lamarck, 1819 (middle panel) collected from Posjet Bay, USSR, and *M. trossulus* Gould, 1850 (bottom panel) collected from Magadan, USSR. Shells deposited in the British Museum of Natural History (accession number 2377) from the study of McDonald et al. (1991). Scale bars at bottom of each panel (photo credit – Jonathan Gardner).

genetic integrity of independent lineages, evolutionary origin, and ultimately the taxonomy and systematics of Southern hemisphere blue mussels. This new knowledge has a direct bearing on other aspects of the study of blue mussels, including biosecurity, aquaculture production and food labelling. This review, the first of its kind with a focus on Southern hemisphere blue mussels, builds on previous reviews (e.g., Koehn 1991, Gardner 1992, Gosling 1992a,b, Seed 1992). The work that we describe, from the earliest days to the present, is truly a global effort, with many different research teams from across the world having contributed. Progress has often been limited and incremental – one small step at a time – but is also occasionally characterised by a profound leap that has changed the world view. The story also highlights the natural tension that exists within the science community about what constitutes a species, especially in light of extensive hybridisation and introgression. There are also questions of taxonomic priority and, dare we say it, of national identity being linked to a native blue mussel. The ongoing process of blue mussel speciation in the sea is rarely clear-cut

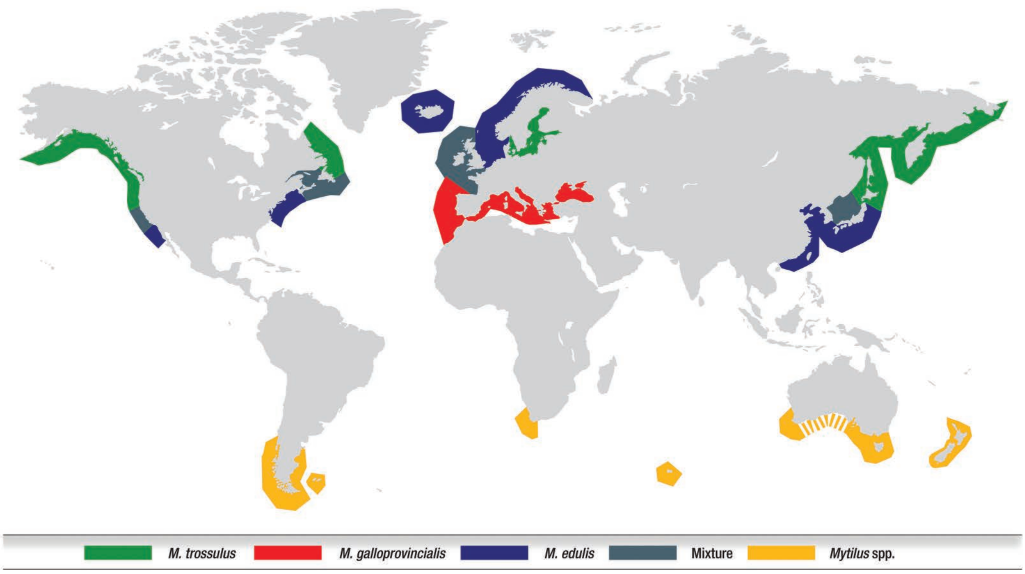

Figure 2 Map of broad regional differences in distributions of smooth-shelled mussels of the genus *Mytilus*. The three Northern hemisphere species (*M. edulis*, *M. galloprovincialis*, *M. trossulus*) and areas of sympatry between them are shown. All Southern hemisphere blue mussels (native and introduced) are shown in yellow – specific details for each region are discussed below.

and has been substantially muddied by anthropogenic activities that have deliberately and accidentally moved blue mussels around the world, in particular during the last 300 years. This chapter focusses on the native mussels from South America and Australasia (blue mussels are not native to southern Africa), including remote offshore islands in the Southern Ocean, but in the context of Northern hemisphere species (Figure 2). We review the fossil and midden records to establish where blue mussels are likely to be native, review the extensive body of literature, examine Southern hemisphere mussel phylogeography based on markers before SNPs, and then describe the recent work using SNPs and how this has confirmed earlier interpretations or added a new view of Southern hemisphere mussel phylogeography. In an evolutionary context, we question how many different native species may be said to exist in the Southern hemisphere, we examine the role of hybridisation in speciation, we discuss the role of new approaches to recognising species – the species delimitation (SD) models, and we seek to determine whether physical oceanography may contribute to or even explain species distributions in the Southern hemisphere. In a broader context, because blue mussels are ecologically and economically important throughout the world, we then review biosecurity threats, old and new, natural and manmade, before finally taking a look at aquaculture production of blue mussels and the importance of correct taxonomy to food labelling, marketing, traceability and production statistics. We conclude with a brief section that focusses on our view of some important future research directions.

The evolutionary origin of modern smooth-shelled blue mussels

The earliest attempts to understand the origin of modern blue mussels focussed on fossil evidence and interpretations of the timing of the opening of major sea passages or major basins such as the Bering Strait, the Mediterranean Sea and the Baltic Sea. From this work, hypotheses were ultimately developed to allow for molecular testing (DNA sequence analyses) of the natural range expansion of blue mussels within the Northern hemisphere and from the Northern to the Southern hemisphere.

Evidence suggests that speciation among the three closely related Northern hemisphere species of the *Mytilus edulis* species complex – that is, *M. edulis*, *M. galloprovincialis* and *M. trossulus* – was most likely allopatric (Figure 3). The molecular evidence shows that *M. trossulus* is the oldest of the three Northern hemisphere smooth-shelled species (Hilbish et al. 2000, Gérard et al. 2008). *Mytilus trossulus* (or its immediate ancestor – some form of proto-*trossulus*) was restricted in its range to the North Pacific region (Lindberg 1991, Vermeij 1991). The first major range expansion, which led to the first allopatric speciation event giving rise to North Atlantic *M. edulis*, occurred ~3.5 M ybp (years before present) with the opening of the Bering Strait between the North Pacific Ocean and the North Atlantic Ocean (Lindberg 1991, Vermeij 1991, Dunton 1992, Cunningham & Collins 1994). This was a period of major biotic interchange, with most movement being west to east, but some also occurring east to west (Vermeij 1991). According to Vermeij (1991), *Mytilus* fossils first appear in the North Atlantic in the early Pliocene. This earliest form of *M. edulis* spread throughout the North Atlantic region during periods of sea level change and colonised the Mediterranean Sea by the Pleistocene (Vermeij 1991). Barsotti & Meluzzi (1968) suggest that the mussels of the North Atlantic were separated from and then reconnected to the mussels of the Mediterranean Sea something like 17 times during periods of major sea level change over a period of ~1.7 M years. More recently, Roux et al. (2014) date the time of divergence of *M. galloprovincialis* from *M. edulis* at 2.5 M ybp. During this period, sea level dropped by as much as 100 m (Lindberg 1991), and this phenomenon is known to have given rise to separation among groups of mussels or between major geographic regions such as the North Atlantic Ocean and the Mediterranean Sea. This separation among mussel regional groups gave rise to genetic differences among members of the different groups. Ultimately, speciation between the northern North Atlantic *M. edulis*, the southern North Atlantic lineage of *M. galloprovincialis* and the Mediterranean Sea lineage of *M. galloprovincialis* was therefore vicariant (Barsotti & Meluzzi 1968, Riginos & Cunningham 2005).

A second natural range expansion from the North Pacific Ocean to the North Atlantic Ocean, again via the Bering Strait, has occurred more recently, during the Pleistocene or the Holocene (Riginos & Cunningham 2005). This invasion gave rise to *M. trossulus* (i.e., this was not a speciation event) on the North American Atlantic coast with a centre of distribution in the Canadian Maritime provinces (Koehn et al. 1984, McDonald & Koehn 1988, McDonald et al. 1991) and in the Baltic Sea (Varvio et al. 1988, Väinölä & Hvilsom 1991). These two disjunct distributions of North Atlantic *M. trossulus* appear to be separate (genetically differentiated) lineages of the original North Pacific form of *M. trossulus* (Riginos & Cunningham 2005) and display different environmental tolerances of, for example, salinity variation (e.g., Kautsky et al. 1990, Gardner & Thompson 2001, Qiu et al. 2002, Braby & Somero 2006).

The molecular and the fossil evidence points very strongly to a Northern hemisphere origin of modern smooth-shelled blue mussels. The North Pacific Ocean *M. trossulus* form is the oldest form (the ancestral lineage), and the two North Atlantic species, *M. edulis* and *M. galloprovincialis*, are much more recent forms. Importantly, there are now two clearly recognised lineages of Northern hemisphere *M. galloprovincialis*, one which is from the Mediterranean Sea and the other from the North Atlantic Ocean, and which shows greater affinity to North Atlantic *M. edulis* than the former (e.g., Sanjuan et al. 1997, Daguin & Borsa 2000, Hilbish et al. 2000, Larraín et al. 2018, Zbawicka et al. 2019, 2021, Popovic et al. 2020). An understanding of the distributions and ages of the Northern hemisphere species is important for our understanding of the origin of modern-day Southern hemisphere *Mytilus*. It is important to note that there is increasing evidence of *Mytilus* taxa (e.g., *M. trigonus*) from southern South America on both the Pacific Ocean and Atlantic Ocean coasts, in particular around Patagonia, which dates to the Miocene epoch and, as such, may predate the origin of modern *M. trossulus* (del Río et al. 2001). This fossil form needs further investigation, given that it may be the ancestral form of modern-day smooth-shelled blue mussels.

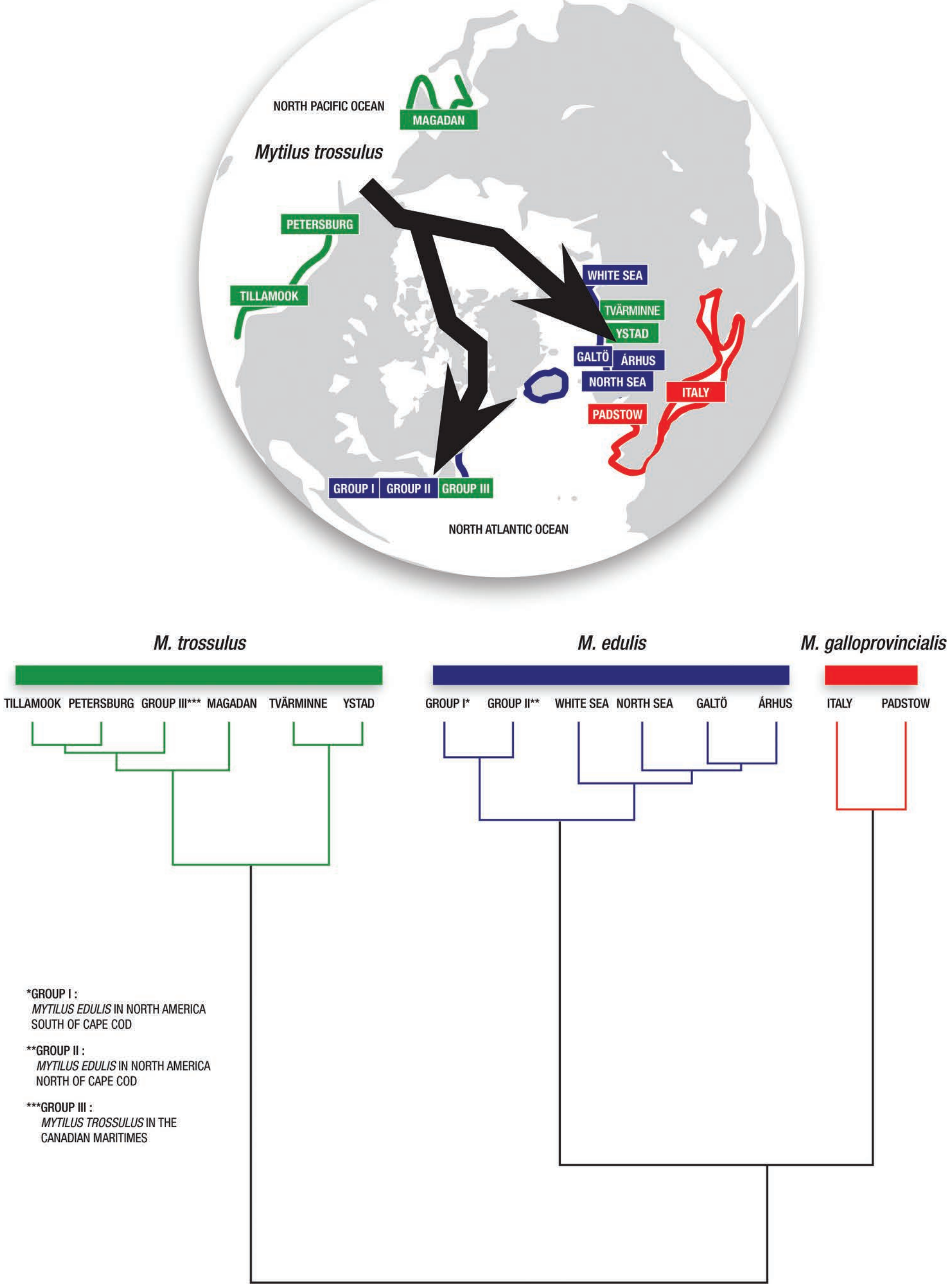

Figure 3 Evolutionary relationships among *Mytilus* species as shown by a UPGMA tree based on Cavalli-Sforza chord distances from five allozyme loci (*Ap*, *Gpi*, *Lap*, *Mpi*, and *Pgm*). Populations are as follows: *M. trossulus* – (1) Tillamook, (2) Petersburg, (3) Magadan, (4) Group III (*Mytilus trossulus* in the Canadian Maritimes), (5) Tvärminne, (6) Ystad (note separation of North Atlantic Ocean from Baltic Sea populations; *M. edulis* – (7) Group I (*Mytilus edulis* in North America south of Cape Cod), (8) White Sea, (9) North Sea, (10) Galtö, (11) Group II (*M. edulis* in North America north of Cape Cod), (12) Århus; *M. galloprovincialis* – (13) Italy, and (14) Padstow. Arrows on the globe represent the recent invasion(s) of Pacific *M. trossulus* into the North Atlantic Ocean. Modified from Riginos & Cunningham (2005).

Establishing the foundation – early genetics-based studies of biogeography and taxonomy

Early work based on allozyme and shell trait and/or shape variation identified three distinct groupings of smooth-shelled blue mussels in the Northern hemisphere: *M. edulis* from the North Atlantic, including the coasts of Europe and North America, *M. galloprovincialis* from the Mediterranean Sea and extending north to SW England and southern Ireland, and south at least as far as southern Morocco on the Atlantic Ocean, and *M. trossulus* from the Baltic Sea and also from parts of the Atlantic seaboard of North America (Koehn et al. 1984, McDonald & Koehn 1988, Varvio et al. 1988, McDonald et al. 1991). During this period, several authors noted that despite extensive hybridisation and varying levels of introgression between pairs of species, each maintained its genetic integrity across large parts of the world and as such they all warranted recognition as distinct species (e.g., McDonald & Koehn 1988, Varvio et al. 1988).

By the early 1990s, there were already five separate reviews of the taxonomy of one or more of the *Mytilus edulis* species complex in the Northern hemisphere (Gosling 1984, 1992a, Koehn 1991, Gardner 1992, Seed 1992). Subsequently, as summarised in Table 1, the application of more modern approaches such as mtDNA and nuclear DNA (nDNA) RFLP analysis (Edwards & Skibinski 1987, Gardner & Skibinski 1991, Inoue et al. 1995, Toro 1998a, Santaclara et al. 2006, Westfall et al. 2010), DNA sequencing (Geller et al. 1993, Hilbish et al. 2000, Gérard et al. 2008), sperm protein analysis (Riginos & McDonald 2003) and microsatellites (Presa et al. 2002, Varela et al. 2007) all confirmed the interpretation of the earlier allozyme-based surveys that three distinct species (*M. trossulus*, *M. edulis* and *M. galloprovincialis*) exist in the Northern hemisphere.

In comparison to the Northern hemisphere, much less work of a similar nature was conducted in the Southern hemisphere, despite the occurrence of blue mussels of the *Mytilus edulis* species complex existing in all Southern continents except Antarctica. The interpretation of the *Mytilus edulis* complex problem in the Southern hemisphere was very much influenced by the very large body of research being conducted in the Northern hemisphere at the time and the major taxonomic advances being made there.

Table 1 Summary table of molecular markers that have been used in the identification of *Mytilus edulis* complex species

DNA Markers	Species	References
Me15/16 (n)	Me, Mg, Mt	Inoue et al. (1995)
Me15/16 RFLP assay (n)	Mc[a], Me, Mg, Mt	Santaclara et al. (2006)
COIXba RFLP assay (mt)	Mc,Mg	Fernández-Tajes et al. (2011)
Myti RFLP assay (n)	Mc, Me, Mg, Mt	Fernández-Tajes et al. (2011)
16S RFLP assay (mt)	MgS, MgN, MgN/Me, Mt	Westfall et al. (2010)
M7 (n)	Me, Mg, Mt	Kijewski et al. (2009)
Mac-1 (n)	Me, Mg	Daguin et al. (2001)
EFbis (n)	Me, Mg	Bierne et al. (2003)
EFbis RFLP assay (n)	Me, Mg, Mt	Kijewski et al. (2009)
16S (n)	Me, Mg, Me/Mg	Bendezu et al. (2005)
ITS RFLP assay (n)	Me/Mg, Mt	Heath et al. (1995)
PLIIa RFLP assay (n)	Me, Mg, Mt	Heath et al. (1995)

DNA type – n, nuclear; mt, mitochondrial; Mc, *Mytilus chilensis*; Me, *M. edulis*; Mg, *M. galloprovincialis*; Mt=*M. trossulus*; MgS, Southern hemisphere *M. galloprovincialis*; MgN, Northern hemisphere *M. galloprovincialis*; MgN/Me, “North Atlantic” haplotype as defined by Hilbish et al. (2000).

[a] This is the same as the MgS pattern of Westfall et al. (2010).

Levinton & Koehn (1976) compared allele frequencies at three allozyme loci (LAP, GPI, AP) in mussels (which, at the time, they called *M. edulis*) from Melbourne, Australia, with mussels from five locations in the Northern hemisphere. They noted several regional differences in the occurrence of alleles at highest frequency that today reflect what we know about the occurrence of *M. edulis*, *M. galloprovincialis* and *M. trossulus* in the Northern hemisphere. Levinton & Koehn (1976) concluded by stating that the three locus-specific alleles at highest frequency in the Australian mussels were the same as those at highest frequency in their sample from south of Cape Cod (*M. edulis* from the Atlantic coast of North America), all of which showed considerable difference to samples from the Gulf of Maine (*M. trossulus* from the Atlantic coast of North America).

The first study of genetic variation focussing specifically on Southern hemisphere blue mussels was that carried out by Grant & Cherry (1985). This work was of interest and importance because the authors demonstrated that blue mussels found in South Africa are not native, but are introduced Northern hemisphere *M. galloprovincialis*, as based on both shell morphometric trait analysis and allozyme electrophoresis. They also noted the absence of *Mytilus* sp. from two large shell deposits, both of which predate European arrival. Subsequently, Blot et al. (1988) examined allozyme variation in native blue mussels from the Kerguelen Islands (southern Indian Ocean, 70°E, 49°S) that, at the time, were called *Mytilus desolationis* Lamy, 1936. They compared *M. desolationis* with reference samples of Northern hemisphere *M. edulis* and *M. galloprovincialis*. Correspondence analysis (CA) (Figure 4) revealed that the two Kerguelen populations were very clearly differentiated from the Northern hemisphere *M. edulis* and *M. galloprovincialis*, but other analyses based on genetic distance revealed limited differentiation among all three mussel types, such that Blot et al. (1988) concluded that *M. desolationis* does not exhibit enough differentiation from *M. edulis* to warrant the rank of species. Blot et al. (1988) noted that Thiriot-Quiévreux (1984) had previously demonstrated the existence of karyotypic differences among *M. desolationis*, *M. edulis* and

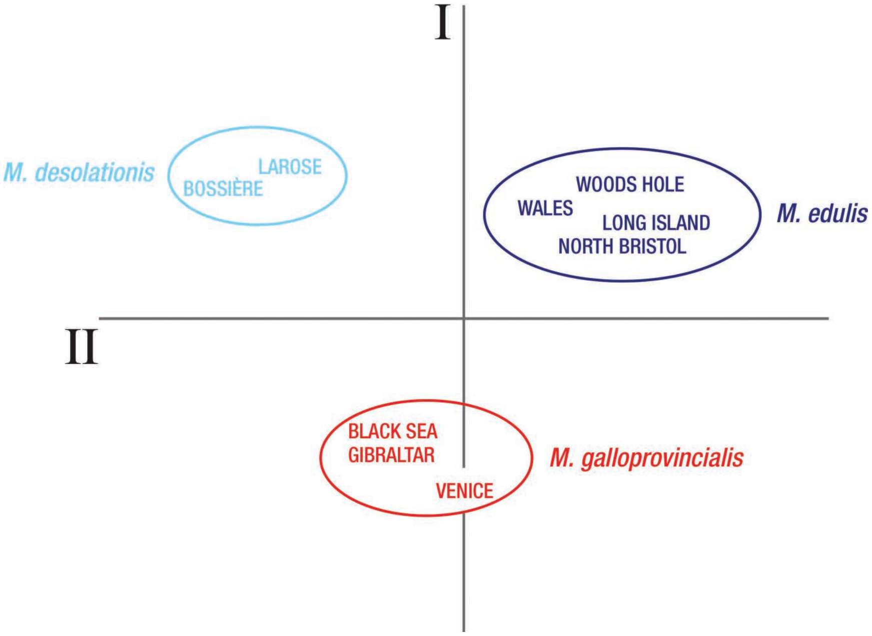

Figure 4 Correspondence analysis plot of allozyme data for mussels from the Kerguelen Islands (*Mytilus desolationis* – Bossière, Larosse), the Mediterranean Sea (*M. galloprovincialis* – Gibraltar, Venice, Black Sea) and the North Atlantic Ocean (*M. edulis* – Long Island, Woods Hole, North Bristol, Wales). Modified from Blot et al. (1988).

M. galloprovincialis (i.e., alongside their own allozyme data, there were additional karyotypic data pointing to what might be interpreted as subspecies differences). Blot et al. (1988) concluded that *M. desolationis* is best considered as a semi-species (following Mayr 1970) of the super-species *M. edulis*. Significantly, the potential limitations of this conclusion based on the best methodology of the day are recognised by the authors, who state that this semi-species status should hold "… until species-specific characters are found …" (Blot et al. 1988, p. 246).

A new global perspective – the 1990s to the early 2000s

Taking a more global view of the *Mytilus* taxonomic problem, which was at least starting to be resolved in the Northern hemisphere by now, McDonald et al. (1991) identified two distinct groups of Southern hemisphere mussels – a South America group including mussels from Chile, Argentina, the Falkland Islands and the Kerguelen Islands, and an Australasian group including mussels from Australia and New Zealand (Figure 5). The former group was most similar to Northern hemisphere *M. edulis*, whereas the latter group was most similar to Northern hemisphere *M. galloprovincialis*. The allozyme-based results were confirmed by analyses of shell trait variation, although not to the same extent of differentiation because the South American group was intermediate between Northern hemisphere *M. edulis* and *M. trossulus*.

Subsequent work based on allozymes and then on molecular markers tended to confirm the earlier interpretation of three species in the Northern hemisphere and also the results of McDonald et al. (1991) for the Southern hemisphere. Sanjuan et al. (1997) reviewed published allozyme data for the mussel *Mytilus galloprovincialis*. At a global scale, their analyses revealed three groups, including (1) Mediterranean, Asian and North American Pacific populations, (2) a group of European North Atlantic populations and (3) a group of Australasian samples that the authors said did not constitute a well-defined cluster. Multi-dimensional scaling (MDS) analysis showed that the two Australian samples were, in fact, quite distinct from the one New Zealand sample (Figure 6). Subsequently, Daguin & Borsa (2000) analysed variation at two nuclear DNA markers, the polyphenolic adhesive protein gene *Glu-5′* and the first intron of the actin gene *mac-1*, to examine the three recognised groups (based on allozyme variation – McDonald et al. 1991, Sanjuan et al. 1997) of *M. galloprovincialis* in the world at the time – a NE Atlantic group, a Mediterranean group, and an Australasian group (invasive *M. galloprovincialis* had already been reported in both of the first two named groups by this time and also from South Africa). It was hoped that the use of molecular markers would provide a new, more in-depth view of *M. galloprovincialis* than that developed only three years previously by the allozyme variation review of Sanjuan et al. (1997). While the *Glu-5′* marker was fixed, or nearly so, for the diagnostic *G* (*M. galloprovincialis*) marker, the *mac-1* marker confirmed the existence of the three already recognised groups, and also identified the likelihood of introduction of Northern hemisphere *M. galloprovincialis* to Chile. Significantly, the analysis of allele variation at the *mac-1* locus highlighted the distinctness of the Australasian *M. galloprovincialis*-like mussels relative to the two Northern hemisphere groups of *M. galloprovincialis* (Figure 7). This led Daguin & Borsa (2000) to suggest that Australasian mussels (i.e., those from both Australia and New Zealand) are derived from what they called a proto-*M. galloprovincialis* population that was already introgressed by *M. edulis*-like genes. They argued that this Australasian mussel should be considered as a subspecies of *M. galloprovincialis*; that is, it is native and is not introduced from the Northern hemisphere. Clustering analyses revealed clear separation of the Southern from the Northern hemisphere mussels, but statistics of differentiation (e.g., F_{ST} or Φ_{ST} or G_{ST}) produced low values (often <0.03) that did not tend to support the idea of different species. The *mac-1* locus did not provide any evidence of substantive differentiation between the Australian and the New Zealand samples, and therefore tended to confirm that the Australasian mussels all fall within one group.

While interpreting the results from these studies, it is important to appreciate that individual sample sizes were often not very large, that a very small spatial extent of the Southern hemisphere

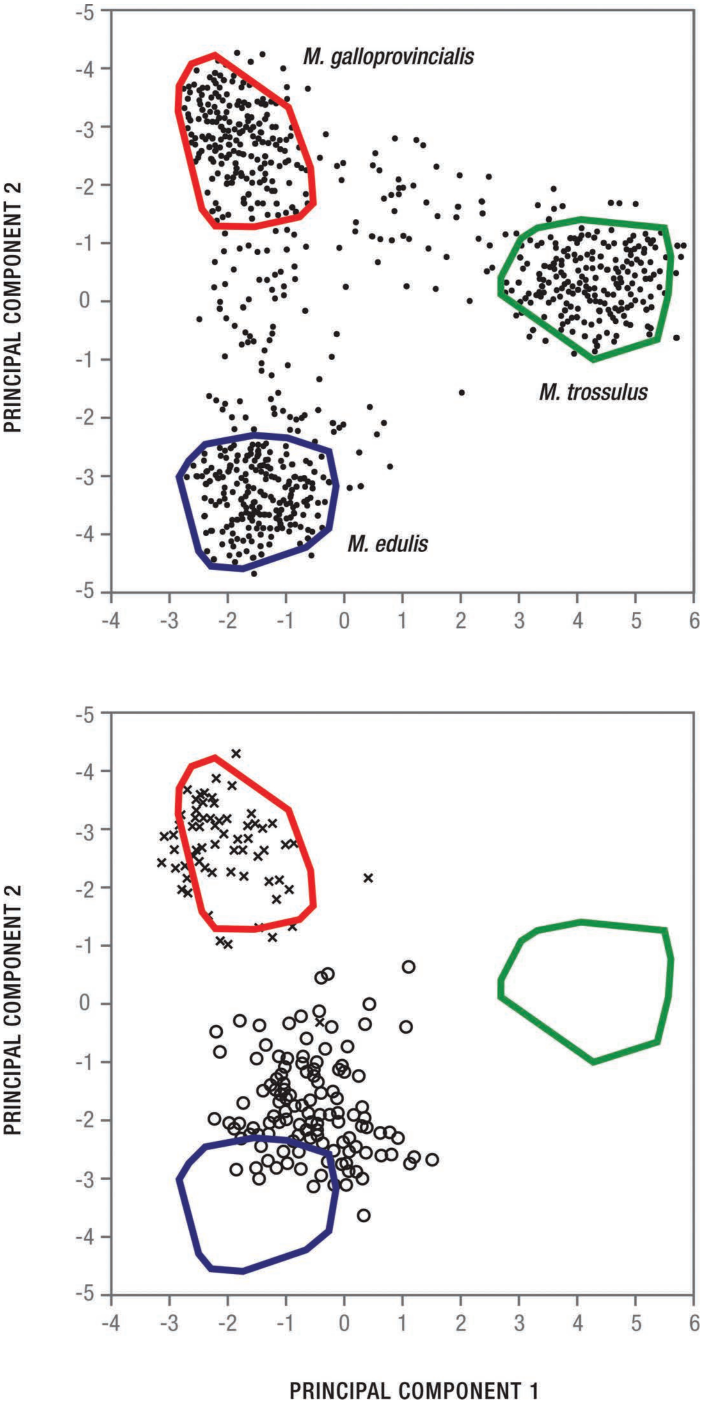

Figure 5 Principal components analysis of allozyme data for mussels from Northern and Southern hemispheres. Top panel showing only individuals from the Northern hemisphere (that is, reference Northern hemisphere samples). Bottom panel same as top panel except only individuals from the Southern hemisphere are shown with polygons for reference Northern hemisphere taxa. (o) Mussels from Chile, Argentina, the Falkland Islands and the Kerguelen Islands; (x) mussels from Australia and New Zealand. Modified from McDonald et al. (1991).

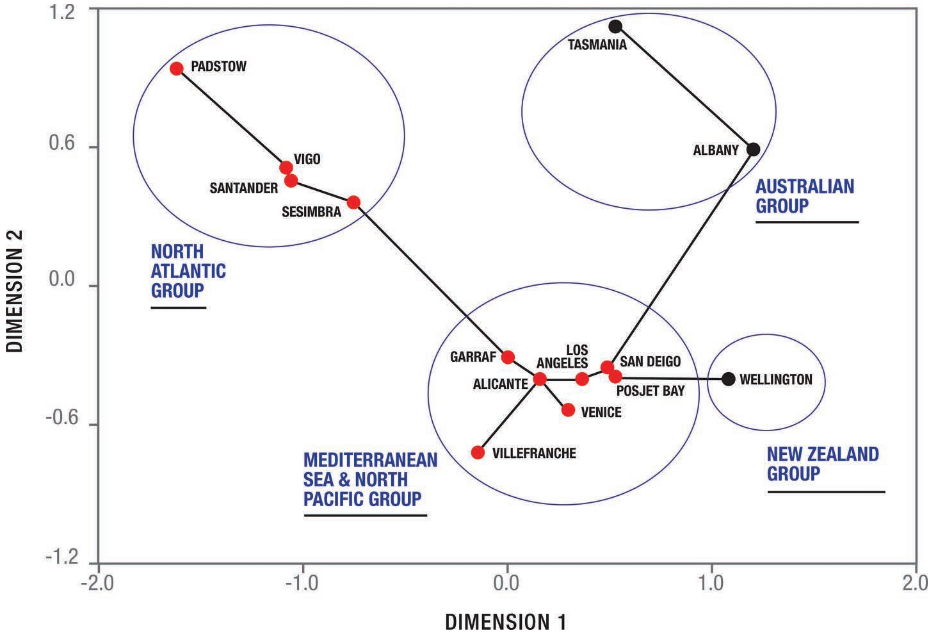

Figure 6 Linear multi-dimensional scaling (MDS) plot of genetic distance among *Mytilus galloprovincialis* populations, with minimum spanning tree superimposed on the MDS plot. Populations: **North Atlantic group** – Padstow, SW England; Santander, Spain; Vigo, Spain; Sesimbra, Portugal: **Mediterranean Sea and North Pacific group** – Alicante, Spain; Garraf, Spain; Villefranche, France; Venice, Italy; Los Angeles, USA; San Diego, USA; Posjet Bay, Russia: **Australian group** – Albany, Western Australia; Tasmania, Australia: **New Zealand** – Wellington, New Zealand. Note that samples from Los Angeles, San Diego and Posjet Bay are now viewed as being introduced (non-native). Modified from Sanjuan et al. (1997).

had been sampled and that today we recognise that Northern hemisphere *M. galloprovincialis* has invaded many areas in the Northern and Southern hemispheres. Nonetheless, what was rapidly becoming apparent was that native Southern hemisphere mussels were different across a range of different marker types to their Northern hemisphere counterparts and that two distinct groups of Southern hemisphere mussels could be identified (South America and Australasia). All native Southern hemisphere mussels were judged to be derived from the Northern hemisphere and to be (1) members of *M. edulis* or *M. galloprovincialis* (note that there was no evidence of *M. trossulus* from the Southern hemisphere), or (2) *M. edulis*-like or *M. galloprovincialis*-like, or (3) subspecies of these two species – e.g., *M. edulis chilensis* Hupé, 1854 (Pacific coast of South America) or *M. edulis platensis* d'Orbigny, 1842 (Atlantic coast of South America) or *M. galloprovincialis* subspecies unspecified (Australasia) or *M. edulis planulatus* Lamarck, 1819 (Australia). Note that WoRMS (http://www.marinespecies.org/) does not accept *M. edulis chilensis*, *M. edulis platensis* or *M. edulis planulatus*.

The evolutionary origin of Southern hemisphere blue mussels

Understanding the origin of Southern hemisphere blue mussels, and thereby perhaps explaining the antitropical distribution of the genus, has been a challenge. A full explanation of the origin of Southern hemisphere blue mussels should shed light on the timing or timings of the origin or origins as well as on the route or routes taken to reach the present-day distributions. Ideally, the methodological approach taken will test hypotheses that permit clear differentiation among putative

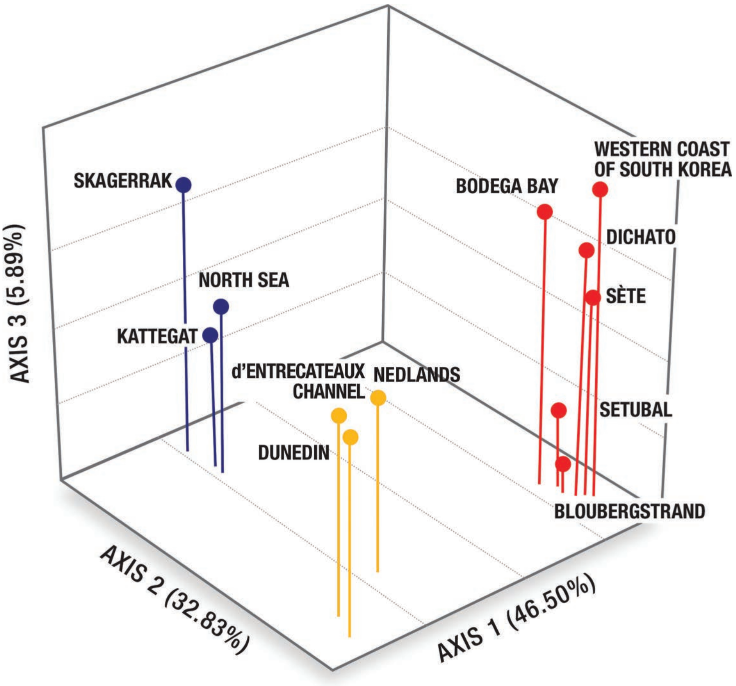

Figure 7 Three-dimensional plot of *mac-1* allelic frequency variation for Northern and Southern hemisphere mussels. Reference *Mytilus edulis* (in blue – Skagerrak, Kattegat, North Sea); Australasian mussels (in yellow – Nedlands (Western Australia), d'Entrecasteaux Channel (Tasmania), Dunedin (New Zealand); *M. galloprovincialis*, both native and introduced (in red – Bodega Bay (California, USA), Dichato (central Chile), Setubal (Portugal), Sète (France), Bloubergstrand (South Africa), western coast of South Korea. Modified from Daguin & Borsa (2000).

timings of colonisation and putative routes of range expansion. We would expect that molecular results are supported by the fossil and midden information available from each major geographic location. Beyond this, we would also like to see an approach that is able to identify recent anthropogenic introductions and differentiate these from natural range expansion events.

Perhaps not surprisingly, there are relatively few predictions about the colonisation of the Southern hemisphere by blue mussels based on non-molecular analyses. Building on earlier work that looked at bipolarity (e.g., Powell 1965), in his evaluation of the marine biotic exchange between the Northern and Southern hemispheres, Lindberg (1991) suggested that Australasian *Mytilus edulis planulatus* may have diverged in the Pliocene (2.58–5.33 M ybp) and might have been dispersed from the eastern North Pacific to Australia and New Zealand by circumpolar currents (the West Wind Drift) as has been hypothesised for several different groups, including the nudibranch *Acanthodoris*, the gastropod *Fusitriton* and the crab *Cancer*. One possible mechanism for this range expansion across the tropics, which is normally a barrier to movement for cooler water species such as *Mytilus*, is increased upwelling along the east Pacific margin and the establishment of a series of stepping stone like cold water refugia (Lindberg 1991). However, Lindberg (1991) notes that whether the ~100 m drop in sea level at the time (~1 M ybp) increased or decreased the number of upwelling sites along the eastern Pacific coast remains unknown, and this may influence the spreading success of certain genera.

This earlier body of work, based on fossil or midden remains, provided a set of testable hypotheses for the molecular researchers who were to follow. The fossil record also provides a reasonably robust framework against which to build molecular hypotheses and to make further predictions. This approach was not, however, implemented until some years later when molecular advances permitted the testing of specific hypotheses, often of a nuanced nature.

In some of the earliest DNA sequencing work of its type, Kenchington et al. (1995) examined 18S sequence variation among representatives of the Northern hemisphere *Mytilus edulis* complex, with one representative from Australia that was recognised as *M. e. planulatus* (collected from Cloudy Bay Lagoon, Tasmania). As we recognise today, the 18S gene is a slowly evolving region that is better suited to exploration of more ancient speciation events than to recent (e.g., less than 3–4 M ybp) speciation events and as such may not be particularly informative for the *Mytilus edulis* species complex. However, Kenchington et al. (1995) concluded that their phylogeny strongly suggested an early separation of Northern hemisphere *M. galloprovincialis* from the other smooth-shelled *Mytilus* spp., including *M. edulis*, *M. trossulus* and Australasian *M. galloprovincialis*. Subsequently, Sanjuan et al. (1997), in their review of published allozyme variation for *M. galloprovincialis* at a global scale, suggested that their data indicated the existence of two main events: first, a natural and ancient transequatorial migration through the Pacific Ocean, and second, a subsequent trans-Arctic migration. They note that these hypotheses assumed a Pacific origin of *M. galloprovincialis*. These two studies were soon superseded by more sophisticated analyses using more informative markers, which illustrates both the rapid pace of marker and data analysis development, as well as how our understanding of "the *Mytilus* problem" could change so rapidly and dramatically.

In the first paper to explicitly test the origin of Southern hemisphere blue mussels, and arguably the one that advanced our understanding the most, Hilbish et al. (2000) used mitochondrial DNA (mtDNA – the 16S rRNA mitochondrial gene) in a phylogenetics framework to test four separate hypotheses (Figure 8). They were able to reject hypotheses indicating that Southern hemisphere blue mussels migrated via the northern equatorial Pacific region to the southern Pacific Ocean region, and that what they viewed as being native blue mussels had been accidentally introduced into the Southern hemisphere. They confirmed the Northern hemisphere origin of native blue mussels, highlighted the route of colonisation being via the Atlantic Ocean from the north to the south and dated the primary migration to ~1.2 M ybp, during the Pleistocene. They went on to note, however, that overall, their data supported the hypothesis of two separate migration events, rather than one, both from the Northern to the Southern hemisphere, with most haplotypes being derived from the first migration 1.2 M ybp, and far fewer being derived from a more recent migration event, also via the Atlantic Ocean route. Unfortunately, Hilbish et al. (2000) were unable to determine the exact origin or timing of this second event, but did note that it predates human activity (i.e., native Southern hemisphere mussels are genuinely native and not a result of human introduction). This two-invasion scenario is best interpreted as representing the older colonisation of South America, including the Falkland Islands and the Kerguelen Islands, and the more recent colonisation of Australasia, including Australia, mainland New Zealand and its offshore islands. This molecular interpretation is consistent with the findings of McDonald et al. (1991) and Sanjuan et al. (1997) based on allozyme variation, and also of Daguin & Borsa et al. (2000) based on two nDNA markers. In addressing the Pleistocene-Pacific hypothesis (e.g., as proposed by Lindberg 1991), Hilbish et al. (2000) were very clear that their results reject any suggestion of transequatorial migration through the Pacific and that the greater affinity of Southern hemisphere mussel mtDNA lineages with those found in Northern hemisphere *M. edulis* and *M. galloprovincialis* clearly indicates an Atlantic route of migration for colonisation of the Southern hemisphere. If this is the case, then the primary colonisation event of South America (via a North Atlantic to South Atlantic Ocean route) seems sensible because it is direct and geographically nearest to the North Atlantic centre of origin, and the subsequent secondary colonisation event of Australasia is also intuitively appealing because it is more remote from the North Atlantic centre of origin, and Australasia is connected to South America via the West Wind Drift.

While the work of Borsa et al. (2007) using *Glu-5′/Glu-3′* and *mac-1* (both are nuclear DNA markers) did not specifically examine the timing of origin nor the routes of colonisation of Southern

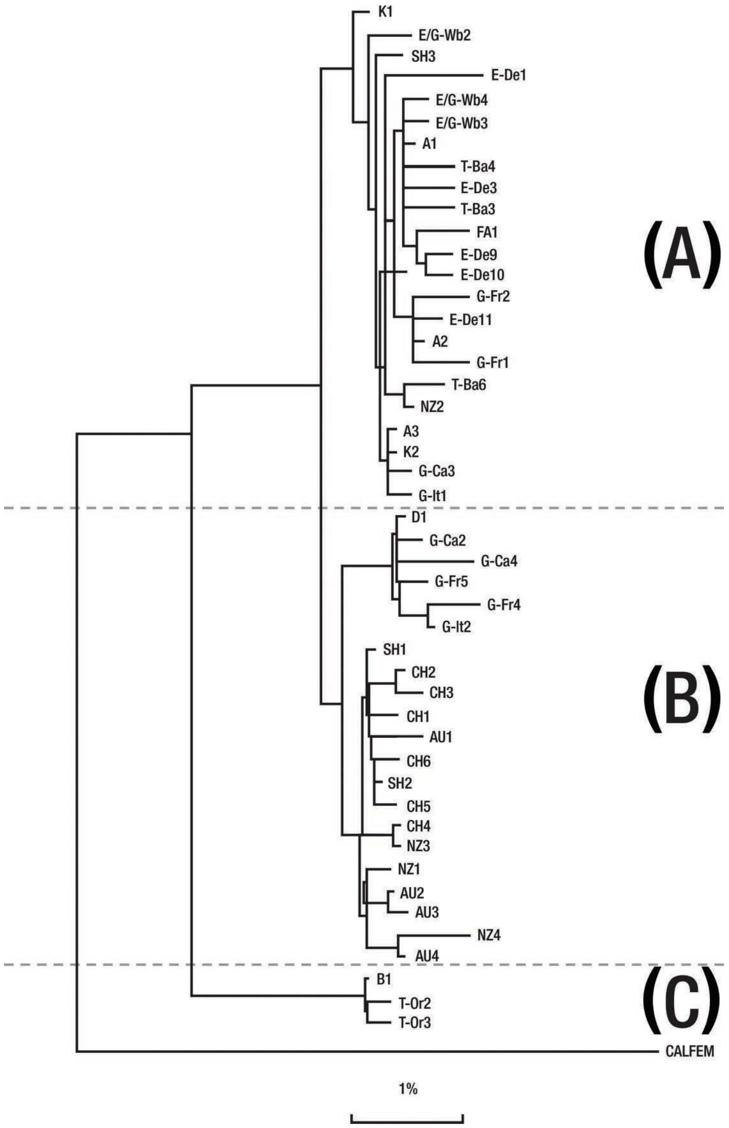

Figure 8 Neighbour-joining phylogeny for the *Mytilus* 16S rRNA maternal mitochondrial lineage sequences from Northern and Southern hemisphere mussel populations, taken from Hilbish et al. (2000). **Clade A** – Northern hemisphere *M. edulis* and *M. galloprovincialis*, but also including some mussels from the Falkland Islands, Kerguelen Islands, Western Australia and New Zealand. On average, these sequences are 0.3% divergent from other A haplotypes found in the northern hemisphere. **Clade B** – Northern hemisphere *M. galloprovincialis* mussels and all Southern hemisphere mussels except those from the Kerguelen Islands. The parsimony and maximum-likelihood analyses, however, both showed that the Northern hemisphere B clade is significantly distinguished from Southern hemisphere B haplotypes. This Southern hemisphere clade is, on average, 1.4% divergent from the next closest B clade of *M. galloprovincialis*. **Clade C** – Northern hemisphere *M. trossulus*. Outgroup (CALFEM) = female *M. californianus*. Modified from Hilbish et al. (2000).

hemisphere mussels, their work did, nonetheless, shed new light on the matter. The authors confirmed the native (endemic) status of mussels from Tasmania and the Kerguelen Islands (i.e., these mussels are not accidentally introduced), and they suggested that the great affinity of Australasian mussels with *Mytilus galloprovincialis* from the western Mediterranean (the type locality for this species) indicates a rapid expansion from the Mediterranean Sea to Australia and New Zealand with very little time for genetic exchange. This interpretation is consistent with the idea of a second, more recent colonisation event of the Southern hemisphere as proposed by Hilbish et al. (2000).

The following year, Gérard et al. (2008) analysed both 16S and COI (both are mtDNA regions) sequence variation, but focussed on COI because it is more variable and therefore more informative. They highlighted pronounced genetic differentiation among the mussels from South America and the Kerguelen Islands, Australia (Tasmania), and New Zealand, consistent with two independent colonisation events (e.g., Hilbish et al. 2000), confirmed the divergence between mussels from the Northern and Southern hemispheres, and suggested that this divergence predated the divergence of Northern hemisphere *M. edulis* and *M. galloprovincialis* (Figure 9). Using the trans-Arctic interchange as a molecular clock calibration, Gérard et al. (2008) estimated the time since divergence to be between 0.5 M and 1.3 M ybp (average 0.84 M ybp). This estimate dates from the Pleistocene (0.01–1.8 M ybp) and is consistent with the estimate produced by Hilbish et al. (2000) of 1.2 M ybp based on sequence variation of the 16S gene. In terms of identifying a route or routes of invasion, Gérard et al. (2008) noted that results obtained with the single mitochondrial genome do not permit the inference of a general history of population divergence (Figure 10). They also noted that comparison of published nuclear and mitochondrial results suggested two different scenarios, the first involving two separate colonisation events and the second involving one event but biased by taxonomic preconception. This latter point has been, and continues to be, a key point of contention in the interpretation of *Mytilus* spp. in the Southern hemisphere.

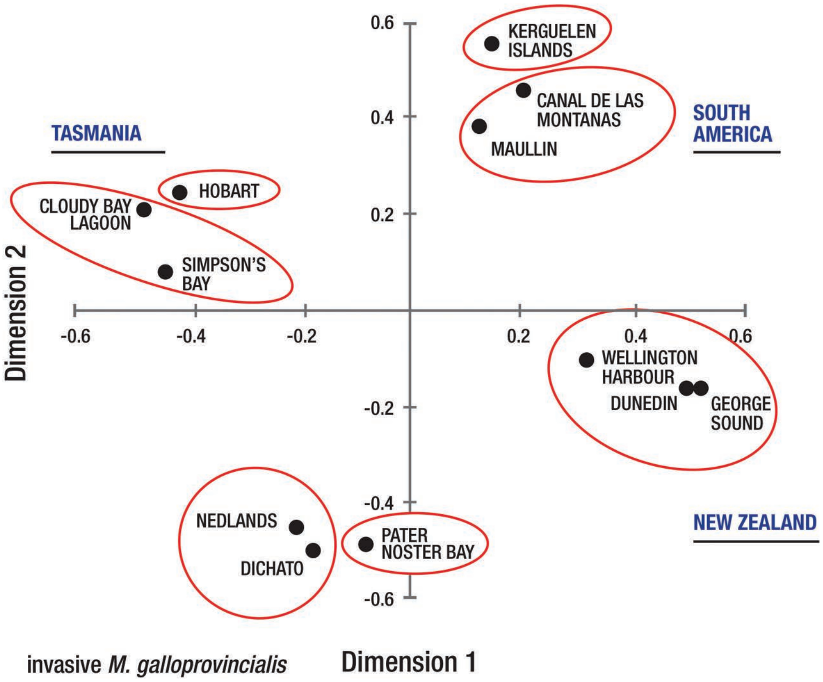

Figure 9 Four groups of differentiated mussels based on COI sequence variation. Tasmania group – Cloudy Bay Lagoon, Tasmania; Hobart, Tasmania; Simpson's Bay, Tasmania. South America group – Kerguelen Islands; Maullin, Chile; Canal de las Montañas, Patagonia, Chile. New Zealand group – Dunedin, South Island; George Sound, South Island; Wellington Harbour, North Island. Invasive Northern hemisphere *M. galloprovincialis* – Pater Noster Bay, South Africa; Nedlands, Australia; Dichato, Chile. Samples within the same circle are not significantly different ($P > 0.05$), whereas samples in different circles are different ($P < 0.05$) based on Φ_{ST} values. Modified from Gérard et al. (2008).

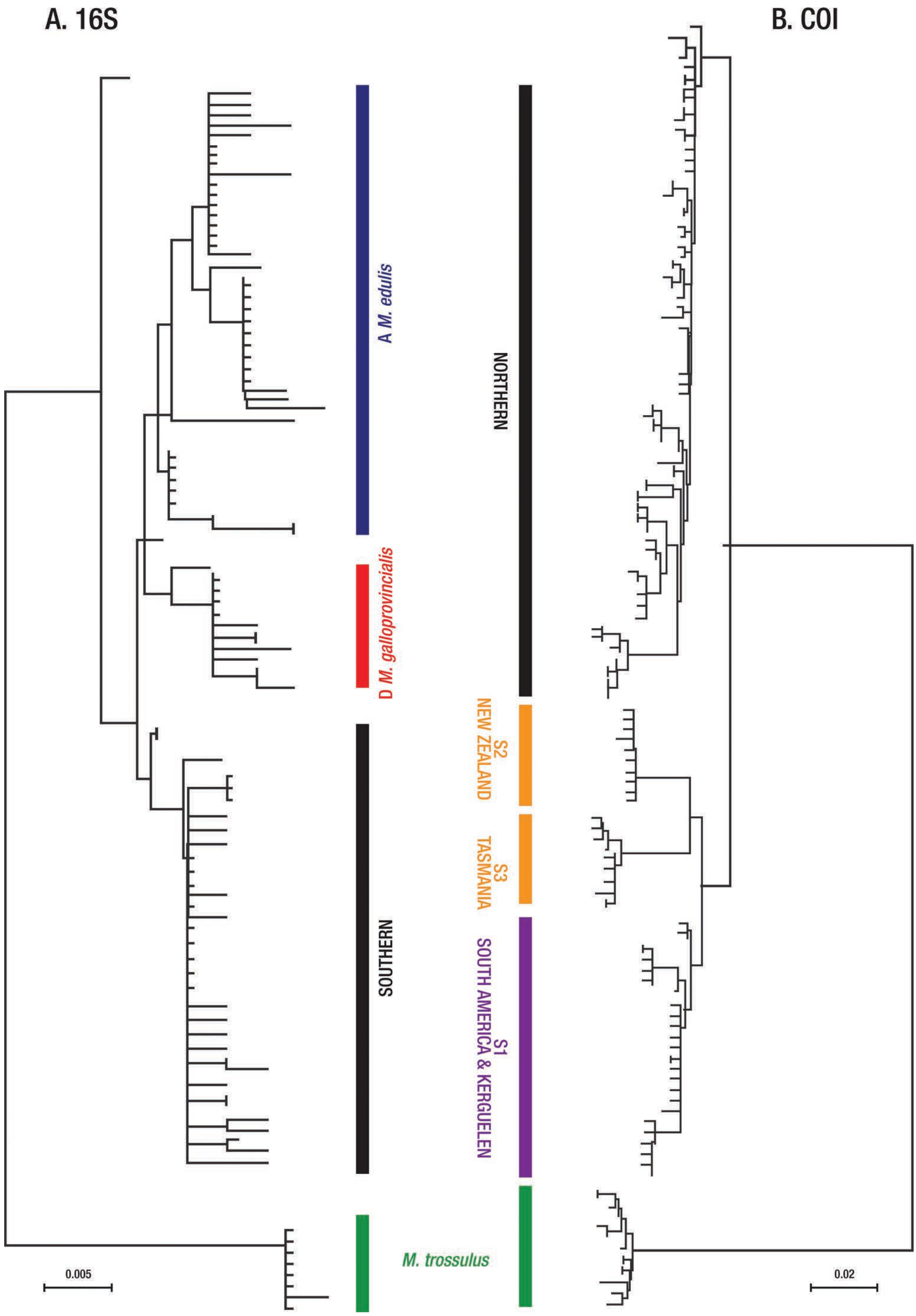

Figure 10 Phylogenetic relationships of *Mytilus* spp. mussels based on (A) 16S rDNA and (B) COI haplotypic variation. Bootstrap scores>50% are indicated on branches for NJ (neighbour-joining) and ML (maximum-likelihood) trees, respectively. Tree-length scales given at the bottom of each tree. Note that the scale of the 16S tree is four times larger than that of the COI tree. Clade interpretations are given down the centre of the figure. Modified from Gérard et al. (2008).

Pickett & David (2018) failed to detect a Northern versus Southern hemisphere split based on COI sequence variation alone (360-bp fragment with 157 variable sites – Figure 31) in sequences downloaded from GenBank (we note that all such DNA sequence data are only as good as the meta-data). The authors did, however, detect four well-differentiated haplogroups (Australasia, including all New Zealand samples, all Tasmanian samples and some mainland Australia samples; Turkey; southern Korea; southern China) that diverged from a central cluster of haplotypes that showed no real evidence of geographic structure. They suggested that the absence of a distinct Northern versus Southern hemisphere split as previously reported by Hilbish et al. (2000) and Gérard et al. (2008) and as also indicated by Westfall et al. (2010) might be explained by dilution of the signal due to what they called cryptic dispersal, that is frequent and ongoing anthropogenic movement of mussels. Nonetheless, Pickett & David (2018) did identify a very strong Australasian grouping that is quite distinct from all other groups (separated by at least 20 mutational steps from its nearest haplogroup neighbour), as well as provide confirmation of the presence of invasive Northern hemisphere *M. galloprovincialis* in several Southern hemisphere locations such as Chile, South Africa and eastern Australia.

Most recently, Popovic et al. (2020) have used transcriptome-wide markers (a panel of 20,509 SNPs) in an Approximate Bayesian Computing (ABC) framework to test multiple hypotheses of the origin of native Australian (but not New Zealand) mussels. They showed that native mussels from Tasmania are representative of the endemic Australian taxon (*M. planulatus*) and that these mussels exhibit the greatest affinity to Northern hemisphere *M. galloprovincialis*. Based on model testing, Popovic et al. (2020) suggested that Australian *M. planulatus* diverged in allopatry from Northern hemisphere *M. galloprovincialis* between 0.1 and 0.6 M ybp, under a model of historical gene flow followed by divergence in isolation. These findings are consistent with earlier work (e.g., Hilbish et al. 2000, Gérard et al. 2008, Pickett & David 2018), in particular with the suggestion of a second, more recent, range expansion by Mediterranean Sea *M. galloprovincialis* into Australasia (e.g., Hilbish et al. 2000).

While the interpretation of the evolution of Southern hemisphere blue mussels is still not entirely clear, what is apparent is that most studies, regardless of the approach that they have taken, have tended to arrive at similar conclusions. The big picture is relatively clear, but the details are still not always either known or agreed upon by all workers in the field. We can summarise this body of work in five key points: (1) Southern hemisphere mussels are native and do not originate from recent human transport, either accidental or deliberate; (2) Southern hemisphere mussels are derived from Northern hemisphere mussels; (3) the colonisation of the Southern hemisphere first occurred ~1 M ybp (1.2 M ybp according to Hilbish et al. 2000 based on 16S variation; 0.84 M ybp according to Gérard et al. 2008 based on COI variation) during the Pleistocene; (4) the route of invasion was via the Atlantic Ocean and not via the Pacific Ocean; and (5) there is evidence of a second, more recent, colonisation event – unable to be dated by Hilbish et al. (2000) but more recent than 1.2 M ybp, supported by the work of Popovic et al. (2020) who reported a date of 0.1–0.6 M ybp for Australian mussels. It remains unclear, however, whether the two invasions are linked or are independent events, although increasingly the body of evidence is now pointing to two independent events. For example, it is possible that (1) there was one invasion from the Northern hemisphere that gave rise to South American mussels, which subsequently and at an unknown date then gave rise to the Australasian mussels, versus (2) there were two independent invasion events from the Northern hemisphere, the first of which (derived from *M. edulis*) gave rise to the South American mussels and the second of which (derived from *M. galloprovincialis*) gave rise to the Australasian mussels. A recent analysis of transcriptome sequencing and identification of putative biomineralisation genes might provide a new insight (Malachowicz & Wenne 2019). The phylogenetic relationships within some, but not all, members of the genus *Mytilus* were defined on the basis of concatenated, aligned nucleotide sequences of 202 homologous genes using the neighbour-joining (NJ) method (Figure 11). As expected, *M. californianus* and *M. coruscus* are genetically more distant from the other taxa, being equivalent to outgroups for their smooth-shelled mussel congenerics. Again, as expected, *M. trossulus* is the oldest and most distinct species among the smooth-shelled mussels. Detail within the NJ tree

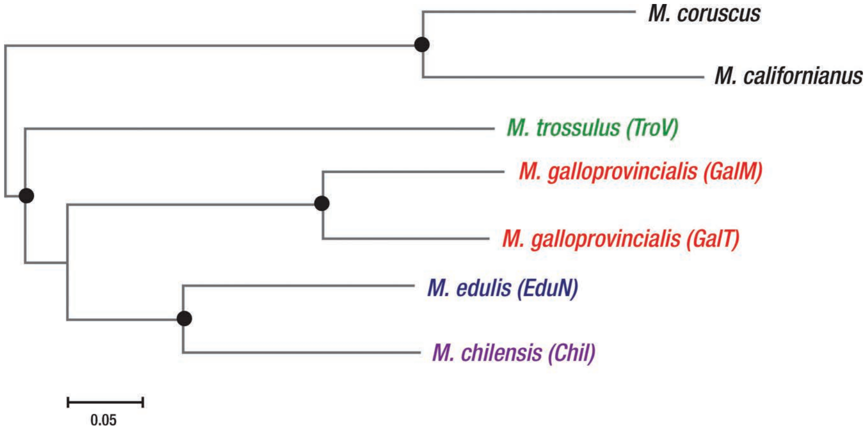

Figure 11 Phylogenetic relationships of six *Mytilus* taxa based on alignment of 202 homologous DNA sequences. A black dot at the node represents bootstrap values >90%. TroV – *M. trossulus* (Vancouver, Pacific coast of Canada), GalM – *M. galloprovincialis* (Trieste and Chioggia, Mediterranean Sea), GalT – *M. galloprovincialis* (Spring Bay, Tasmania, Australia), EduN – *M. edulis* (Oosterschelde estuary, North Sea), Chil – *M. chilensis* (Punta Arenas and Concepción, Chile). Modified from Malachowicz & Wenne (2019).

reveals that *M. galloprovincialis* from the Mediterranean Sea clusters with Southern hemisphere *M. galloprovincialis* from Tasmania (Australia), whereas *M. edulis* from the North Sea clusters with *M. chilensis* from Chile (Malachowicz & Wenne 2019). Thus, this NJ tree provides evidence of two separate invasions of the Southern hemisphere, the first involving Northern hemisphere *M. edulis* that gave rise to the South American native mussels and the second invasion involving Northern hemisphere *M. galloprovincialis* that gave rise to the Australasian native mussels (Malachowicz & Wenne 2019). This interpretation is consistent with the findings of Hilbish et al. (2000), the suggestion of Gérard et al. (2008) and the dating of the origin of the Australian native mussels by Popovic et al. (2020). The presence of two distinct Southern hemisphere groups of native mussels (South America versus Australasia) in the NJ tree is consistent with multiple reports from numerous different authors of this apparent biogeographic split. The inclusion of other native taxa (e.g., from New Zealand, Argentina, the Falkland Islands, the Kerguelen Islands, western Australia) in this sort of analysis would be informative and may help to clarify the one-invasion or two-invasion scenarios that, at present, remain unresolved. On the weight of evidence available, we support the two-invasion scenario.

The recent and ongoing application of SNPs to mussels from all regions of the Southern hemisphere, and the use of reference Northern hemisphere taxa for comparative purposes, sheds new light on the situation in the Southern hemisphere. While markers such as SNPs do not have great utility for determining either the timing of the colonisation or the number of such events (but see Popovic et al. 2020), they are nonetheless particularly informative in terms of providing new information about genetic affinities (relatedness) of Southern and Northern hemisphere mussels, of genetic differentiation among mussels from different Southern hemisphere regions, and may also provide new insights into evolutionary processes such as hybrid speciation (reticulate evolution – Borsa et al. 2007, Arnold & Fogarty 2009, Mallet et al. 2016) and bioinvasions.

Southern hemisphere mussel taxonomy has long been embedded in Northern hemisphere thinking and interpretation

Because the *Mytilus edulis* species complex was much better known and understood at any given time in the Northern hemisphere than in the Southern hemisphere, the nomenclature applied in the north was generally widely applied to the south as well. That is, the species-level taxonomy of Southern hemisphere mussels was often not viewed as being separate from the north, but was viewed as being part of the north. This situation had not always been the case (e.g., taxonomies based on shell characters alone – d'Orbigny 1846, Hupé 1854, Lamy 1936, Powell 1958), but increasing evidence of species-level regional differences when allozyme and the first generations of molecular markers were applied started to change this interpretation.

In considering the taxonomic status of mussels of the Southern hemisphere, it is important to appreciate that taxonomic interpretation is only as good as the traits or the markers being used, in particular given that very few, if any, anatomical or behavioural differences exist among the species. If the marker in question is not informative, then the interpretation has to be that there is no difference at a taxonomic level between the two samples being examined. It is also important to appreciate that the first colonisation event giving rise to Southern hemisphere mussels (*M. edulis* to South America) is judged to be reasonably recent (~1 M ybp) and therefore profound (species-specific diagnostic) differences between Southern and Northern hemisphere mussels may not have had sufficient time to evolve. This will be particularly true if Australasian mussels (*M. planulatus* and *M. aoteanus*) are derived from a much more recent (perhaps in the range 0.1–0.6 M ybp) range expansion from the Northern hemisphere, meaning that even less time has occurred for them to differentiate from *M. galloprovincialis*. Thus, many markers of whatever type may not yet be diagnostically different because of ongoing speciation. Taken in isolation, as they usually were, a single marker may not contain enough information to differentiate between species, but in conjunction with other markers, perhaps the multi-marker approach is sufficient to point to a level of differentiation that is enough to identify different evolutionary lineages. Dealing with incipient speciation is therefore challenging given that in an evolutionary context, not much time may have passed since a split, and also given that for blue mussels, the processes of hybridisation and introgression may blur or retard the formation of new species boundaries. The question of whether speciation occurred without gene flow (allopatrically) or in the face of ongoing gene flow is also important, in this regard.

One of the key points made by Gérard et al. (2008) was that the combined published multi-marker mitochondrial and nuclear DNA data point to two different scenarios. They defined the first scenario as two separate invasion events from the north to the south and the second as "… a single trans-equatorial migration and a view of the composition of the nuclear genome **biased by taxonomic preconception**" (Gérard et al. 2008, p. 84 – emphasis added in bold). They concluded by stating that for the single colonisation event "Under this scenario the distinction, based on nuclear markers, of *M. edulis*-like and *M. galloprovincialis*-like mussels in the Southern Hemisphere would be merely virtual, constrained by human's wish to always assign new samples to reference populations assumed to represent the genetic composition of a given taxon …" (Gérard et al. 2008, p. 90). That is, that genetic differences of Southern hemisphere mussels at the species level might not be recognised as such and would only be interpreted in terms of existing Northern hemisphere species. Perhaps not surprisingly, because the history of marker development and application and the fact that most of the *M. edulis* species complex research has been carried out in the Northern hemisphere, a lot of the interpretation of the Southern hemisphere situation has been strongly embedded in the interpretation of the species in the Northern hemisphere. For example, based on marker types available at the time Blot et al. (1988) concluded that native mussels from the Kerguelen Islands (*M. desolationis*) are part of the *M. edulis* species complex, and many authors noted the similarities between Northern hemisphere *M. edulis* or *M. galloprovincialis* and mussels from different regions and continents in the Southern hemisphere (e.g., McDonald et al. 1991, Sanjuan et al. 1997, Daguin & Borsa 2000). However, they also noted several differences, but often of a subtle nature that was difficult to interpret. In the end, all of these authors tended to favour a taxonomic interpretation of similarity to Northern hemisphere species rather than a separate identity for the Southern hemisphere mussels. This seems to have been as true of mussels from Australasia as it was for mussels from South America (both coasts) and from remote island locations. Even more recently, although a 16S RFLP revealed a clear difference between Northern and Southern hemisphere mussels, a nomenclature based on similarity rather than difference – Northern hemisphere *M. galloprovincialis* and Southern hemisphere *M. galloprovincialis* – was employed (Westfall & Gardner 2010, Westfall et al. 2010, Dias et al. 2014, Ab Rahim et al. 2016). These examples highlight the difficulties faced by workers when using only partially diagnostic markers (often one at a time) that cover only a tiny fraction of the genome to allow the recognition of new species that are endemic to the Southern hemisphere.

In more recent work, Borsa et al. (2007) noted that allozyme and/or *mac-1* (nuclear DNA marker) variation separated placing Southern hemisphere mussels into two clusters, consistent with earlier interpretation (e.g., Hilbish et al. 2000). One cluster was from South America and included the Falkland and Kerguelen populations, having greatest affinity to Northern hemisphere *M. edulis*. The second cluster was composed of populations from mainland Australia, Tasmania and New Zealand (Australasia), having the greatest affinity to *M. galloprovincialis* from the western Mediterranean (the type locality for this species). Borsa et al. (2007) noted that this latter affinity suggests rapid expansion of *M. galloprovincialis* from the Mediterranean to Australasia, presumably with sufficient time for genetic differentiation of the two lineages. Gérard et al. (2008) provided strong evidence of separation among regional groups (New Zealand versus Australia versus South America and the Kerguelen Islands) within the Southern hemisphere and between taxa of the two hemispheres. Ultimately, Gérard et al. (2008) were cautious in their interpretation, noting that gene trees are not species trees (*sensu* Nichols 2001), particularly in the *Mytilus* species complex where hybridisation and introgression are common. Westfall et al. (2010) developed a single marker (16S rRNA RFLP) assay that was able to differentiate Northern hemisphere *M. galloprovincialis*, *M. edulis* and *M. trossulus* from what they called native Southern hemisphere *M. galloprovincialis*. This assay could not, however, differentiate between or among native Southern hemisphere mussels from Chile, Argentina, Australia and New Zealand. The authors suggested that sequencing of each 16S fragment may be helpful in differentiating among regional Southern hemisphere mussels and may be informative in terms of their phylogeography. Thus, the interpretation at the time was still that Southern hemisphere mussels were all similar because they could not be differentiated based on this assay alone (Westfall & Gardner 2010) and were most like Northern hemisphere *M. galloprovincialis*, but that they were clearly different from all Northern hemisphere species (Westfall et al. 2010). Most recently, Astorga et al. (2015) analysed both COI and 16S sequence variation in mussels from South America based on newly collected material (from Chile, Argentina and Uruguay) and GenBank sequence data, including reference Northern hemisphere taxa. As expected, *M. trossulus* was most different from all other groups. Beyond this, COI sequence divergence estimates were of similar magnitudes, such that all four groups (South American *Mytilus*, Northern hemisphere *M. galloprovincialis*, Southern hemisphere *M. galloprovincialis* and *M. edulis*) were equally differentiated. For 16S sequence divergence, again there was evidence of divergence among all pairwise comparisons of the four groups, but the South American *Mytilus* were more similar to other Southern hemisphere mussels than any other pairwise comparison (refer to Table 2 for details). A minimum spanning network of COI haplotypes clearly resolved separate groups: Northern hemisphere *M. trossulus* (black), *M. edulis* (dark blue) and *M. galloprovincialis* (light blue) from their Southern hemisphere counterparts of South American mussels (red) and other Southern hemisphere (Australia and New Zealand) mussels (green) (Figure 12). Consistent with previous analyses (e.g., Hilbish et al. 2000, Gérard et al. 2008), Astorga et al. (2015) reported that there are great differences between Southern hemisphere mussels (two distinct groups were recognised, South America and Australasia) and that samples from South America, including the Kerguelen Islands "… are taxonomically independent" (Astorga et al. 2015, p. 924). Finally, Astorga et al. (2015) noted the complex and, at times, tangled taxonomy of the global *M. edulis* species complex (they dismissed use of regional-specific subspecific status (*M. edulis edulis*, *M. edulis galloprovincialis*, *M. edulis planulatus* and *M. edulis platensis*) and concluded somewhat uncertainly that "In the southern hemisphere, *Mytilus planulatus* should be the name used for specimens from South America, Kerguelen, and

Table 2 Percentage genetic distance between regional taxa of *Mytilus*, as reported by Astorga et al. (2015)

	South American *Mytilus*	Northern hemisphere *M. galloprovincialis*	Southern hemisphere *M. galloprovincialis*	*Mytilus edulis*	*Mytilus trossulus*
South American *Mytilus*	–	0.035	0.033	0.030	0.438
Northern hemisphere *M. galloprovincialis*	0.019	–	0.041	0.015	0.472
Southern hemisphere *M. galloprovincialis*	0.005	0.021	–	0.039	0.490
Mytilus edulis	0.034	0.038	0.036	–	0.448
Mytilus trossulus	0.098	0.103	0.107	0.100	–

The number of base substitutions per site averaged over all sequence pairs between groups are shown. For COI, analyses were conducted using the Tamura-Nei 93 model+G. The rate variation among sites was modelled with a gamma distribution (shape parameter=0.241). For 16S, analyses were conducted using the Tamura-3-parameters model. The rate variation among sites was modelled with a gamma distribution (shape parameter=0.319).
Values for COI above and values for 16S below the diagonal.

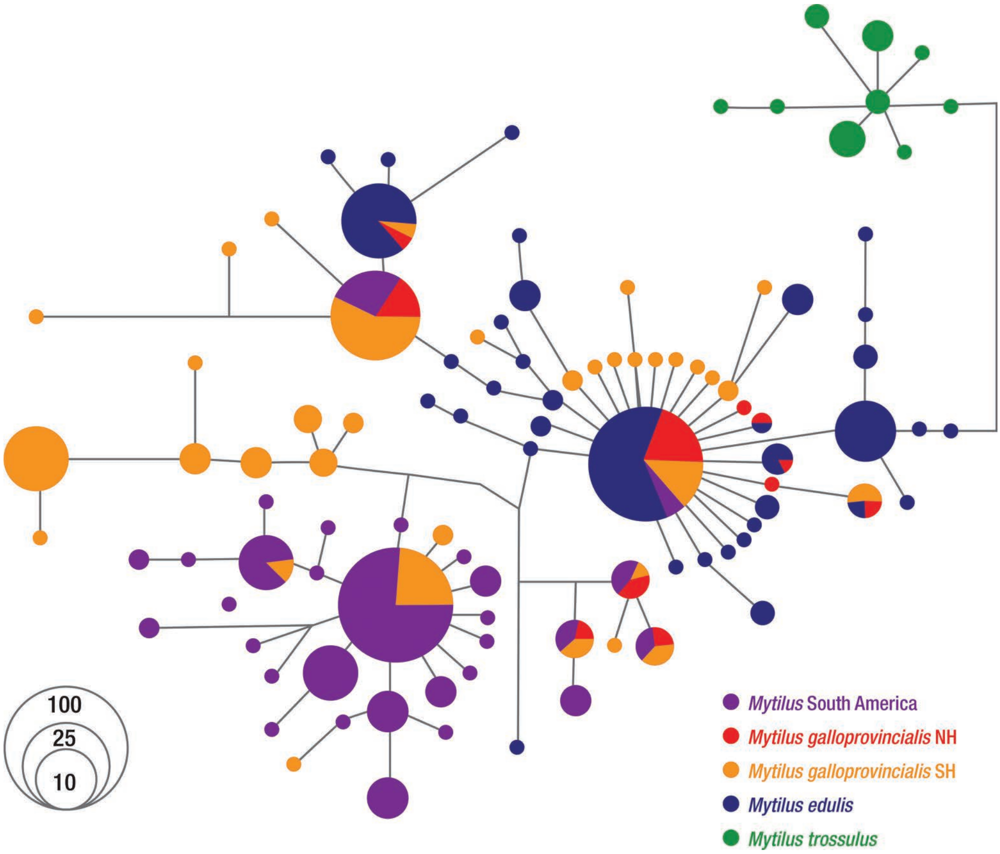

Figure 12 Minimum spanning network of haplotypes derived from variation at the COI gene for *Mytilus* species. The size of each circle is proportional to the absolute haplotype frequency, and the total number of individuals in each haplotype is indicated inside the circle (see graphic bottom left). The branch lengths are proportional to the mutational steps. Modified from Astorga et al. (2015).

the southwest Pacific (eastern Australia, Tasmania and New Zealand); or perhaps two differentiated groups should exist for the southern hemisphere, namely *planulatus* and *platensis*" (Astorga et al. 2015, pp. 927–928). Thus, based on taxonomic priority, the name *M. chilensis* would cease to be used for mussels from the Pacific coast of South America (Astorga et al. 2015).

Overall, there has long been evidence of differentiation between mussels from the Northern and Southern hemispheres (all studies have reported this, to greater or lesser degrees) and of differentiation between South America and Australasia within the Southern hemisphere (most, but not all studies have reported this). However, there was still, at this time, no definitive evidence that quite clearly pointed to differentiation among between-region or within-region mussel groups in the Southern hemisphere consistent with mussels of different species.

What constitutes a species within the *Mytilus edulis* species complex?

Understanding the diversity and biogeography of native Southern hemisphere blue mussels requires an understanding and appreciation of what constitutes a species. The idea and application of the species concept is, of course, a topic in its own right and one that has been debated over many decades. The detail of this debate is beyond the scope of the present review, and the reader is directed towards other papers for further discussion of this topic (e.g., Mallet 1995, Hey 2001a,b, de Queiroz 2007, Häuser 2009, Hausdorf 2011, Chambers 2012, Harrison & Larson 2014, Hohenegger 2014, Stanton et al. 2019). However, much of the longstanding debate about the taxonomy of the *Mytilus edulis* species concept in a global sense can really only be understood in the light of what various authors consider to be a species. As noted by Hey (2001a,b) and also indirectly by Gérard et al. (2008), this may be a personal view, rather than a purely objective view.

Changing views of the taxonomy of Southern hemisphere blue mussels

Many, but not all, of the native smooth-shelled blue mussels from the Southern hemisphere were named in the nineteenth century, during one of the great periods of global exploration and scientific discovery. Of course, these different mussels were named based on shell shape variation and with reference to descriptions provided for Northern hemisphere taxa (e.g., *M. edulis* Linnaeus, 1758, *M. galloprovincialis* Lamarck, 1819 and *M. trossulus* Gould, 1850) as these existed at the time. Many different taxa were described (refer to WoRMS for more detail – http://www.marinespecies.org/) and often on what may best be described as minor shell morphological differences. While this classification of global blue mussels may not seem to be of great importance, ultimately it is very relevant to the recognition of Southern hemisphere species, at least in part because of the concept of taxonomic priority (International Commission for Zoological Nomenclature 1999) and also as taxonomy relates to food labelling and biosecurity issues (see subsequent sections). These factors – the recognition of geographically isolated species and the concept of taxonomic priority – combined with individual views of what constitutes a species, have led to a series of debates and disagreements in the literature about the global taxonomic status of smooth-shelled blue mussels.

Two of the most important reviews of the subject of native Southern hemisphere mussel taxonomy are provided by Lamy (1936) and Soot-Ryen (1955), in the days before the application of genetic markers. In some respects, these two reviews provide an important framework, based on morphometric differences, for testing using modern molecular approaches. Lamy (1936) recognised the three Northern hemisphere taxa *Mytilus edulis* Linnaeus, 1758, *M. galloprovincialis* Lamarck, 1819 from the Mediterranean Sea, *M. trossulus* Gould, 1850 from the Pacific coast of North America, and also several Southern hemisphere taxa, including *M. chilensis* Hupé, 1854 from Chile, *M. platensis* d'Orbigny, 1846 from Argentina and Uruguay, and *M. planulatus* Lamarck, 1819 from Australia (but no mention of New Zealand), and then also described *M. desolationis* from the

Kerguelen Islands (Lamy 1936). In contrast, Soot-Ryen (1955) considered most of the above listed taxa as subspecies of Northern hemisphere *M. edulis*. In his extensive review of the littoral ecology and biogeography of the Southern oceans, Knox (1960, pp. 591–592) notes that while the blue mussels of the Southern hemisphere had formerly been split into separate species, they are now "… but subspecies of the cosmopolitan *Mytilus edulis*". Knox (1960, his figure 64) recognised five distinct subspecies – *M. e. chilensis*, *M. e. platensis*, *M. e. planulatus*, *M. e. aoteanus* Powell, 1958 and *M. e. desolationis* – consistent with the suggestions of the time made by Soot-Ryen (1955, 1957) and Fleming (1959) that had superseded the interpretation of Lamy (1936).

While the concept of the species may be in the eye of the beholder (Hey 2001a,b), there is one line of thinking that seems to be shared among most workers in the field in terms of species-level recognition and that is the concept of differentiated evolutionary lineages that maintain their identity even in the face of hybridisation and introgression. Thus, distinct genetic groupings with different evolutionary histories, despite gene flow between them, are the most commonly accepted interpretation of a "species" within the *M. edulis* species complex (e.g., Varvio et al. 1988, Koehn 1991, Daguin & Borsa 2000, Riginos & Cunningham 2005). Numerous more modern reviews of the species problem and of what constitutes a species boundary tend to agree with this interpretation. For example, Harrison & Larson (2014, p. 795) note in their review that species may be defined as "… populations that are diagnosably distinct, reproductively isolated, cohesive, or exclusive groups of organisms", that species boundaries are not uniform in space, in time or across the genome, and that species boundaries may be maintained despite hybridisation and introgression (i.e., species boundaries may be semi-permeable). However, the application of this framework does not guarantee a consistent approach across all workers. For example, when applied to mussels from Chile, Borsa et al. (2012) recognised the distinction between what they called Southern hemisphere *M. edulis* and Northern hemisphere *M. edulis* that gave rise to a "… separate, geographically isolated entity" (Borsa et al. 2012, p. 7) and concluded that these Southern hemisphere mussels warranted subspecific status as *M. edulis platensis* d'Orbigny 1846 and that the name *chilensis* (as in *M. chilensis* or *M. edulis chilensis*) should be dropped. In a similar vein, they argued that what they called Southern hemisphere *M. galloprovincialis* (e.g., so-called *M. desolationis* Lamy, 1936 for mussels from the Kerguelen Islands) should be called *M. galloprovincialis planulatus* Lamarck, 1819. Their argument was based, quite correctly, on the principle of taxonomic priority, but their interpretation of subspecific status for Southern hemisphere mussels was not widely accepted or applied. This example highlights the problem of taxonomic designations within the *M. edulis* species complex, and how, as noted above, the concept of the species may be in the eye of the beholder (Hey 2001a, b).

In their appraisal of blue mussels from the Pacific coast of North America, McDonald & Koehn (1988) make the point about taxonomy and specific status for Northern hemisphere smooth-shelled blue mussels that scientific clarity (i.e., the avoidance of confusion) is an important consideration. Revisions of taxonomy are based on rules (International Commission for Zoological Nomenclature 1999), but nonetheless revisions of taxonomy need to be mindful of longstanding practice and must not generate confusion. Given the difficulty of recognising distinct species in a species complex where speciation is recent and ongoing, and where both hybridisation and introgression often occur at high frequencies, an interpretation based on distinct evolutionary histories and genetic differences that are maintained despite gene flow seems to be entirely appropriate. We suggest that this approach now needs to be applied to Southern hemisphere mussels in the light of newly published data based on SNPs.

Interpretation of Southern hemisphere species and problems with taxonomy

Borsa et al. (2012) make the point that "Given the morphological variation encountered within Northern-Hemisphere *M. edulis* (McDonald et al. 1991), it remains to be proven that the reportedly flatter shell of Hupé's *M. chilensis* constitutes a character strong enough to distinguish it from

M. edulis and assign it specific rank" (Borsa et al. 2012, p. 3). The same reasoning about shell morphometry also applies to the recognition of other putatively endemic Southern hemisphere taxa (e.g., *M. platensis* in Argentina and Uruguay, *M. planulatus* in Australia, *M. aoteanus* in New Zealand, *M. desolationis* at the Kerguelen Islands) and their differentiation from Northern hemisphere taxa and, of course, among themselves. To some extent, the answer to this question will depend on the species concept applied, but it will also depend on the supporting evidence derived from other sources, such as new molecular markers.

While applying their 16S RNA RFLP assay to native Southern hemisphere mussels, Westfall & Gardner (2010, 2013) noted that all native Southern hemisphere mussels that they tested (from Australia, Chile and New Zealand) were distinct from Northern hemisphere mussels. However, the 16S RFLP assay could not differentiate among the different Southern hemisphere regional populations. This led them to apply the concept of different evolutionary lineages of mussels (i.e., a Southern hemisphere *M. galloprovincialis* versus a Northern hemisphere *M. galloprovincialis*). While this approach was informative for identifying non-native Northern hemisphere mussels in the Southern hemisphere, it was not informative in terms of identifying native Southern hemisphere region-specific differences.

Those who consider the differences to be important (e.g., Lamy (1936) who was more of a "splitter") and those who consider the similarities to be more important (e.g., Soot-Ryen (1955) who was more of a "lumper") may help to explain the absence of consensus about the specific status of Southern hemisphere mussels (refer to species delimitation review by Stanton et al. 2019). In some respects, molecular workers have also tended towards one or other of these schools of thought (lots of different regional differentiated taxa versus a relatively few species of Northern hemisphere origin, into which all Southern hemisphere taxa are fitted as subspecies). This dichotomy reflects, in the minds of some workers, what has been called "taxonomic inflation" (Isaac et al. 2004) and has real consequences across a range of different fields and management options. These two contrasting viewpoints provide an opportunity for testing ideas about speciation and biogeography, and this is very much the background that helped spur the development and application of a panel of new SNP markers (Zbawicka et al. 2012) to Southern hemisphere mussels (Gardner et al. 2016, Larraín et al. 2018, Zbawicka et al. 2018, 2019, 2021).

The fossil and midden records of *Mytilus* spp. in the Southern hemisphere

A number of authorities have noted that *Mytilus* shells are found as fossils or in middens that predate European arrival in all Southern hemisphere countries so far examined, with the notable exception of South Africa (e.g., McDonald et al. 1991 and references therein). The coverage for fossil or midden valves of *Mytilus* sp. is patchy, with several important regions having no information about them at all. Thus, interpretation needs to be made with care, but the evidence overwhelmingly supports the view that fossils and/or midden valves that predate European arrival in all regions point to the native status of blue mussels in the Southern hemisphere.

Surprisingly, few analyses of shell trait or shape variation among Southern hemisphere shells in the context of reference Northern hemisphere shells have been carried out, despite the fact that shell trait and shape variability may be informative at the species level (e.g., McDonald et al. 1991, Gardner 2004, Gardner & Thompson 2009, Illesca et al. 2018). Thus, interpretation of Southern hemisphere shells may, at times, be difficult given the absence of reference samples.

Intriguingly, there is evidence from both coasts of South America of what appear to be very old deposits (Miocene epoch, ~5.333–23.030 M ybp) that contain native blue mussels. The specific status of these mussels is often unclear, but their presence on both coasts suggests that blue mussels may be older than much of the present literature suggests. Given a presumed origin of *M. trossulus* approximately 3.5 M ybp, which is thought to be the ancestral species of contemporary smooth-shelled blue mussels in the North Pacific Ocean region (Riginos & Cunningham 2005), the occurrence of a relative in Chilean middens can be explained, but the presence of a relative in Argentina that predates *M. trossulus* is harder to explain. Such fossil remains need further investigation, and new interpretation may, once again, revise our thinking about the evolutionary origin of the *Mytilus edulis* species complex.

Chile

Mytilus sp. fossils have been reported from several sites on the Chilean coast. The oldest records date from the early Miocene, in the Navidad formation (33°55′S) on Ipún Island (Los Chonos – 44°36′S) (Kiel & Nielsen 2010), at Lo Abarca in central Chile – (33°31′S) (Covacevich & Frassinetti 1990) and at Tubul (37°S) an early Pleistocene *Mytilus* fossil has been recorded (Nielsen & Valdovinos 2008, Kiel & Nilsen 2010). In the south, near the Strait of Magellan, molluscs of the genus *Mytilus* are the most important macroinvertebrates of the modern benthic fauna (Aldea & Rosenfeld 2011). They have been a key ecological component of the coastline since at least the Holocene period (Estevez et al. 2001, Rabassa et al. 2009, Gordillo et al. 2010), and the fossil record indicates that a smooth-shelled blue mussel (*Mytilus* sp.) may date back to the late Miocene (~10 Myr BP) in this region (Martínez & del Río 2002, Aguirre et al. 2008). The molecular data (Bayesian Skyline Plot) indicate that population increase of *Mytilus* in Chile happened 20,000 years ago after the Last Glacial Maximum (Figure 13). It is likely that the colonising populations settled in discrete refuges (e.g., Ipún Island) and subsequently colonised the south as the glaciers retreated. This would indicate that the fossil records of *Mytilus* in South America are

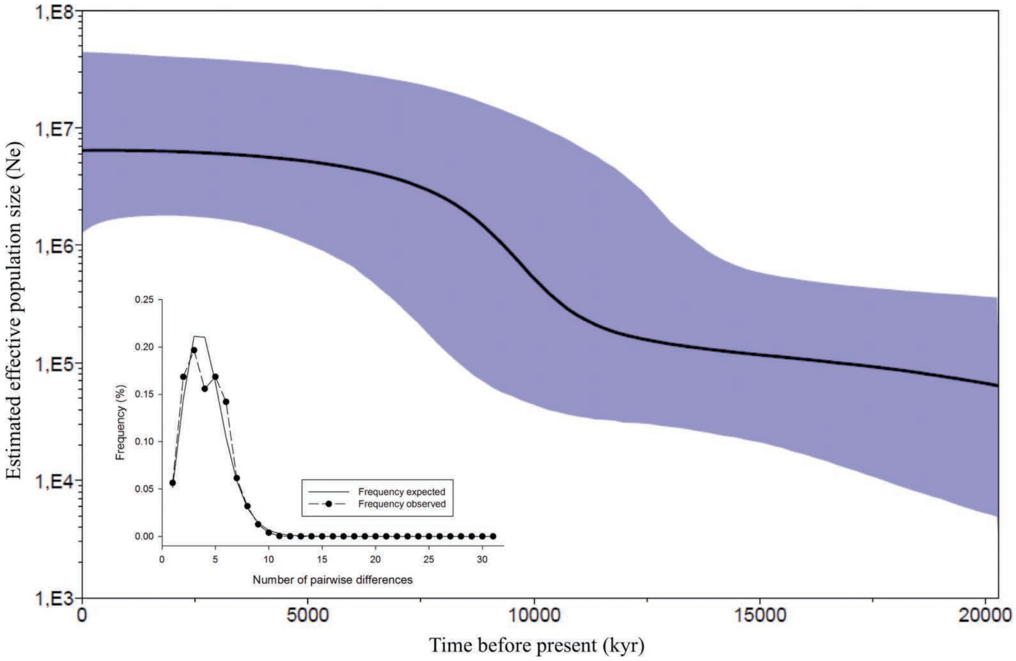

Figure 13 Bayesian skyline plot showing the demographic history of *Mytilus chilensis* on the Chilean coast. The dark line (solid black line) represents the median value of the population size (Ne), and the blue area represents the 95% highest probability density interval. Inset, lower left – the mismatch analysis represents the frequency distribution of pairwise differences among cytochrome oxidase subunit I (COI) haplotypes in *Mytilus*. Modified from Oyarzún et al. (2019).

older than those reported in the Northern hemisphere (e.g., Vermeij 1991). This interpretation may have some bearing on the origin of modern smooth-shelled blue mussels, but does not, as things presently stand, argue against or disprove the molecular interpretation of the origin of modern smooth-shelled blue mussels.

Argentina and Uruguay

McDonald et al. (1991) noted that pre-Columbian fossil shell deposits and/or middens are reported from Uruguay (Sprechemann 1978) and Argentina (Johnson 1976). More recently, del Río et al. (2001) have reported the presence of *M. trigonus* that inhabited the Miocene sea in northern Patagonia, Argentina. Subsequently, Savoya et al. (2015) used Fourier analysis to show that pre-European and modern *Mytilus* sp. shells from Patagonia are different from one another, possibly suggesting that modern native blue mussels in Argentina are, in fact, invaders rather than genuinely native. However, the authors note that alternative explanations also exist, including the fact that environmental change may result in a change in shell shape over evolutionary time. The question of a possible cryptic invasion requires the application of modern molecular markers to answer it and thereby to inform management (e.g., protection) practices (Savoya et al. 2015). We are unaware of any evidence of fossil or midden valves from the Falkland Islands.

New Zealand

Pre-European fossil shell deposits and/or middens are reported from numerous locations throughout mainland New Zealand (Fleming 1959, Fleming & Suggate 1964, McDonald et al. 1991, Gardner 2004). However, we are unaware of any such records from the numerous offshore islands in the Southern Ocean, although these were infrequently inhabited (e.g., as summer fishing and hunting camps).

In New Zealand, the fossil record for *Mytilus* dates back a little over 1.0 M ybp, to the early Castlecliffian (Sutherland et al. 1995). An analysis of one fossil valve and 83 midden valves from New Zealand (Gardner 2004) in comparison to reference Northern hemisphere valves, indicated that native New Zealand mussels were best interpreted as *M. galloprovincialis*-like. That is, consistent with genetic markers being employed at the time, native New Zealand mussels showed the greatest affinity in terms of shell trait variation to Northern hemisphere *M. galloprovincialis*. Interestingly, the Bay of Islands region (far north of New Zealand) was identified by the analysis of shell trait variation to have the greatest affinity with reference Northern hemisphere *M. edulis*. Subsequently, this region has been shown to have been very heavily invaded by Northern hemisphere *M. galloprovincialis* (Gardner & Westfall 2012, Gardner et al. 2016), so we speculate that it is possible that the NZ shells with the greatest affinity to *M. edulis* were non-native Northern hemisphere mussels or perhaps were hybrids and/or backcrosses between native and introduced mussels.

Australia

McDonald et al. (1991) note that pre-European fossil shell deposits and/or middens are reported from mainland Australia and Tasmania (Hope et al. 1977, Donner & Jungner 1981, Colhoun et al. 1982, Kerrison & Binns 1984). However, all of these reports relate to sites in eastern Australia (New South Wales, Victoria, South Australia, Tasmania), and there appear to be no records of such shells from Western Australia. Svane (2011) noted that because blue mussel valves may be difficult to identify (even to genus level) and to age from archeological material, the identification of the shells and fragments has not been independently verified. In the context of blue mussels in Australia, all authors have noted that the presence of valves in middens that predate European arrival strongly supports the contention that such mussels are native to Australia or at least some parts of it.

South Africa

Several different authors have noted that blue mussel valves are not found in fossil or shell midden deposits (e.g., Grant & Cherry 1985, McDonald et al. 1991, and references therein). This information has been interpreted as meaning that the genus is naturally absent from southern Africa. This interpretation is consistent with the physical oceanographic data that explains contemporary blue mussel distributions in the Southern hemisphere.

Offshore islands

Reports of fossils from remote offshore Southern hemisphere islands are harder to find, but nonetheless, Fletcher (1938) has reported marine fossils, including a recent *Mytilus* sp., from a late Tertiary bed at the Kerguelen Islands (Powell 1965). The natural (i.e., pre-human) distributions of blue mussels across the many islands in the Southern Ocean are hard to establish, and there is only limited evidence that clearly points to their native presence. Nonetheless, it appears to be widely accepted or believed that blue mussels are native to many, but not all, remote offshore islands in the Southern hemisphere.

Southern hemisphere mussel phylogeography based on markers before the use of SNPs

Chile

In South America, blue mussels occur naturally from approximately the latitude of Concepción, Chile (36°49′S; 73°03′W) on the Pacific coast, along the southern Chilean coast line and around Cape Horn (55°58′S; 67°17′W), and then extend north along the Atlantic coastline of Argentina, to a northern limit at approximately Punta del Este, Uruguay (34°58′S; 54°57′W) (Hernández & González 1976, Oyarzún 2016).

The native blue mussel from the Pacific coast of South America (Chile) was described by Hupé in 1854 as *M. chilensis*. This was soon after the description of the native blue mussel from the Atlantic coast of South America (Uruguay), described by d'Orbigny in 1846 as *M. platensis*. As noted by Borsa et al. (2012) when addressing this point "… Hupé mentioned the presence of *M. chilensis* '*en la costa*, *en Valparaíso, etc*.' and recognised that *M. chilensis* '*tiene enteramente el aspecto del Mytilus edulis de las mares de Europa*' except that '*su forma es más aplastada*'" (Borsa et al. 2012, p. 3). In other words, Hupé (1854) described a mussel that he felt was different from *M. edulis* as found in Europe (this is specifically mentioned), and presumably also from *M. platensis* described only eight years earlier by d'Orbigny (1846) from Uruguay. So although Hupé does not specifically mention *M. platensis* in his description of *M. chilensis*, it is reasonable to assume that he was aware of d'Orbigny's (1846) description of *M. platensis* (Larraín et al. 2018). Consistent with the scientific practices of the day, it warranted specific status – *M. chilensis*.

Mussel phylogeography in the Southern hemisphere, specifically in Chile, but also in Argentina and Uruguay, has been based on the use of markers such as allozymes (McDonald et al. 1991, Toro et al. 2006, Borsa et al. 2012), diagnostic nuclear DNA regions (Daguin & Borsa 2000), RAPDs (Toro et al. 2004a), RFLPs (Toro 1998b, Toro et al. 2005, Westfall et al. 2010, Larraín et al. 2012, Oyarzún et al. 2016), microsatellites (Ouagajjou et al. 2011, Larraín et al. 2015), F mtDNA sequencing (Gaitán-Espitia et al. 2016), 16S rRNA sequencing (Astorga et al. 2015) and COI sequencing (Pickett & David 2018, Astorga et al. 2018) to obtain evidence about the macro- and micro-distributions of species. Based on this body of research, and very much depending on its interpretation, there is evidence of three *Mytilus* species on the Pacific coast and into the Strait of Magellan region. First, the Chilean mussel *Mytilus chilensis* (Hupé, 1854) has been reported from many locations (from 36°S to 54°S) along the southern Pacific coast of Chile (Toro et al. 2006, Santaclara et al. 2006, Larraín et al. 2012, Śmietanka & Burzyński 2017) and the Strait of Magellan (Oyarzún et al. 2016). Second, the mussel *Mytilus edulis* (Linnaeus, 1758) has been reported in southern Chile (McDonald et al. 1991, Hilbish et al. 2000, Santaclara et al. 2006, Fernández-Tajes et al. 2011). Oyarzún et al. (2016) reported a cline with a high proportion of mussel samples being classified as *M. edulis* from the east of the Strait of Magellan declining towards the west of the Magellan Channel. Third, the invasive Northern hemisphere *Mytilus galloprovincialis* (Lamarck, 1819) has been reported from the central coast of Chile (Daguin & Borsa 2000, Toro et al. 2005, Westfall & Gardner 2010, Borsa et al. 2012, Tarifeño et al. 2012, Pickett & David 2018) and also in the Strait of Magellan (Oyarzún et al. 2016). Despite all these data, the interpretation of the spatial distribution of native blue mussels around the coasts of South America is still controversial, complicated by a dispersive larval pelagic stage (four to five weeks), the ability of mussels to hybridise and the contribution that processes such as rafting may have on natural range expansion and gene flow between sites or regions (e.g., Ó Foighil et al. 1999, Miller et al. 2018). In addition, some species have been used for aquaculture, and the transfer of juveniles from a few sites of spat collection to the grow-out sites is another important human-mediated form of gene flow (Holmberg 2012, Astorga et al. 2018).

Argentina and Uruguay

On the Atlantic coast of South America, smooth-shelled blue mussels are present from the south of Brazil (Klappenbach 1965), along the coasts of Uruguay and Argentina south to Tierra del Fuego (Castellanos 1962, Amaro-Padilla 1967) and around Cape Horn. This Atlantic Ocean natural (native) distribution also includes the Falkland Islands (Davenport et al. 1984), but not apparently any other South Atlantic Ocean islands.

The native blue mussel from the Atlantic coast of South America (Uruguay) was first described by d'Orbigny in 1846 as *M. platensis*. As described previously, the situation on the Atlantic coast of South America and into the Strait of Magellan has received a lot of attention (but less than for Chilean mussels), based on a variety of different marker types. The native Argentine mussel *Mytilus platensis* (d'Orbigny, 1846) has been reported from Montevideo, Uruguay (34°50′S; 56°10′W) (Astorga et al. 2015), Mar del Plata, Argentina (38°10′S; 57°27′W) (Gaitán Espitia et al. 2016), Puerto Deseado, Argentina (47°45′S; 65°53′W) (Astorga et al. 2015) and along much of the Atlantic coast. *Mytilus edulis* has been reported from southern Argentina (McDonald et al. 1991, Hilbish et al. 2000, Santaclara et al. 2006, Fernández-Tajes et al. 2011), where (as noted previously) it forms a natural hybrid zone with *M. chilensis* in the Strait of Magellan (Oyarzún et al. 2016). Invasive Northern hemisphere *Mytilus galloprovincialis* has now also been reported from the central coast of Argentina (42°46′S; 64°59′W) (Zbawicka et al. 2018).

New Zealand

Smooth-shelled blue mussels of the genus *Mytilus* are distributed throughout New Zealand, from the Bay of Islands in the north (35°S), as far south as the Campbell Islands (52°S). This distribution includes all offshore (sub-Antarctic) islands, the Chatham Islands to the east and the three main islands – Stewart Island, the South Island and the North Island (Powell 1955, Morton & Miller 1968, Gardner & Westfall 2012, and references therein). This distribution spans 17° of latitude (1,800 km) and includes subtropical, warm temperate, cold temperate and subantarctic waters (Gardner 2004). For reasons that remain unclear (possibly related to environmental conditions), there is a major discontinuity in mussel distribution from 41°S to 35°S (Morton & Miller 1968, Gardner & Westfall 2012). A single New Zealand fossil valve has been dated to ~1 M ybp (references in Gardner 2004), an age that is consistent with molecular phylogenetic analyses that place the Southern hemisphere origin of so-called *M. galloprovincialis* between 0.84 M ybp (Gérard et al. 2008) and 1.2 M ybp

(Hilbish et al. 2000). Interestingly, this fossil valve considerably predates the estimate of Popovic et al. (2020) of an Australian (and therefore, by extension, a New Zealand?) origin of native blue mussels dating to 0.1–0.6 M ybp.

Based on shell morphometric differences, Powell (1958) described the native blue mussel from New Zealand as the endemic species, *M. aoteanus*. Powell (1958) differentiated the New Zealand *Mytilus* (the type locality is Wellington Harbour, in the North Island, which is important in the use of this binomial for New Zealand mainland and also offshore island locations) from native Australian *Mytilus* by variation in several shell traits, including dorsal slope (longer in New Zealand shells), hinge teeth (fewer in New Zealand shells), shape of the posterior retractor scar (narrower in New Zealand shells) and the anterior adductor scar (larger in New Zealand shells) (Figure 14). These are all relatively minor differences but were consistent enough across samples to convince Powell of a specific difference between native New Zealand and Australian shells. This status was subsequently reduced to subspecific status – *M. edulis aoteanus* – by Fleming (1959), who followed Soot-Ryen (1955) in the application of trinomial taxonomy, in large part because of the close similarity of shell form, habitat preference and zonal distribution of both Northern hemisphere *M. edulis* Linnaeus, 1758 and the many Southern hemisphere varieties. Many workers have employed this changing taxonomy over the years (e.g., Duff 1967, Morton & Miller 1968, Kennedy 1977).

Subsequent work based on both allozyme and nuclear DNA marker variation (e.g., McDonald et al. 1991, Sanjuan et al. 1997, Daguin & Borsa 2000) and also on fossil and middens remains (Gardner 2004) tended to highlight a degree of separation of native New Zealand mussels from reference Northern hemisphere *M. galloprovincialis*, but greater affinity to *M. galloprovincialis* than to any other Northern hemisphere species (Figures 5–7). Consistent with this, Hilbish et al. (2000) and Gérard et al. (2008), using 16S and COI sequencing, respectively, both noted the separation of New Zealand native mussels from Northern hemisphere mussels within a clade composed of all *M. galloprovincialis* (Figures 8 and 9). Overall, these findings resulted in calls for native New Zealand mussels to be recognised as a subspecies of Northern hemisphere *M. galloprovincialis* or as equivalent to (indistinguishable from) Northern hemisphere *M. galloprovincialis*. This taxonomy has been followed reasonably closely by most workers (e.g., Gardner & Kathiravetpillai 1997, Gardner 2000, Rogers 2003, Petes et al. 2007). However, on occasions, a broader geographic interpretation of New Zealand blue mussel taxonomy has been applied. For example, Morley & Hayward (2010), who noted the unstable taxonomy of New Zealand *Mytilus* sp., used the trinomial *M. galloprovincialis planulatus*, following Crowe (2010) who recorded this particular trinomial for mussels from Tasmania and southern Australia. Interestingly, Morley & Hayward (2010) describe an apparent range expansion of native New Zealand blue mussels around Auckland (36.8485°S, in northern New

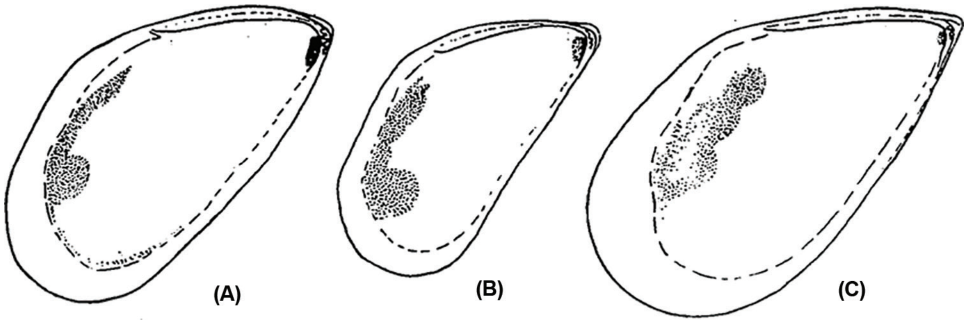

Figure 14 Examples of interior shell characteristics of native blue mussels from the Campbell Islands (at 52°S in the Southern Ocean), New Zealand (A), the Atlantic coast of the United States of America (B) and Tasmania, Australia (C). Taken from Fleming (1959).

Zealand), an area where it has traditionally been found in low abundance or not at all. It cannot be determined from their work whether this range expansion refers to native New Zealand mussels or to the morphologically very similar form of the invasive Northern hemisphere *M. galloprovincialis*: this would need to be tested with molecular markers.

Westfall et al. (2010), using a 16S RFLP assay, reported the presence of native New Zealand *M. galloprovincialis*-like mussels that were different from Northern hemisphere *M. galloprovincialis*. Based on Me15/16 results, they also reported the presence of two *M. galloprovincialis*/*M. edulis* hybrid genotypes, both from the Auckland Islands in the Southern Ocean (Westfall & Gardner 2010). A significant proportion of invasive Northern hemisphere *M. galloprovincialis* were reported from a number of different sites and regions, principally in the north of the country. Subsequently, using the Me15/16 and 16S RFLP assays, Gardner & Westfall (2012) reported a new meta-population of native New Zealand blue mussels (Southern hemisphere lineage of *M. galloprovincialis*) in the far north of the country. They also noted the presence of invasive Northern hemisphere *M. galloprovincialis* at many of these far north sites. Spencer et al. (2009), in their "Key to New Zealand molluscs" (last updated May 2017), and following a number of authorities, list the native New Zealand blue mussels as *M. galloprovincialis*.

Australia

In Australia, *Mytilus* is common in the temperate waters of southern Australia and around Tasmania, and extends into northern New South Wales (Cape Hawk or Port Stephens ~ 32.4°S) on the east coast, and to Perth at ~ 32.2°S on the west coast (Gardner & Westfall 2012, Dias et al. 2014, Ab Rahim et al. 2016 and references therein). At the moment, it is unclear whether this distribution is continuous or whether there exists a discontinuous distribution, with centres of distribution around southeastern and southwestern Australia, and an absence along the Great Australian Bight. This point needs checking and clarifying. Svane (2011) notes that in Australia, the blue mussel may be found on the rocky coastline of the temperate region "… but the species has until recently only been found in environments associated with marinas and harbours" (Svane 2011, p. 134).

Lamarck (1819) described multiple *Mytilus* species from Australian waters that at the time were called Nouvelle-Hollande (present day Albany, southwestern Australia), including *M. angustanus*, *M. corneus*, *M. planulatus* and *M. ungularis* (cited by McDonald & Koehn 1988). Because of morphological similarity of shells, Australian populations of *Mytilus*, including those from Tasmania, were, at times, considered to be *M. edulis* Linnaeus, 1758 (Wallis 1975). However, it is the name *M. planulatus* Lamarck, 1819 (Lamarck's type locality was King George Sound, Western Australia) that was extensively used, at least until the assessment of allozyme variation (e.g., Lamy 1936 in McDonald et al. 1991, McDonald et al. 1991, Sanjuan et al. 1997) and nuclear DNA markers (Daguin & Borsa 2000) for Australian mussels, at which time differences between Northern hemisphere *M. galloprovincialis* and native Australian mussels became less clear and often resulted in calls for subspecific status (i.e., *M. galloprovincialis planulatus*).

Allozyme variation in mussels from Australia was more similar in allele frequencies to *M. galloprovincialis* from the Northern hemisphere than to *M. edulis* (McDonald et al. 1991 – Figure 5). Sanjuan et al. (1997 – Figure 6) and Daguin & Borsa (2000 – Figure 7) both reported the separation of Australian mussels from their Northern hemisphere counterparts based on global analyses of *M. galloprovincialis* allozyme alleles. Daguin & Borsa (2000) also examined two nuclear DNA markers (*Glu-5′* and *mac-1*) in their study of global *M. galloprovincialis* populations and found that the *mac-1* allele *G* was diagnostic for Australian mussels, which led them to suggest that Australian *M. galloprovincialis* had mixed genetic architecture, with a high frequency of *M. edulis*-like and *M. galloprovincialis*-like alleles ("patchy genetic architecture") and was distinct from northern *M. galloprovincialis*. They suggested that native Australian *Mytilus* populations should be considered as a "regional subspecies of *M. galloprovincialis*". Sequencing of mitochondrial DNA led both Hilbish et al. (2000) and Gérard et al. (2008) to highlight the distinctness of native Australian mussels and their greater affinity to *M. galloprovincialis* than any other species among the Northern hemisphere reference taxa. Analysis of what was called native *M. galloprovincialis* from Tasmania revealed the presence of both *M. edulis* (at the *mac-1* locus) and *M. galloprovincialis* (at the *Glu-5′/Glu-3′* locus) allele frequencies that were nearly fixed, indicating a possible hybrid origin of these mussels (Borsa et al. 2007).

Westfall & Gardner (2010) combined the use of the Me15/16 and 16S RFLP assays to describe native mussels from Port Arthur (Tasmania) and Melbourne (Victoria) as Southern hemisphere *M. galloprovincialis*, and also reported the presence of introduced Northern hemisphere *M. galloprovincialis* at 10% and 20%, respectively. Phylogenetic analysis of COI sequence variation revealed the occurrence of Northern hemisphere *Mytilus* haplotypes in southeastern Australia populations (Colgan & Middelfart 2011) and based on F-type COI variation, in mussels from three hatcheries in South Australia, Victoria and Tasmania, and in four wild populations from Western Australia (Dias et al. 2014). Most recently, Ab Rahim et al. (2016) identified both native and introduced Northern hemisphere *M. galloprovincialis* in Australian populations. Svane (2011) hypothesised that Northern hemisphere *M. galloprovincialis* was introduced into Australia with the first ships that arrived from Europe, most probably into Western Australia which is the type location of *Mytilus* in Australia (i.e., *Mytilus planulatus* Lamarck 1819). Interestingly, Svane (2011) went on to suggest that native mussels in South Australia might have died out as a consequence of post-Ice Age climate change, only to be replaced by what we would now consider to be invasive *M. galloprovincialis* from Europe. However, as noted above, the results of several studies do not support this contention because all report a mix of what appears to be native and what are identified as invasive mussels. More recently, Pickett & David (2018) who analysed global records of COI variation noted that Tasmanian mussels did not share haplotypes with any other population and were even genetically isolated from nearby South Australian and New Zealand individuals (refer to Figure 31). Overall, these results are difficult to interpret, but strongly suggest that native blue mussels in Australia were originally only found in the southeast of the country, in particular in the island state of Tasmania. Today's disjunct distribution of blue mussels (if that is, in fact, what it is), in the southeast and the southwest of the country may reflect native (southeast) and introduced (southwest) mussels.

Offshore islands

Offshore islands in the Southern Ocean are usually characterised by high levels of endemism. However, this is not always the case for marine species capable of dispersal over large geographic distances. So the question of island endemism for mussels of the genus *Mytilus* remains unresolved, despite the fact that mussels have been reported from many, but not all, remote Southern Ocean islands, including some near to Antarctica. Whereas offshore islands such as the Falklands Islands (52°S, 58°W) have reasonably clear affiliations both in terms of geographic distance and biogeography with the neighbouring continent of South America (in particular with the Atlantic coast of Argentina), the situation is much less clear for the more remote Kerguelen Islands (49°S, 70°E) in the South Indian Ocean. To the best of our knowledge, there is no information about native blue mussels from any other island or island groups in the Southern Ocean.

Mussels from the Kerguelen Islands were described as belonging to the endemic species *Mytilus desolationis* by Lamy in 1936 and then *M. kerguelensis* by Fletcher in 1938 (if they are an endemic species, then Lamy's nomenclature will have priority). As discussed previously, the comparison of allozyme variation of the native Kerguelen mussels with *M. edulis* and *M. galloprovincialis* from the Northern hemisphere (Blot et al. 1988) revealed that all alleles found in Kerguelen Islands populations were also observed in Northern hemisphere *Mytilus* taxa, and the only real difference was in the number of rare alleles. No unique alleles were found in Kerguelen Island mussels. According to Blot et al. (1988, p. 246), these results indicated that *M. desolationis* is not a separate taxon, but rather a "semi-species in the super-species *M. edulis*". These allozyme results contrasted with the earlier description of karyotypic differences among *M. desolationis*, *M. edulis* and *M. galloprovincialis* (Thiriot-Quiévreux 1984). Later, McDonald et al. (1991) reported that mussels from the Kerguelen Islands and the Falkland Islands were not different from *Mytilus* populations in Chile and Argentina based on allozyme variation, and referred to them being *M. edulis*-like. These mussels were morphologically intermediate between Northern hemisphere *M. edulis* and *M. trossulus*, but they contained alleles characteristic of all three Northern hemisphere species but with the greatest similarity to *M. edulis* from the Northern hemisphere.

Analysis of 16S sequence variation of Kerguelen Island and Falkland Island mussels in comparison to Northern hemisphere *Mytilus* populations was inconclusive and indicative of the necessity of using markers with much higher resolution power (Hilbish et al. 2000). In contrast, analysis of COI sequence variation revealed that Kerguelen Islands mussels grouped with South American populations and created one subclade (Gérard et al. 2008). Analysis of what was called native *M. edulis* from the Kerguelen Islands by Borsa et al. (2007) revealed the presence of both *M. edulis* (at the *mac-1* locus) and *M. galloprovincialis* (at the *Glu-5′/Glu-3′* locus) alleles, indicating a possible hybrid origin of these mussels (i.e., reticulate evolution). The taxonomy of mussels from islands groups such as the Falkland Islands and, in particular, the Kerguelen Islands, has therefore been tangled and represents both a major challenge and a major opportunity to better understand Southern hemisphere phylogeography and also, possibly, hybrid speciation.

SNP markers applied to Southern hemisphere mussels – phylogeography, taxonomy and cryptic species

Single-nucleotide polymorphisms

SNPs are, as the name suggests, single base pair changes in a length of DNA (see reviews by Davey et al. 2011, DeFaveri et al. 2013, da Fonseca et al. 2016). Several different sets of SNPs have now been developed for use with *Mytilus* spp. (e.g., Zbawicka et al. 2012, Saarman & Pogson 2015, Araneda et al. 2016, Fraïsse et al. 2016, Mathiesen et al. 2017, Wilson et al. 2018, Popovic et al. 2020) and the number of papers describing results from SNP analyses, both in the Northern and Southern hemispheres, is increasing rapidly. SNPs are, most usually, nuclear DNA co-dominant variants, and as such may be very informative in terms of genetic variation, population genetic structure, gene flow (connectivity) and evolutionary processes such as hybridisation and introgression (Wenne et al. 2020), whereas the non-neutral SNPs may be informative about adaptation to environmental variation. In particular, SNPs are appropriate markers for the identification and analysis of genetic relationship between closely related species (Daïnou et al. 2016 and references therein). The application of SNPs to resolve taxonomic and biogeographic uncertainty within the *Mytilus edulis* species complex may well overcome the low genomic representativeness of markers such as allozymes, RFLPs and even DNA sequencing.

Chile

SNP markers have been applied to nine populations of mussels from Chile, spanning almost the entire natural distribution of ~2,500 km (Larraín et al. 2018). Consistent with the approach employed in other studies (Gardner et al. 2016, Zbawicka et al. 2018, 2019, 2021), a set of reference Northern hemisphere mussels (*M. trossulus* from the Pacific coast of Canada, *M. edulis* from the United Kingdom (Northern Ireland), *M. galloprovincialis* from Italy and Spain) and Southern hemisphere mussels (*M. galloprovincialis*-like from New Zealand) was also tested. In total, 338 mussels were assayed for variation at 49 informative SNP loci. Both neighbour-joining

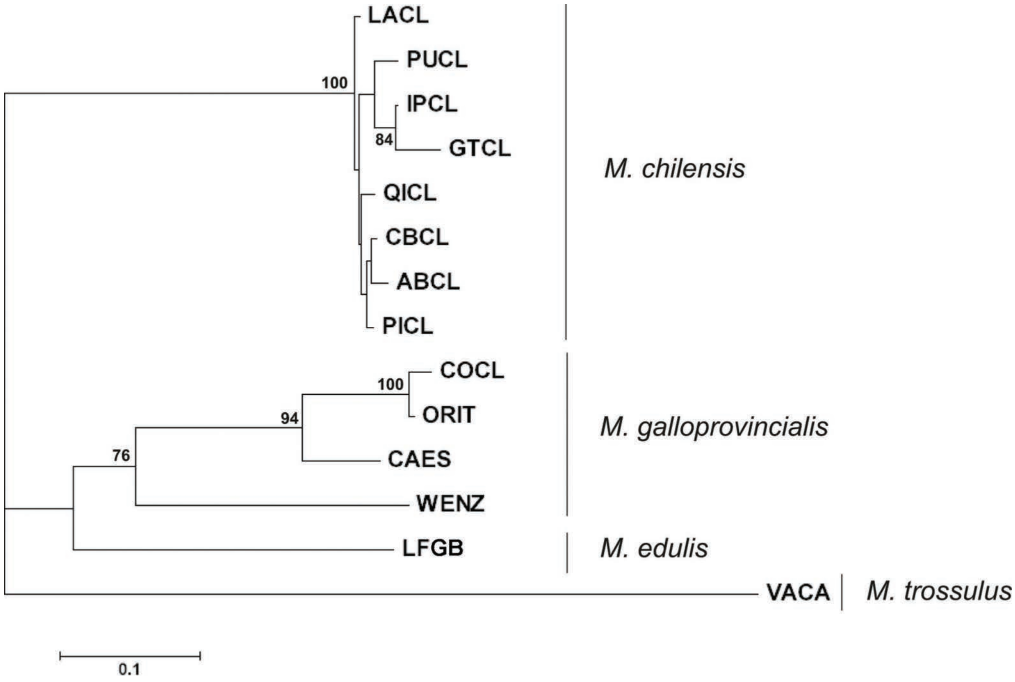

Figure 15 Neighbour-joining tree of *Mytilus* populations based on F_{ST} distance matrix for the analysis of nine Chilean populations using SNP markers. Taken from Larraín et al. (2018).

tree analysis (Figure 15) and also DAPC (not shown) revealed clear differences among the putative mussel species. The Northern hemisphere reference *M. trossulus* (VACA), *M. edulis* (LF) and the *M. galloprovincialis* (ORIT – Mediterranean Sea lineage, CAES – North Atlantic Ocean lineage) and the Southern hemisphere reference *M. galloprovincialis*-like mussels (WENZ) formed very distinct groupings. The Chilean population of Cocholgue (COCL) displayed clear evidence of being recently introduced Northern hemisphere *M. galloprovincialis*, most likely from the Mediterranean Sea. The eight "pure" Chilean populations formed a distinct group with 100% bootstrap support, which Larraín et al. (2018) identified as being native *M. chilensis*. Similarly, clear-cut results were reported for other analysis methods, including DAPC, assignment testing and Structure (Figure 16).

Depending on the criterion used (the value of minor allele frequency, MAF, ranging from >0.1 to > 0.4) as few as three SNP loci could be employed to accurately assign random individual mussels to their correct species designation.

Consistent with a range of reports from different workers employing different approaches, Larraín et al. (2018) concluded that their SNP markers provided unequivocal evidence of the differentiation of native Chilean mussels from all other reference mussels. That is, that the native mussel of the Pacific coast of South America is indeed *M. chilensis*, consistent with the designation provided by Hupé in 1854. Consistent with their application elsewhere, e.g., New Zealand (Gardner et al. 2016) and more recently Argentina (Zbawicka et al. 2018), Southern Ocean islands (Zbawicka et al. 2019) and also Australia (Zbawicka et al. 2021), the SNP panel quite clearly differentiates the native reference Northern hemisphere species (and the two *M. galloprovincialis* lineages), it identifies known cases of invasion (e.g., the Northern hemisphere *M. galloprovincialis* on northern Chile), it detects hybrids and backcrosses and it clearly identifies a distinct group of native Chilean mussels that must now be recognised as a separate species, *M. chilensis*.

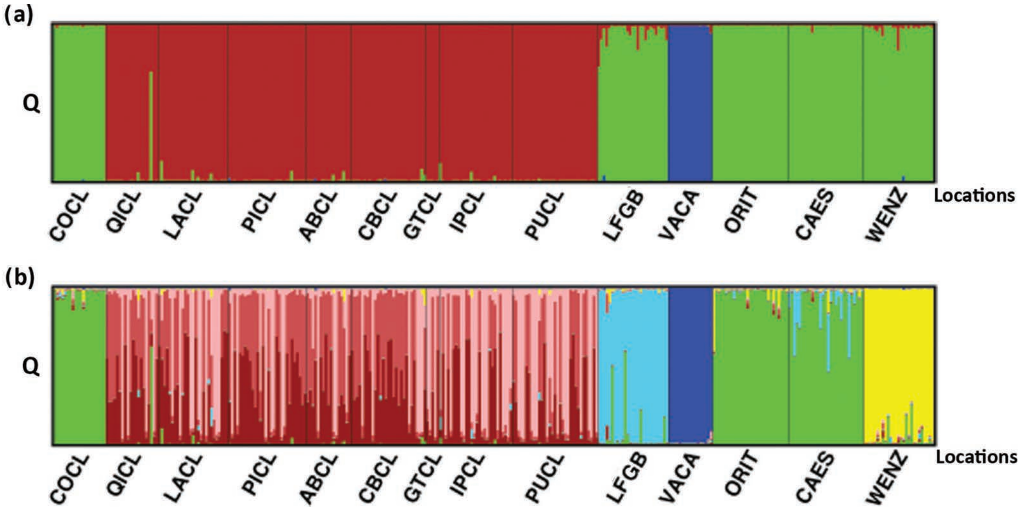

Figure 16 Structure plot showing proportional membership (Q) of each of three (panel a) and seven (panel b) clusters inferred from the analysis of nine Chilean populations using SNP markers. Population codes – COCL (Cocholgue, Chile), QICL to PUCL (Chile), LFGB (Lough Fyne, Northern Ireland, United Kingdom), VACA (Vancouver, Pacific coast of Canada), ORIT and CAES (Italy Mediterranean Sea and Spain Atlantic Ocean, respectively), WENZ (New Zealand). Colour codes for the groups – green is Northern hemisphere *M. galloprovincialis*, red-brown is *M. chilensis*, light blue is Northern hemisphere *M. edulis*, dark blue is Northern hemisphere *M. trossulus*, and yellow is Southern hemisphere *M. galloprovincialis*-like from New Zealand. Taken from Larraín et al. (2018).

Argentina and Uruguay

Fifty-one polymorphic SNP loci have recently been used to examine native smooth-shelled mussels along the Atlantic coast of South America and from Patagonia (Zbawicka et al. 2018). *Mytilus* spp. samples from ten localities in Argentina were analysed alongside reference samples from Northern and Southern hemisphere locations (e.g., Gardner et al. 2016, Larraín et al. 2018, Zbawicka et al. 2019, 2021). Correspondence analysis (CA) revealed clear distinction among five major groupings: reference *M. edulis* and *M. galloprovincialis* from the Northern hemisphere, *M. chilensis* from Chile, *M. galloprovincialis*-like Southern hemisphere mussels from New Zealand and *M. platensis* from the Atlantic coast of Argentina (Figure 17). The Argentinian Atlantic coast population of Puerto Madryn (PMD) sat in the middle of the plot, with no obvious affiliation to any of the five main groupings. Structure analysis (Figure 18) revealed that eight populations from Argentina clustered together (these are interpreted as being *M. platensis*). The sample from Ushuaia (Strait of Magellan) clustered with *M. chilensis* from Chile, consistent with interpretation of other workers (e.g., Oyarzún et al. 2016) of the existence of this species in the far south. All individuals in the Puerto Madryn (PMD) sample were identified as F2 hybrids (*M. platensis*×*M. galloprovincialis*), except one which was classified as invasive Northern hemisphere *M. galloprovincialis*. Zbawicka et al. (2018) suggested that European *M. galloprovincialis* had probably been introduced by ship traffic. Overall, *Mytilus* from Argentina is composed of three groups: native *M. platensis* (Atlantic coast south of Rio de La Plata), native *M. chilensis* in the south (area of Tierra del Fuego, Strait of Magellan) and hybrid individuals (native *M. platensis*×introduced *M. galloprovincialis*) in the vicinity of Puerto Madryn.

Neighbour-joining tree analysis (Figure 19) confirmed the differentiation of *M. trossulus* from all other groups, the known Northern versus Southern hemisphere split within the *M. galloprovincialis*-like mussels, the identity of the reference *M. edulis* and the separation of *M. chilensis* from *M. platensis*.

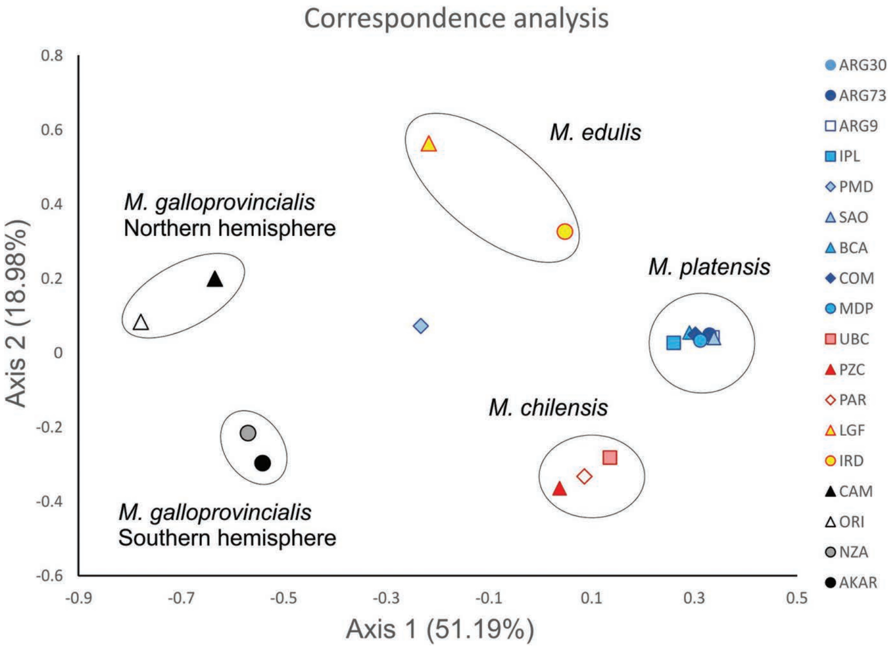

Figure 17 Correspondence analysis plot of mussel populations from the Atlantic coast of South America, with reference Northern hemisphere populations of *M. edulis* and *M. galloprovincialis* plus reference Southern hemisphere populations from Chile (Pacific coast of South America) and New Zealand, both the mainland and the offshore islands (Southern Ocean). Population codes – *M. platensis* ARG30, ARG73, ARG9, IPL, SAO, BCA, COM, MDP; mixed *M. galloprovincialis* and *M. platensis* – PMD; native mussels from Chile, *M. chilensis* – UBC, PZC, PAR; reference Northern hemisphere *M. edulis* – LGF, IRD; reference Northern hemisphere *M. galloprovincialis* – CAM, ORI; native New Zealand mussels, mainland – AKAR, offshore islands – NZA. Taken from Zbawicka et al. (2018).

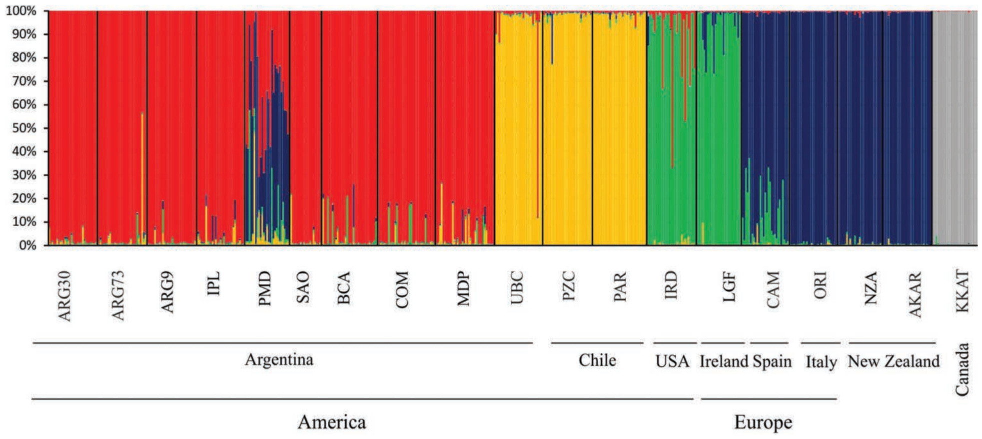

Figure 18 Structure plot ($k=5$) for ten Argentinian mussel populations (ARG30 to UBC), with the inclusion of reference populations. Colour groups: red=native *M. platensis* from Argentina; yellow=native *M. chilensis* from Chile (PZC, PAR); green=native Northern hemisphere *M. edulis* (IRD, LGF); blue=native Northern hemisphere *M. galloprovincialis* (CAM, ORI) plus introduced Northern hemisphere *M. galloprovincialis* in the Argentinian population of PMD and also native Southern hemisphere *M. galloprovincialis*-like mussels from New Zealand (NZA, AKAR); grey=native Northern hemisphere *M. trossulus* (KKAT). Taken from Zbawicka et al. (2018).

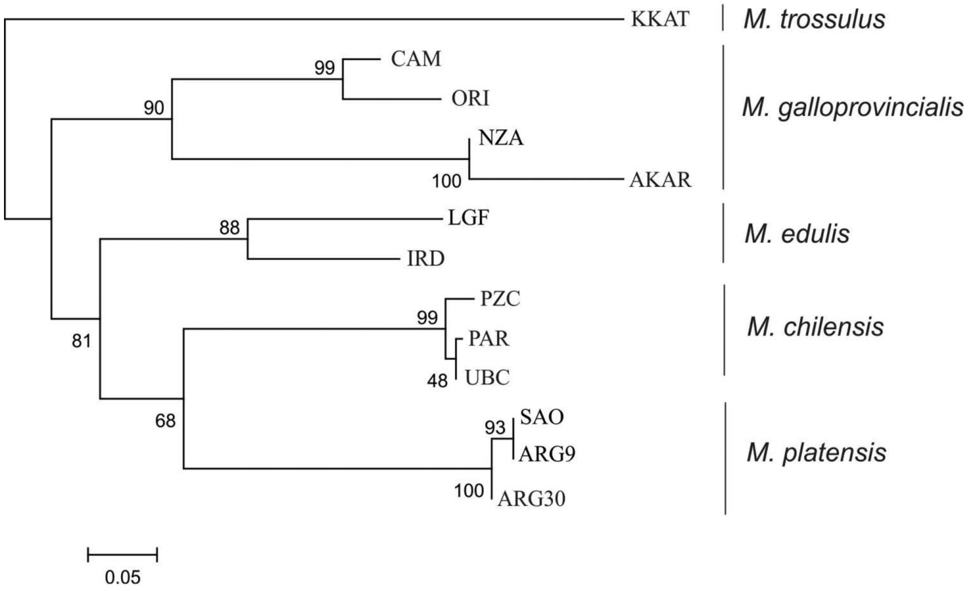

Figure 19 Neighbour-joining tree of *Mytilus* spp. samples from Argentina and reference populations of *M. edulis*, *M. trossulus*, *M. galloprovincialis* and *M. chilensis* from North America, Europe and New Zealand based on F_{ST} values. Tree constructed using individuals without admixture ($q>0.8$ or $q<0.2$) identified by Structure analysis ($K=5$). Taken from Zbawicka et al. (2018).

Overall, this study demonstrates that *M. platensis* and *M. chilensis* are clearly distinguishable native taxa in South America, the former from the Atlantic coast and the latter from the Pacific coast. In total, 19 SNP loci were involved in differentiating between native Argentine *M. platensis* and the mussels of all other regions. Five SNPs were identified as highly informative – BM106B, BM12A, BM151A, BM21B and BM6C – indicating that even relatively small panels of SNPs can be used to differentiate among species.

New Zealand

SNPs were applied to Southern hemisphere blue mussels for the first time from New Zealand (Gardner et al. 2016). This work built on the earlier use of microsatellite markers (Westfall 2010) and the application of the Me15/16 and 16S RFLPs to clarify the status of the native blue mussel and also the presence of invasive Northern hemisphere blue mussels (Westfall & Gardner 2010, Westfall et al. 2013). Mussels from 39 sites (= populations) were collected from throughout mainland New Zealand and also from the offshore islands, and their SNP profiles at 44 loci were compared against reference Northern hemisphere blue mussels (refer also to Larraín et al. 2018, Zbawicka et al. 2018, 2019, 2021). In total, 57 loci were assayed, but 13 were dropped because they were variable only in *M. trossulus* mussels and were therefore uninformative in the Southern hemisphere context.

A range of different analyses revealed clear and consistent differences among individual mussels and populations from different regions, with the New Zealand mussels being differentiated from Northern hemisphere reference taxa (Figure 20). The New Zealand mussels do not form a single homogeneous group, but in fact, three groups are apparent: (1) the remote offshore island mussels collected from the Auckland Islands and Campbell Islands are differentiated from all other mussels, (2) the Chatham Island mussels, all the South Island mussels and a limited number of North Island populations form a separate group and (3) several North Island populations, in particular those from the far north (the Bay of Islands) plus Wellington Harbour, are partially differentiated

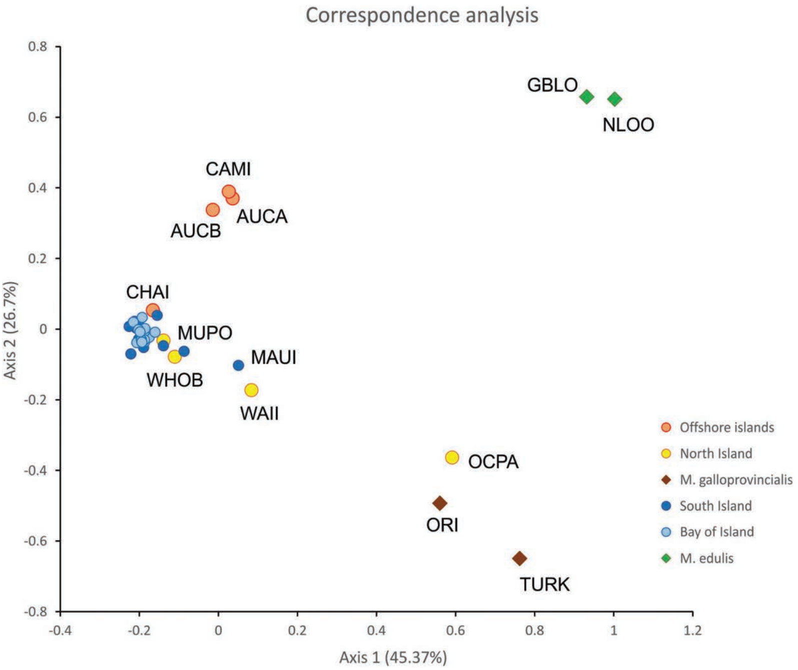

Figure 20 Correspondence analysis plot computed from the SNP data of two reference *Mytilus* spp. taxa (*M. edulis* – GBLO and NLOO – green diamonds; *Mytilus galloprovincialis* – ORI and TURK – dark brown diamonds), with all New Zealand mussel populations (offshore islands=orange circles; North Islands samples=yellow circles; South Island samples=blue circles). Each dot denotes a site sample. Note that in this figure, the reference *M. trossulus* from the Northern hemisphere have not been included because they are very different from all other mussels. OCPA=a moveable oil rig with Northern hemisphere *M. galloprovincialis* as biofouling. Taken from Gardner et al. (2016).

from all other mussels (refer to NJ tree – Figure 21). One sample collected from a moveable oil rig (OCPA) that had recently arrived in New Zealand from South Africa via Australia had biofouling mussels that were identified as Northern hemisphere *M. galloprovincialis*.

These analyses, with or without the inclusion of the reference *M. trossulus*, highlight the considerable differentiation of the New Zealand mussels from all reference mussels. The New Zealand mussels are at least as differentiated from the reference taxa as the three reference taxa are differentiated among themselves. This degree of separation raises questions about the specific status of the native New Zealand mussels. If the three reference Northern hemisphere taxa are now widely recognised as distinct species, then should not also the native New Zealand mussels be recognised as a separate species. And what then is the status of the remote offshore mussels, given that they too form a distinct grouping? While these two questions were not explicitly answered by Gardner et al. (2016), the application of SNPs to mussels from other Southern hemisphere locations helps to develop the picture and draws into focus the uncertain status of the native New Zealand mussels, both on the mainland and on the offshore islands.

The Structure plot (Figure 22) and the NewHybrids analysis both highlight the extent of hybridisation and introgression that is occurring within New Zealand between the native mussels and introduced Northern hemisphere *M. galloprovincialis*. While the majority of mussels (~90%) were identified as being native, ~10% were identified as being non-native or admixed (individuals of mixed ancestry). Nine individuals (~2%) were identified as pure Northern hemisphere *M. galloprovincialis*, and while no F1 hybrids were detected, ~9% of mussels were identified as F2 hybrids, and nine mussels were identified as being backcrosses to native New Zealand mussels.

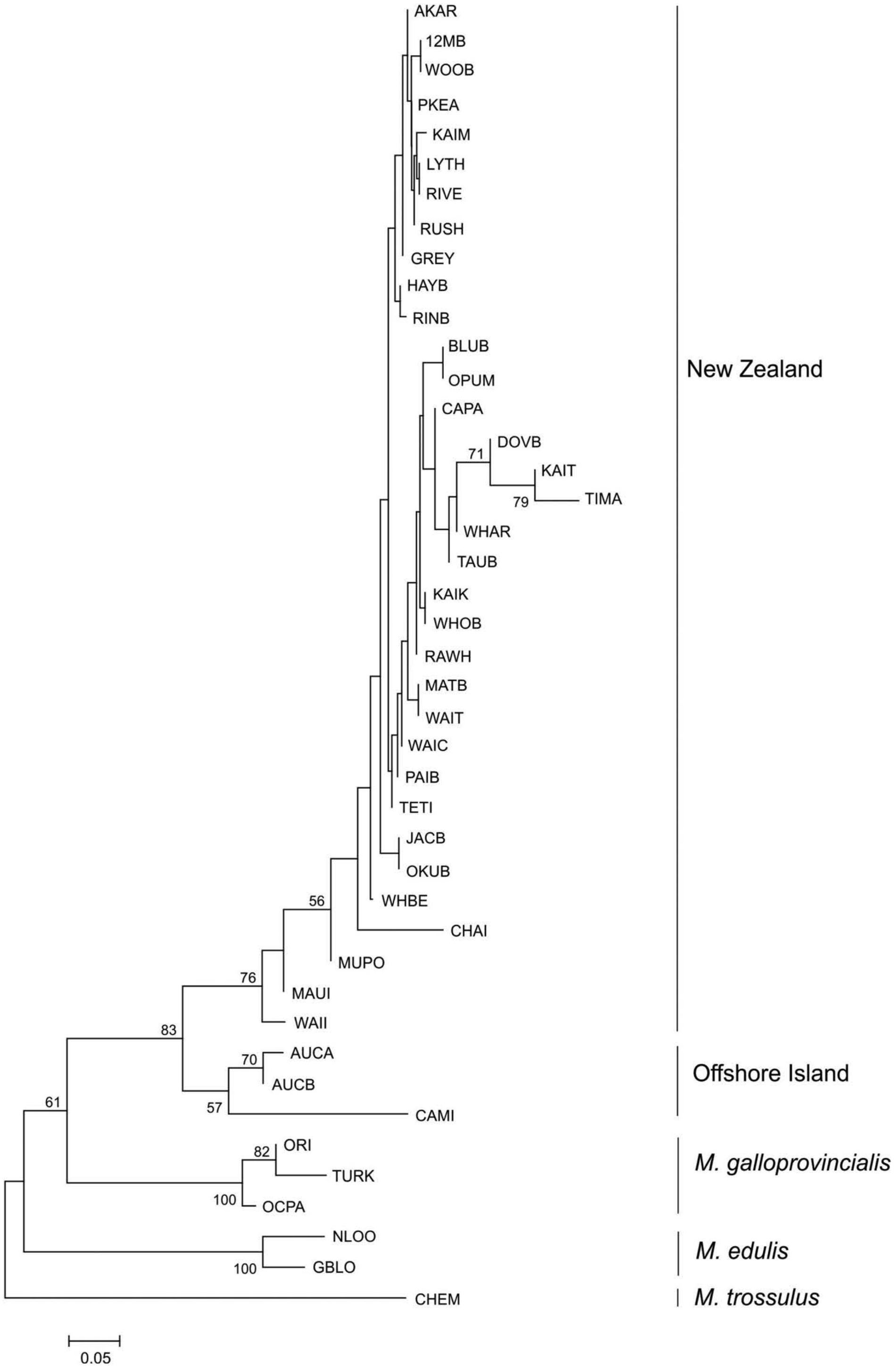

Figure 21 Neighbour-joining tree of 43 *Mytilus* populations from New Zealand and reference samples of *Mytilus edulis*, *Mytilus galloprovincialis* and *Mytilus trossulus* based on the F_{ST} distance matrix from allele frequencies of the SNP loci. Tree shows clear separation of all mainland and offshore New Zealand population samples from the three reference taxa. Taken from Gardner et al. (2016).

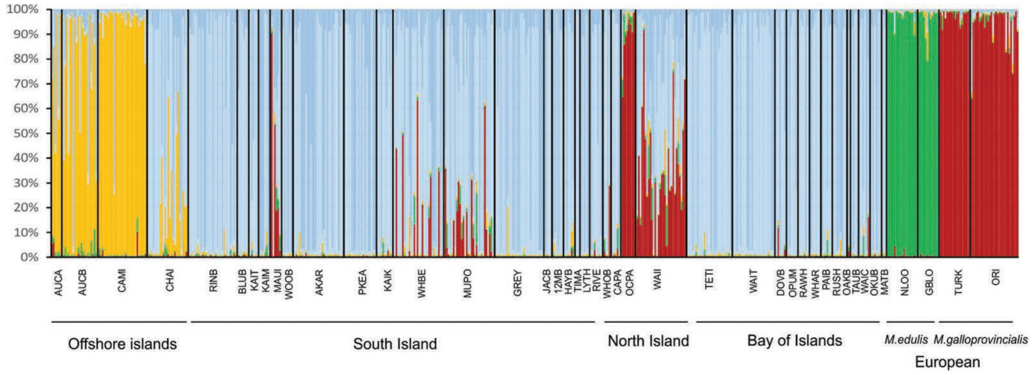

Figure 22 Plot from Structure analysis at $K=5$ showing group affinities of all New Zealand populations (the Southern Ocean offshore islands, South Island, North Island and the Bay of Islands), the two reference *Mytilus edulis* populations and the two reference *Mytilus galloprovincialis* populations. Taken from Gardner et al. (2016).

Interestingly, there was limited evidence of the presence of both *M. trossulus* and *M. edulis* alleles (but not actual mussels) within the populations of the two remote offshore island groups in the Southern Ocean, although an explanation of common ancestry for the SNP alleles in question is probably most likely.

Overall, the SNP analyses of the New Zealand mussels highlighted the considerable separation of the native mussels from the reference Northern hemisphere taxa and also the prevalence of hybridisation and introgression between the native mussels and the introduced Northern hemisphere *M. galloprovincialis*, in particular, in the north of the country, but also in proximity to the major port cities of Auckland, Wellington and Nelson.

Australia

Popovic et al. (2020) applied a panel of 20,509 SNPs to representative samples of Australian mussels from one site in Tasmania and two sites in New South Wales, to test for bioinvasion and to estimate the timing of origin of native Australian blue mussels. They identified the presence of invasive Mediterranean Sea lineage *M. galloprovincialis* in Sydney Harbour and North Atlantic lineage *M. galloprovincialis* at Batemans Bay, and also highlighted the distinct nature of the native Australian mussel, *M. planulatus*, from Tasmania. Unfortunately, this study did not include samples from Australia's west coast. The authors estimated the time of divergence of *M. planulatus* from Northern hemisphere *M. galloprovincialis* to 0.1–0.6 M ybp must likely under a model of historical gene flow followed by divergence in isolation.

SNP testing has been applied to mussel samples from ten localities in Australia, in comparison with reference taxa, to examine native Australian blue mussel species diversity, biogeography and taxonomy (Zbawicka et al. 2021). In total, results were obtained for 53 polymorphic SNPs for samples collected from the states of Western Australia, Victoria, New South Wales, South Australia and Tasmania.

CA revealed that native Australian mussels clustered together and distinct from the reference mussels (Figure 23). In fact, the Australian mussels exhibit the greatest affinity to Northern hemisphere *M. galloprovincialis* from the Mediterranean Sea, and then about equal affinity to Northern hemisphere *M. galloprovincialis* and to what is called Southern hemisphere Northern hemisphere *M. galloprovincialis*-like mussels from mainland New Zealand. Structure analysis (Figure 24) revealed that *Mytilus* in Australia is composed of two groups, native Southern hemisphere *M. galloprovincialis*-like (one sample from Tasmania that showed affinity with the reference

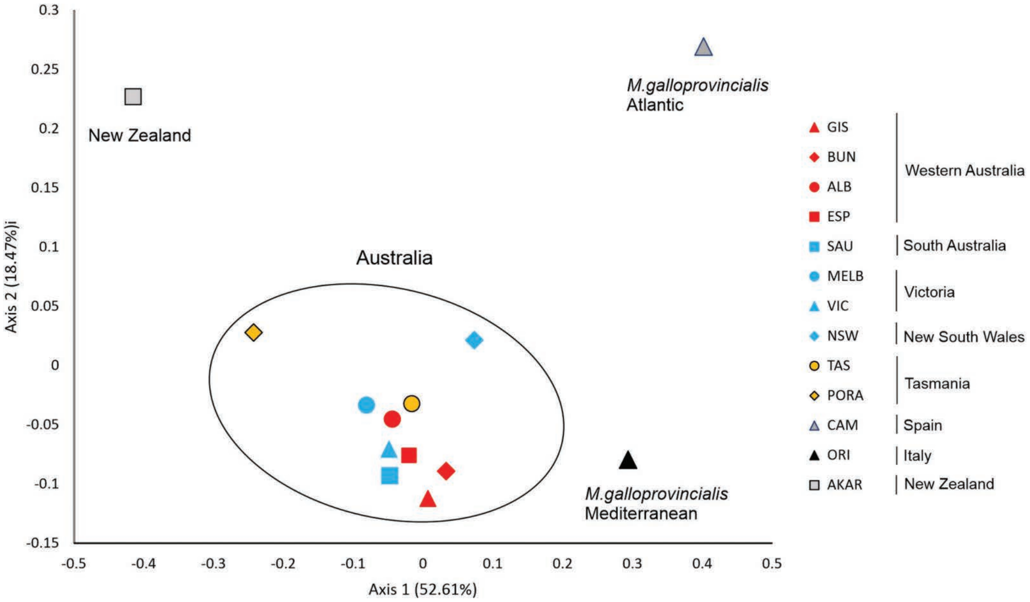

Figure 23 Correspondence analysis plot of mussel populations from mainland Australia and Tasmania, with inclusion of reference populations from the Northern hemisphere and New Zealand. Population codes: GIS=Garden Island, Western Australia; BUN=Bunbury, Western Australia; ALB=Albany, Western Australia; ESP=Esperance, Western Australia; SAU=Port Lincoln, South Australia; MELB=Melbourne, Victoria; VIC=Portarlington, Victoria; NSW=Eden, New South Wales; TAS=Spring Bay, Tasmania; PORA=Port Arthur, Tasmania; CAM=Camarinal, reference Northern hemisphere *M. galloprovincialis* from the Spanish Atlantic coast; ORI=Oristano, reference Northern hemisphere *M. galloprovincialis* from the Mediterranean Sea, Italy; AKAR=Akaroa, New Zealand mainland. Taken from Zbawicka et al. (2021).

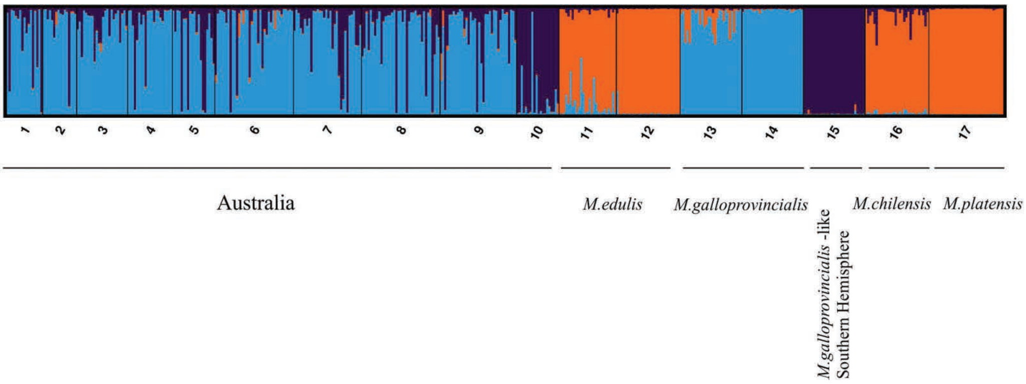

Figure 24 Structure plot ($K=2$) of SNP analysis of Australian mussels. Population codes: 1=ALB, Albany, Western Australia, 2=BUN, Bunbury, Western Australia, 3=ESP, Esperance, Western Australia, 4=GIS, Garden Island, Western Australia, 5=MELB, Melbourne, Victoria, 6=NSW, Eden, New South Wales, 7=SAU, Port Lincoln, South Australia, 8=VIC, Portarlington, Victoria, 9=TAS, Spring Bay, Tasmania, 10=PORA, Port Arthur, Tasmania, 11=reference Northern hemisphere *M. edulis* from Lough Foyle, Northern Ireland, UK, 12=reference Northern hemisphere *M. edulis* from Indian River, Delaware, USA, 13=reference Northern hemisphere *M. galloprovincialis* from Camarinal, Spain, 14=reference Northern hemisphere *M. galloprovincialis* from Oristano, Italy, 15=reference Southern hemisphere mussels from Akaroa, mainland New Zealand, 16=reference *M. chilensis* from Chiloé, Chile, 17=reference *M. platensis* from Comodoro, Argentina. Modified from Zbawicka et al. (2021).

native mussels from New Zealand) and hybrid individuals that showed very high levels of admixture in the other nine populations, that is Southern hemisphere *M. galloprovincialis*-like × Northern hemisphere *M. galloprovincialis*. GeneClass2 analysis of hybrid individuals confirmed the admixed status of the nine populations from the Australian mainland. NewHybrid analysis identified most admixed individuals from Australia as F2 hybrids. These SNP results tend to confirm the results of many of the earlier studies which suggest that the native mussels from Tasmania are distinct from mainland populations and that mainland Australian populations have experienced substantial introgression from invasive (introduced) Northern hemisphere *M. galloprovincialis*. The SNP analyses do, however, clearly point to the difference of the native Australian mussels from reference Northern hemisphere taxa.

Offshore islands

Having investigated native mussels from Chile, Argentina/Uruguay, New Zealand and Australia in the context of reference Northern hemisphere mussels using SNPs (Gardner et al. 2016, Larraín et al. 2018, Zbawicka et al. 2018, 2021), the situation for the remote offshore islands in the Southern Ocean is of particular interest. Zbawicka et al. (2019) examined mussels from the Falkland Islands, the Kerguelen Islands, the Auckland Islands, the Campbell Islands and also Tasmania, and obtained results from 53 polymorphic loci, in the context of SNP variation in reference Northern and Southern hemisphere mussels.

CA of the Chile, Argentina, Falkland Island and Kerguelen Island mussels revealed clear separation of samples based on geography (Figure 25a). Native mussels from the Falkland Islands and the Kerguelen Islands exhibited greater affinity to *M. platensis* from Argentina than to *M. chilensis* from Chile and were clearly separated from all other blue mussel groups of the Northern and Southern hemispheres. The native Tasmanian mussels (*M. planulatus*) clustered with native mainland New Zealand mussels (*M. aoteanus*) in a Southern hemisphere *M. galloprovincialis*-like group, distinct from all other groupings, while the New Zealand Southern Ocean island individuals formed their own cluster distinct from all other groupings, but sitting between the Southern hemisphere *M. galloprovincialis*-like mussels from mainland New Zealand and from Tasmania, and the *M. chilensis* cluster. CA carried out for individuals revealed that mussels from the Kerguelen Islands exhibited overlap with the *M. platensis* and *M. chilensis* individuals, whereas mussels from the Falkland Islands exhibited more overlap with *M. platensis* than with *M. chilensis* (Figure 25b). Finally, CA carried out for only reference *M. chilensis*, *M. platensis* and the mussels from the Falkland Islands and the Kerguelen Islands (these four groups were included to reveal maximum detail – Figure 25c) showed clear separation of the four mussel groups, but with samples from the Falkland Islands and the Kerguelen Islands showing greater affinity to *M. platensis* than to *M. chilensis*.

In the Structure analysis, the individual assignments of mussels from the Falkland Island, Kerguelen Island and Tasmanian samples were often revealed to be influenced by introgression (Figure 26). Most individuals from the Falkland Islands and Kerguelen Islands were assigned to *M. platensis*, while other individuals were considered potentially admixed (*M. chilensis* × *M. platensis*). In total, 94% of individuals were correctly assigned to their location of origin using GeneClass2, indicating the extent of genetic differentiation that exists among them. Potentially admixed individuals from the Falkland Islands and the Kerguelen Islands were assigned to their original location or to the Argentinian sample (*M. platensis*). These results point to a different evolutionary history for New Zealand Southern Ocean island plus Tasmanian mussels compared to the South American (Atlantic and Pacific coasts), Falkland Island plus Kerguelen Island mussels, consistent with earlier suggestions of two separate migration events from the Northern hemisphere into the Southern hemisphere (Hilbish et al. 2000; Gérard et al. 2008). Overall, these results reveal that Southern hemisphere island mussels have mixed genome ancestry and are native, not introduced by human activities. Zbawicka et al. (2019) suggested that the offshore island groups should be treated as separate

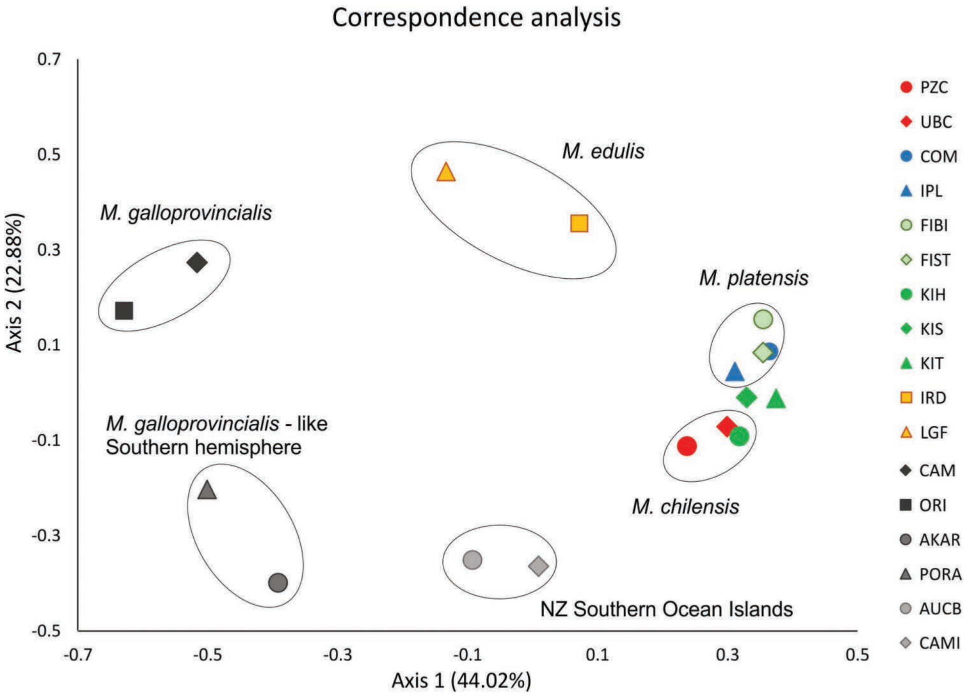

Figure 25a Correspondence analysis plot of Southern hemisphere island populations of native blue mussels, with inclusion of reference taxa populations from the Northern hemisphere. Population codes – Reference Northern hemisphere *M. edulis* – IRD=Indian River, Delaware, USA, Atlantic coast; LGF=Lough Foyle, United Kingdom, Atlantic Ocean; Reference Northern hemisphere *M. galloprovincialis* – CAM=Camarinal, Spain, Atlantic Ocean; ORI=Oristano, Italy, Mediterranean Sea; *M. chilensis* – PZC=Chiloé Island, Chile, Pacific Ocean; UBC=Ushuaia, southern Argentina, Strait of Magellan; *M. platensis* – MYBI – Bense Island, Falkland Islands, Atlantic Ocean; MYST – Port Stanley Wharf, Falkland Islands, Atlantic Ocean; KIH – Henri Bossiere Fjord, Kerguelen Islands, Indian Ocean; KIS – Ile Suhm, Kerguelen Islands, Indian Ocean; KIT – Ilot des Trois Bergers, Kerguelen Islands, Indian Ocean; Southern hemisphere *M. galloprovincialis* – PORA=Port Arthur, Tasmania, Australia, Pacific Ocean; AKAR=Akaroa, New Zealand, Pacific Ocean; Offshore islands – AUCB=Auckland Islands, New Zealand, Southern Ocean; CAMI=Campbell Islands, New Zealand, Southern Ocean; Note – in this figure there are no reference Northern hemisphere *M. trossulus* because all Southern hemisphere mussels were not found to be similar enough to them. Taken from Zbawicka et al. (2019).

evolutionary significant units for the purposes of protecting *Mytilus* taxa of the Southern hemisphere. The invasive Northern hemisphere *M. galloprovincialis* was identified only in Tasmania, among native mussels of a distinct Australian lineage. The preservation of distinct evolutionary lineages (or Southern hemisphere species) needs to be an ongoing focus of conservation efforts, given that population sizes on some of the remote offshore oceanic islands will be small and may be more easily adversely affected by invasion and subsequent hybridisation and introgression than larger populations elsewhere (Gardner et al. 2016).

In conclusion, the application of SNP markers to Southern hemisphere mussels has, as expected, provided much greater detail to the elaboration of smooth-shelled blue mussel diversity. While the earliest study of New Zealand mussels (Gardner et al. 2016) may not have been able to explicitly address the question of taxonomic rank for mainland or for offshore island mussels because of a lack of immediate context, subsequent studies (e.g., Larraín et al. 2018, Zbawicka et al. 2018, 2019, 2021) using both the same reference Northern hemisphere taxa and also some of the same Southern mussels as reference have provided much more context and greater certainty around taxonomic

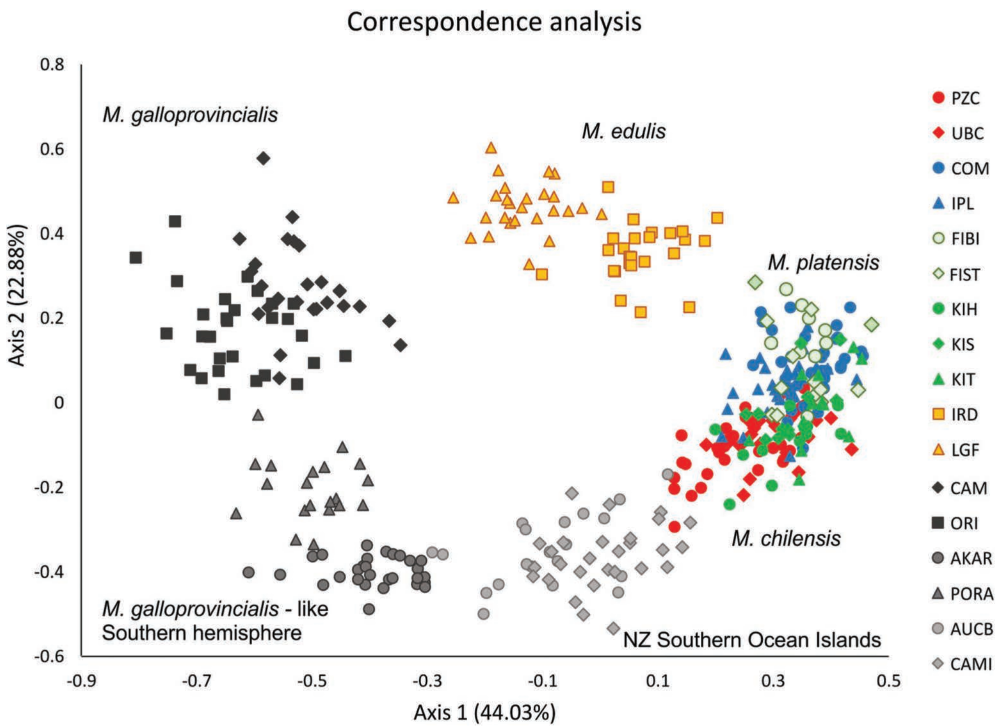

Figure 25b Correspondence analysis plot of Southern hemisphere island individuals of native blue mussels, with inclusion of reference taxa from the Northern hemisphere. Population codes – Reference Northern hemisphere *M. edulis* – IRD=Indian River, Delaware, USA, Atlantic coast; LGF=Lough Foyle, United Kingdom, Atlantic Ocean; Reference Northern hemisphere *M. galloprovincialis* – CAM=Camarinal, Spain, Atlantic Ocean; ORI=Oristano, Italy, Mediterranean Sea; *M. chilensis* – PZC=Chiloé Island, Chile, Pacific Ocean; UBC=Ushuaia, southern Argentina, Strait of Magellan; *M. platensis* – MYBI – Bense Island, Falkland Islands, Atlantic Ocean; MYST – Port Stanley Wharf, Falkland Islands, Atlantic Ocean; KIH – Henri Bossiere Fjord, Kerguelen Islands, Indian Ocean; KIS – Ile Suhm, Kerguelen Islands, Indian Ocean; KIT – Ilot des Trois Bergers, Kerguelen Islands, Indian Ocean; Southern hemisphere *M. galloprovincialis* – PORA=Port Arthur, Tasmania, Australia, Pacific Ocean; AKAR=Akaroa, New Zealand, Pacific Ocean; Offshore islands – AUCB=Auckland Islands, New Zealand, Southern Ocean; CAMI=Campbell Islands, New Zealand, Southern Ocean; Note – in this figure there are no reference Northern hemisphere *M. trossulus* because all Southern hemisphere were not found to be similar enough to them. Taken from Zbawicka et al. (2019).

distinctiveness, as well as hybridisation and introgression, and the presence of non-native taxa. The recent study of Popovic et al. (2020) has also highlighted the distinctness of native Australian mussels and shed light on the likely timing and mechanism of their origin.

How many Southern hemisphere mussel species are there?

Given the vast expanse of the Southern Ocean and the remoteness of many of its landmasses and small islands, it is not surprising that the marine biogeography of the Southern hemisphere is not as well understood as that of the Northern hemisphere. For example, a recent biogeographic study of Antarctic and sub-Antarctic intertidal communities reveals that species accumulation curves for the 11 best sampled regions are not even close to reaching an asymptote (Griffiths & Waller 2016). That is, there are many more new species (across all taxa and phyla) yet to be described.

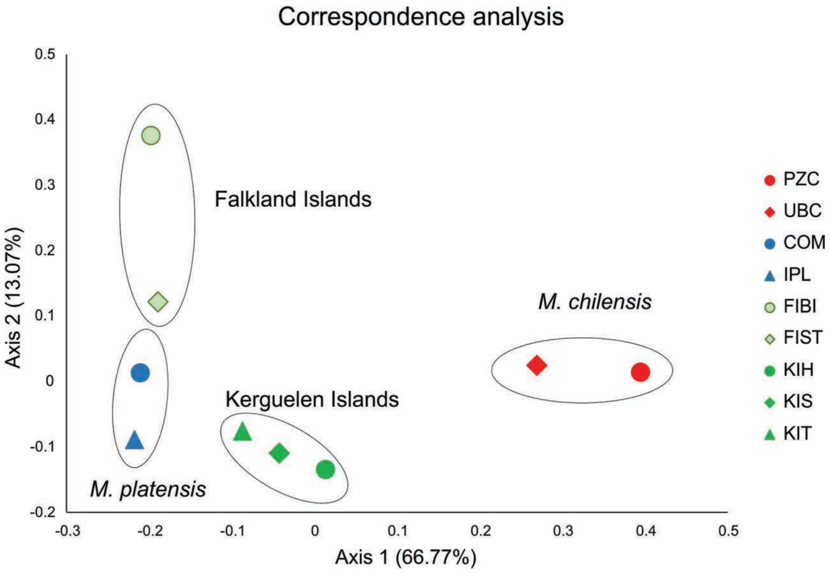

Figure 25c Correspondence analysis plot of Southern hemisphere island populations of native blue mussels from the Falkland Islands (Atlantic Ocean) and the Kerguelen Islands (Indian Ocean), with reference to native *M. chilensis* and *M. platensis* from South America. Population codes: *M. chilensis* – PZC=Chiloé Island, Chile, Pacific Ocean; UBC=Ushuaia, southern Argentina, Strait of Magellan; *M. platensis* – COM=Comodoro Rivadavia, Argentina, Atlantic Ocean; IPL=Isla de los Pajaros, Argentian, Atlantic Ocean; Falkland Islands – MYBI – Bense Island, Falkland Islands, Atlantic Ocean; MYST – Port Stanley Wharf, Falkland Islands, Atlantic Ocean; Kerguelen Islands – KIH – Henri Bossiere Fjord, Kerguelen Islands, Indian Ocean; KIS – Ile Suhm, Kerguelen Islands, Indian Ocean; KIT – Ilot des Trois Bergers, Kerguelen Islands, Indian Ocean. Taken from Zbawicka et al. (2019).

Held (2014) has noted the prevalence of cryptic marine species in the Southern hemisphere and how frequently such cryptic species may be recognised when molecular techniques are employed (e.g., Held 2003, Held & Wägele 2005, Janosik & Halanych 2010, González-Wevar et al. 2019). The general problem of crypticity in biological invasions has been reviewed by Jarić et al. (2019). As noted by Held (2014), even before the advent of molecular techniques, cryptic species were reported from the Southern Ocean using morphological evidence, and of course, this is as true of members of the genus *Mytilus* in the Southern hemisphere (e.g., Lamy 1936, Soot-Ryen 1955, Powell 1958) as it is for many other taxa. In fact, it has been suggested that the identification of cryptic species is now one of the main contributors to the discovery of new species in the Southern Ocean and elsewhere (Bickford et al. 2007). While such newly discovered and described species are an important contribution to our understanding of biogeographic patterns and evolutionary processes such as speciation, and perhaps also hybridisation and introgression, new taxonomies may have implications that extend far beyond taxonomy and systematics (Held 2014), reaching, for example, into fields such as conservation, biodiversity protection, aquaculture and food labelling, and biosecurity (e.g., Gardner et al. 2016, Larraín et al. 2018, Stanton et al. 2019, Zbawicka et al. 2021).

Three Northern hemisphere species are now universally recognised, *M. edulis*, *M. galloprovincialis* and *M. trossulus*. Based largely but not exclusively on the new SNP data, and applying the concept of evolutionary different lineages that maintain some form of genetic distinctness (identity) in the face of hybridisation and introgression as is now widely applied by many different workers, we suggest the following for blue mussels in the Southern hemisphere: *Mytilus chilensis* on the Pacific coast of South America, *M. platensis* on the Atlantic coast of South America, and *M. planulatus* from Australia should be recognised as three distinct species. The native mussels from the Kerguelen

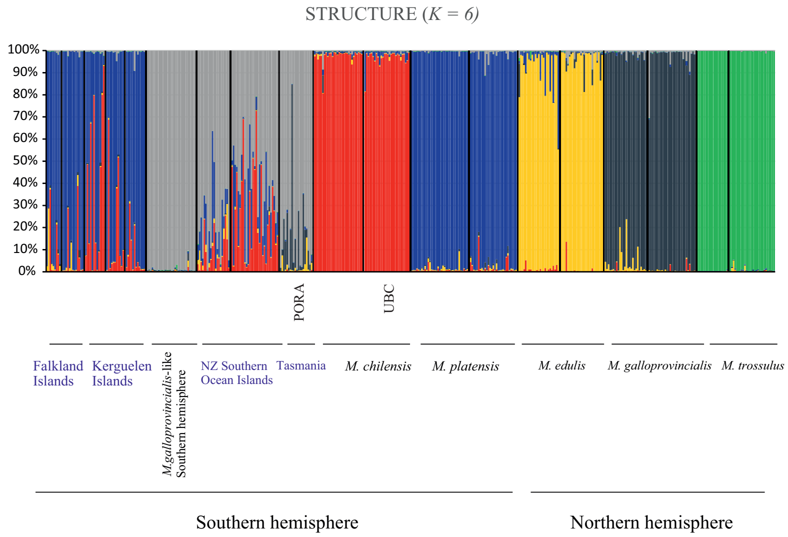

Figure 26 Structure plot (K=6) for 13 native Southern hemisphere and six reference Northern hemisphere mussel populations. Population codes – reference Northern hemisphere *M. edulis* – IRD=Indian River, Delaware, USA, Atlantic coast; LGF=Lough Foyle, United Kingdom, Atlantic Ocean; reference Northern hemisphere *M. galloprovincialis* - CAM=Camarinal, Spain, Atlantic Ocean; ORI=Oristano, Italy, Mediterranean Sea; *M. chilensis* – PZC=Chiloé Island, Chile, Pacific Ocean; UBC=Ushuaia, southern Argentina, Strait of Magellan; *M. platensis* – MYBI – Bense Island, Falkland Islands, Atlantic Ocean; MYST – Port Stanley Wharf, Falkland Islands, Atlantic Ocean; KIH – Henri Bossiere Fjord, Kerguelen Islands, Indian Ocean; KIS – Ile Suhm, Kerguelen Islands, Indian Ocean; KIT – Ilot des Trois Bergers, Kerguelen Islands, Indian Ocean; Southern hemisphere *M. galloprovincialis* – PORA=Port Arthur, Tasmania, Australia, Pacific Ocean; AKAR=Akaroa, mainland New Zealand, Pacific Ocean; Offshore islands – AUCB=Auckland Islands, New Zealand, Southern Ocean; CAMI=Campbell Islands, New Zealand, Southern Ocean. Taken from Zbawicka et al. (2019).

Islands and the Falkland Islands appear to have some sort of hybrid origin (they appear to be derived from reticulate evolution, e.g., Borsa et al. 2007, Zbawicka et al. 2019), are clearly different from populations of the geographically nearest land masses and appear to maintain separate genetic identities. As such, mussels from the Kerguelen Islands and from the Falkland Islands may now warrant specific status as *M. desolationus* Lamy, 1936. Mussels from the New Zealand subantarctic islands also show evidence of a hybrid origin, but it is different from that shown by the Falkland and the Kerguelen mussels (Zbawicka et al. 2019). The New Zealand offshore island mussels have previously been accepted as being the same as mussels from mainland New Zealand – that is, there has been, as far as we are aware, no separate binomial or trinomial applied to the New Zealand mainland versus the offshore island mussels. As such, the island mussels may warrant a new specific name, different from that applied to mussels that are native to mainland New Zealand and the Chatham Islands to the east. We note that Powell (1958) applied the binomial *M. aoteanus* to mussels collected from Wellington Harbour (type locality) as well as the Campbell Islands. Following the principle of avoiding taxonomic confusion (McDonald & Koehn 1988) we suggest that all New Zealand blue mussels (i.e., mainland plus offshore islands) are recognised as *M. aoteanus*. Future work may reveal that the hybrid origin of the offshore mussels requires taxonomic revision. Under this scenario, there are as many as six species of native Southern hemisphere mussels now to be recognised. We acknowledge that this will need further work and confirmation, and that not everyone will agree with this interpretation, but the data from multiple independent studies on which this conclusion is based are very strong.

The recent application of SNP markers to Southern hemisphere mussels has been enlightening. Despite the relatively recent evolutionary origin of all native Southern hemisphere mussels from their Northern counterparts, there are more clearly recognisable Southern hemisphere lineages that maintain their evolutionary identities despite hybridisation and the potential of natural gene flow among them than are recorded in the Northern hemisphere. The most likely explanation for this is not solely to do with evolutionary time, but is also a function of geographic distance. That is, building on a large body of research from many different workers, we suggest that *M. edulis* newly arrived from the Northern hemisphere settled somewhere on the modern-day coastline of Uruguay and/or Argentina and due to a relative absence of gene flow with their Northern hemisphere counterparts gave rise, via genetic drift and mutation, to *M. platensis*. This is the first (oldest) range expansion described by Hilbish et al. (2000). Either the original *M. edulis* or the more newly formed *M. platensis* then spread from the Atlantic to the Pacific coastline of South America, via the Strait of Magellan. The separation between the Pacific and Atlantic coasts, in conjunction with changes in global sea level and regional ice coverage, subsequently gave rise to *M. chilensis* in southern South America (the Strait of Magellan in Argentina and Chile) and along the Pacific coastline. The Atlantic *M. platensis*, with a small input from *M. chilensis* in southern South America, then gave rise to mussel populations on the Falkland Islands and the Kerguelen Islands. Subsequently, and consistent with previous suggestions (e.g., Hilbish et al. 2000, Gérard et al. 2008), there was a second independent invasion event from the Northern hemisphere involving *M. galloprovincialis* that gave rise to *M. planulatus* in Australia (e.g., Popovic et al. 2020) and, we speculate, also to *M. aoteanus* in New Zealand (the modern-day remote offshore Auckland Islands and Campbell Islands populations arose via reticulate evolution after the colonisation of the New Zealand mainland). The similarity of native Australasian mussels to Northern hemisphere *M. galloprovincialis*, and their difference to native South American mussels, as reported by multiple different studies over the years, provides strong supporting evidence for the original hypothesis proposed by Hilbish et al. (2000) of two independent invasion events from the Northern hemisphere.

Distances between the South American and the Australasian landmasses are sufficiently large (1000s of km), and the pelagic larval duration (PLD) of blue mussels is sufficiently short (typically four to five weeks) that gene flow between these regions was rare at best, but could have occurred infrequently via rafting and island hopping. This sort of pattern of island hopping has been described for other Southern Ocean species, including those that are strictly benthic and lacking a pelagic larval stage (Leese et al. 2010), and illustrates the impact and biodiversity importance of what has been called “founder takes all” (Waters et al. 2013). This genetic isolation across the Southern hemisphere allowed for the build-up of regional-specific genetic lineages that in time became new species (*sensu* Held 2014). This model of allopatric speciation for up to four species, in many ways, mirrors the model of allopatric speciation noted for the three North Atlantic species, after the loss of the connection with the North Pacific approx. 3.5 M ybp (Vermeij 1991), while the model of reticulate evolution (speciation by hybridisation) for up to two species on remote Southern Ocean islands is novel.

The role of hybridisation in speciation

It is frequently reported that wherever two or more smooth-shelled *Mytilus* species occur in sympatry they hybridise. The extent of this hybridisation, and any introgression and backcrossing that may follow, varies from region to region, for reasons that are not always understood (e.g., Rawson et al. 1999, Borsa et al. 2007, Brannock et al. 2009, Brannock & Hilbish 2010). Hybridisation as a process is potentially important in the evolution of new species, at least in part because it is thought to generate new genetic combinations (Darwin 1868, Harrison 1990, Mallet 2007). While hybrid unfitness may, in some cases, act against the formation of hybrid individuals (hybridisation often results in co-adapted gene complexes being broken up), in other cases the beneficial combination of genes from two different species may result in viable offspring and a new evolutionary lineage. Hybridisation in the sea is a reasonably common phenomenon across many marine phyla (Gardner 1997), and hybridisation within the genus *Mytilus* has been reported from many regions of the world wherever two or more species, native or introduced, co-exist (Skibinski et al. 1978, Skibinski 1983, Gardner & Skibinski 1988, Väinölä & Hvilsom 1991, Gardner 1994, 1997, Suchanek et al. 1997, Comesaña 1999, Rawson et al. 1999, Daguin et al. 2001, Gardner & Thompson 2001, 2009, Skurikhina et al. 2001, Penney et al. 2002, 2007, 2008, Toro et al. 2002, 2004a,b, 2006, 2012, Bierne et al. 2003, Gilg & Hilbish 2004, Riginos & Cunningham 2005, Braby & Somero 2006, Beaumont et al. 2008, Elliot et al. 2008, Shields et al. 2010, Oyarzún et al. 2013, 2016, Westfall & Gardner 2013, Roux et al. 2014, Zbawicka et al. 2014, 2018, Saarman & Pogson 2015, Ab Rahim et al. 2016, Wenne et al. 2016, to name but a few). The reason for the frequency of blue mussel hybridisation is likely to be the high degree of genetic similarity between pairs of species (or lineages) that results because of the young evolutionary age of the group. That is, the split since the most common recent ancestor (~3.5 M ybp) which is thought to be *M. trossulus* from the North Pacific Ocean (Riginos & Cunningham 2005) has not yet given rise to large and disruptive species-specific differences (i.e., non-compatible genomic combinations) that prevent hybridisation via pre- or post-fertilisation mechanisms. This ongoing divergence of the different lineages (sometimes defined as incipient speciation – e.g., Lawniczak et al. 2010, Andrew & Rieseberg 2013) allows for hybridisation and in many cases also introgression between pairs of species.

The role of reticulate evolution (i.e., introgressive hybridisation) as a mechanism promoting speciation (divergence) in the sea has been questioned given the often large body of evidence of extensive gene flow for many marine species (reviewed by Arnold & Fogarty 2009). Given the prevalence of hybridisation and introgression between pairs of species within the *Mytilus edulis* species complex, it is of interest to know just how important reticulate evolution may be for blue mussels (e.g., Borsa et al. 2007, Zbawicka et al. 2019), and it is also of interest to understand which parts of the genome are most actively involved. Several studies have described the karyotypes of different blue mussel taxa (the diploid number = 28) using a range of different approaches (e.g., Thiriot-Quiévreux 1984, 2002, Dixon & Flavell 1986, Martínez-Lage et al. 1995, 1996, Pérez-Garcia et al. 2014). The first report of polyploidy within the genus *Mytilus* was published for *M. trossulus* (González-Tizón et al. 2000) and as far as we aware this remains the only such report. It is surprising that little work has focussed on the role that chromosomal rearrangements may play in promoting or retarding interbreeding and/or speciation in blue mussels when so much research in this area has been carried out for other taxa (refer to Searle 1998, Edwards et al. 2016, Mallet et al. 2016, Potter et al. 2017, Fuller et al. 2018 and references therein). Notably, with the exception of the work by Thiriot-Quiévreux (1984), all analyses of *Mytilus* karyotypes have been conducted on taxa from the Northern hemisphere, meaning that we know nothing about the karyotypes of most Southern hemisphere blue mussel lineages/taxa. This is clearly an area that needs immediate attention, in particular given the role that chromosomal rearrangements may play in speciation.

Based on an assessment of allozyme (protein) and nuclear DNA (the *mac-1* locus) variation among mussels from the Kerguelen Islands and Tasmania (Australia) relative to reference Northern hemisphere taxa, Borsa et al. (2007) reported extreme interlocus variation in allelic composition. They interpreted this as evidence for the native origin of these Southern hemisphere mussels and also for past introgressive hybridisation that has given rise to the distinct differences between mussels from Tasmania (the Australasian grouping) and the Kerguelen Islands (the South American grouping). While it remains unclear how these patterns of introgression actually arose, the authors suggested that factors such as the founder effect, small effective population size, pseudo-selection (selection at a locus not specifically studied, but linked to the assayed locus) and partial (incomplete) reproductive isolation may have contributed to the hybrid origin of these present-day Southern hemisphere populations (Borsa et al. 2007).

Based on SNP variation, most regional meta-populations of native *Mytilus* spp. in the Southern hemisphere display clear differentiation from one another and also from reference Northern hemisphere taxa. Mussels of the Falkland Islands (South Atlantic Ocean), the Kerguelen Islands (South Indian Ocean), and the Auckland Islands and the Campbell Islands (South Pacific Ocean) all exhibit some form of intermediate (hybrid) status compared to mussels of the nearest main land masses. For example, mussels of the Falkland Islands have the greatest affinity to mussels from Argentina (*M. platensis*), but clearly exhibit a degree of introgression with mussels from Chile (*M. chilensis*) (Zbawicka et al. 2019). Similarly, mussels from the Kerguelen Islands exhibit the greatest affinity to mussels from Argentina (*M. platensis*), but exhibit a larger degree of introgression with mussels from Chile (*M. chilensis*), a finding which is surprising given the greater proximity of the Falkland Islands than the Kerguelen Islands to South America (Zbawicka et al. 2019). Mussels of the New Zealand Auckland Islands and the Campbell Islands exhibit the greatest affinity to the native mainland New Zealand group (*M. aoteanus*) but with lesser affinity to both *M. platensis* and *M. chilensis* (Zbawicka et al. 2019) (Figure 27).

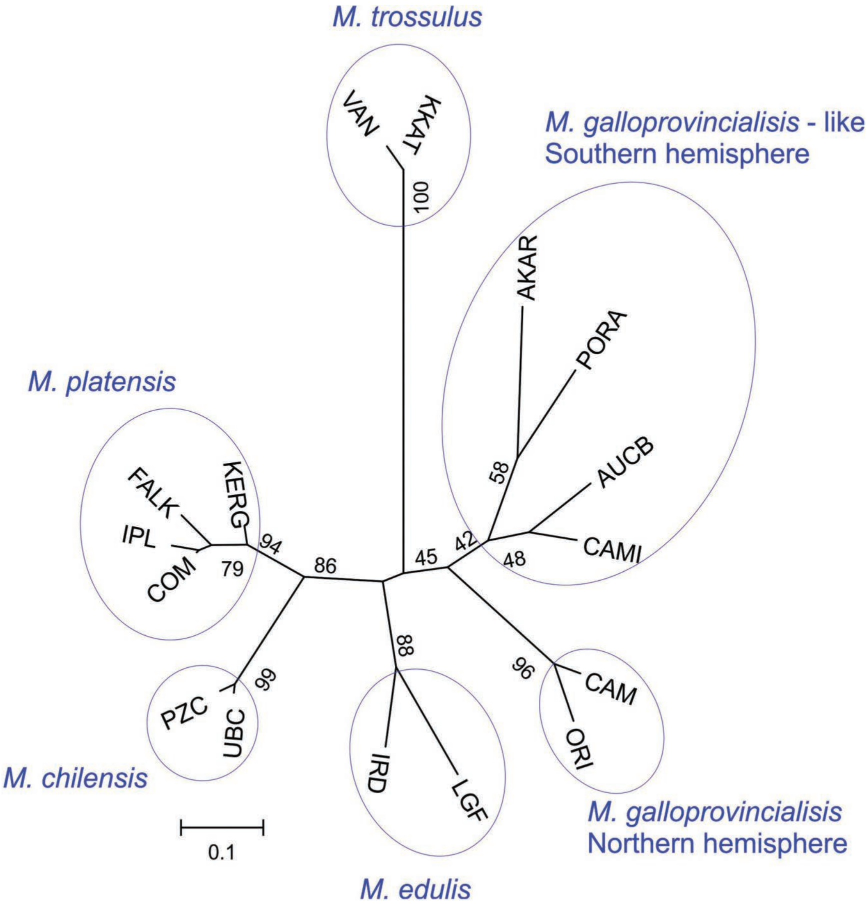

Figure 27 Neighbour-joining phylogenetic tree of SNP variation for Southern hemisphere mussel samples and reference Northern hemisphere samples based on F_{ST} variation. Population codes: *M. platensis* – KERG=Kerguelen Islands, Indian Ocean; FALK=Falkland Islands, Atlantic Ocean; IPL=Isla de los Pajaros, Argentian, Atlantic Ocean; COM=Comodoro Rivadavia, Argentina, Atlantic Ocean; *M. chilensis* – PZC=Chiloé Island, Chile, Pacific Ocean; UBC=Ushuaia, southern Argentina, Strait of Magellan; *M. edulis* – IRD=Indian River, Delaware, USA, Atlantic coast; LGF=Lough Foyle, United Kingdom, Atlantic Ocean; Northern hemisphere *M. galloprovincialis* – CAM=Camarinal, Spain, Atlantic Ocean; ORI=Oristano, Italy, Mediterranean Sea; Southern hemisphere *M. galloprovincialis* – CAMI=Campbell Islands, New Zealand, Southern Ocean; AUCB=Auckland Islands, New Zealand, Southern Ocean; PORA=Port Arthur, Tasmania, Australia, Pacific Ocean; AKAR=Akaroa, New Zealand, Pacific Ocean; *M. trossulus* – KKAT=Halifax, Canada, Atlantic Ocean; VAN=Vancouver, Canada, Pacific Ocean. Taken from Zbawicka et al. (2019).

The SNP analyses identify the existence of unique mussel lineages on the remote offshore islands that span the Southern Ocean in the higher latitudes (Falkland Islands ~ 51°S, Kerguelen Islands ~ 49°S, Auckland Islands ~ 50°S, Campbell Islands ~ 52°S). Levels of introgression for the Falkland Island, Kerguelen Island and Auckland Island plus Campbell Island mussels were estimated to be 23%, 25% and 73%, respectively (Zbawicka et al. 2019), which strongly suggests that hybridisation and the subsequent introgression of the different lineages (*M. chilensis* × *M. platensis* for the Falkland Islands and Kerguelen Islands populations; *M. aoteanus* × *M. chilensis* and also *M. aoteanus* × *M. platensis* for the Auckland Islands and Campbell Islands mussels) are moderately to very common. None of this reported hybridisation and introgression involves introduced Northern hemisphere species, but it all involves native Southern hemisphere species. However, despite this fact, it is not yet apparent whether all Southern hemisphere species arrived at these remote island locations independently (e.g., via rafting as adults or larval dispersal with the anticlockwise flow of the Southern Ocean – Zbawicka et al. 2019) or whether they benefitted from human-mediated (accidental) transfer. The latter is possible, given both the reasonably long history of sailing ship movement for trade and for whaling around the Southern Ocean and the reasonably frequent strandings or wrecking of ships on these remote islands (Gardner 2004, Gardner et al. 2016 and references therein).

The status of the Kerguelen Island mussels is particularly interesting, and several different studies using a range of different markers have highlighted their difference from reference Northern taxa and/or from other Southern hemisphere mussels (e.g., Thiriot-Quiévreux 1984, Blot et al. 1988, Hilbish et al. 2000, Borsa et al. 2007, Roux et al. 2014, Fraïsse et al. 2018). Lamy (1936) described Kerguelen mussels as a distinct species, *M. desolationis*, based on shell characters alone. Several studies have placed the Kerguelen mussels within or closest to the South American mussel grouping, and distinct from Australasian mussels. This mixed ancestry led Borsa et al. (2007) to suggest that the Kerguelen mussels are a product of reticulate evolution (i.e., they have a hybrid origin), a finding that is strongly supported by the most recent SNP analyses (Zbawicka et al. 2019). We can add to this short list the mussels of the Falkland Islands which show similar mixed ancestry, although this seems to be slightly less complicated than the story for the Kerguelen mussels (Borsa et al. 2007) and also the mussels for the New Zealand offshore islands (Zbawicka et al. 2019).

Ultimately, the role that hybridisation and/or introgression may have played in the speciation process of Southern hemisphere blue mussels remains unclear, but there is now a body of evidence that shows that hybridisation and introgression have occurred and are important, although the timing of these events is unknown. Thus, Southern hemisphere mussels from these remote island groups are presently defined by different lineages that are clearly derived from hybridisation and some extent of introgression. As such, the island groups provide a rare opportunity to examine reticulate evolution among evolutionarily young lineages to better understand speciation in the sea. Whether the mussels of the Falkland Islands, the Kerguelen Islands and the NZ offshore islands are distinct species or not, remains to be seen. This matter may be resolved by the use of species delimitation models, the application of new molecular markers (e.g., Ryu et al. 2012, Quattrini et al. 2017, 2019) or greater depth of coverage of SNPs, perhaps involving hundreds or even thousands of loci (e.g., Smith et al. 2020).

Traces of M. trossulus *in the Southern hemisphere*

The traditional view, based on a range of different analyses, is that *M. trossulus* is the oldest of the three *Mytilus edulis* species complex species and that this species is absent from the Southern hemisphere (e.g., McDonald et al. 1991, Hilbish et al. 2000, Gérard et al. 2008). However, there is a small, but growing body of evidence that points to the existence of *M. trossulus*, or at least *M. trossulus*-like alleles, in mussels of the Southern hemisphere. The first report is from Fernández-Tajes et al. (2011) who noted the presence of two *M. chilensis* × *M. trossulus* hybrids in a can of mussels purchased from a local supermarket in Spain and labelled as *M. galloprovincialis* from Galicia, northern Spain. It is unclear what exactly has happened here, but it very much looks as if mussels from Chile (hence the *M. chilensis* component) have been canned and sold in Spain as *M. galloprovincialis*. The confirmed presence of *M. chilensis*×*M. trossulus* hybrids in the can therefore raises the possibility of *M. trossulus* or *M. trossulus*-like genes being present in Chile. Given that there may be only 10 or 12 mussels in a can, this puts the abundance of *M. chilensis*×*M. trossulus* hybrids at ~16%–20%. This might be as far as the story goes, had it not been for the fact that soon after this event, Larraín et al. (2012), using the Me15/16 RFLP assay, reported the presence of *M. chilensis*×*M. trossulus* hybrids from wild mussel populations in Chile. They reported the hybrids (two individuals in each case) from four separate sites (two sites are mussel collecting centres, two are mussel on-growing centres), three on the Chilean mainland and one on the island of Chiloé, which is a major aquaculture centre. Within any given population, the *M. chilensis*×*M. trossulus* hybrids reached a maximum frequency of 4%, but across all 11 populations, they reached only ~1.5% frequency. Subsequently, Astorga et al. (2015) failed to record *M. trossulus* or its hybrids in their survey of Chilean mussel populations, whereas Oyarzún et al. (2016) noted the presence of *M. trossulus*×*M. galloprovincialis* and also *M. trossulus*×*M. chilensis* hybrids at very low frequencies at two separate sites in the Strait of Magellan region. These records, from a range of different groups, working at different sites and using different molecular markers suggest that *M. trossulus* or at least its alleles may be found at very low frequencies in some locations in southern Chile. Clearly, this topic warrants further attention, but the most simple explanation right now is that the supposed "*trossulus*" alleles are not definitively from *M. trossulus*, but actually represent an ancestral shared state.

At New Zealand's remote offshore islands in the Southern Ocean, Gardner et al. (2016) reported the presence of SNP alleles present in *M. trossulus* and reaching moderately high frequencies at the Auckland Island and the Campbell Island sampling locations. They noted, however, that no hybrids involving *M. trossulus* were observed. They highlighted the difficulty faced by workers when trying to determine the presence of "invasive" alleles from, for example Northern hemisphere *Mytilus* populations, because such alleles may not be invasive at all but may be an ancestral polymorphism that reflects the close evolutionary histories of the species. On balance, Gardner et al. (2016) concluded that there was no evidence of *M. trossulus* or its hybrids in New Zealand. Similarly, no evidence was found of *M. trossulus* or its hybrids in mussel samples collected from the Atlantic coast of South America (Zbawicka et al. 2018), from Southern Ocean islands including the Falkland and Kerguelen islands (Zbawicka et al. 2019), or from mainland Australia or Tasmania (Zbawicka et al. 2021).

In conclusion, the range of analyses carried out to date across the Southern hemisphere points to a limited presence of *M. trossulus* alleles and/or hybrids in the Southern hemisphere. It remains to be determined whether this is a reflection of anthropogenically mediated invasion, whether it reflects a natural and historical range expansion, perhaps from the North Pacific Ocean into the South Pacific Ocean (e.g., Lindberg 1991) or whether it is simply a matter of a shared ancestral polymorphism that has not yet been completely recognised as such. Further work addressing these different points will help to clarify the situation and may well provide new insight into Southern hemisphere phylogeography or invasion dynamics (natural or anthropogenically mediated) from the Northern hemisphere.

Are any more new Mytilus *species likely to be identified in the Southern hemisphere?*

Native blue mussels are widely distributed throughout the Southern Ocean, being present on all major land masses except Antarctica and South Africa (Figure 28). While recording the presence of native blue mussels is easy on major land masses, recording their presence or absence on each of the numerous small, isolated islands of the Southern hemisphere is much harder. Knox (1960, p. 592)

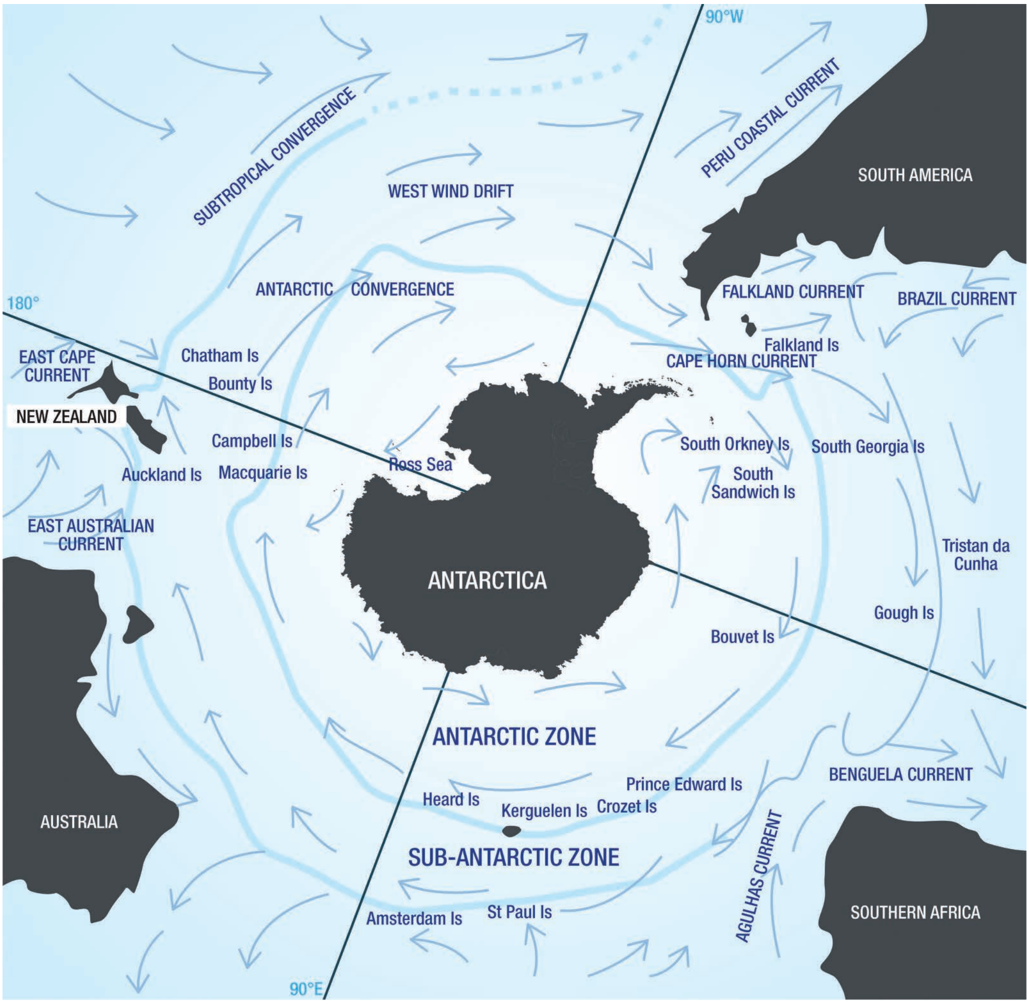

Figure 28 Map of the Southern Ocean showing major landmasses and remote offshore islands in the context of major oceanographic features (Antarctic Convergence, Subtropical Convergence) and major currents.

notes that Southern hemisphere blue mussels occur "… throughout the subantarctic cold temperate of South America and in Kerguelen and the Auckland and Campbell Islands. It appears to be absent from all the other subantarctic islands". Powell (1965) notes that blue mussels are common in most subantarctic waters but are conspicuously absent from Antarctic Seas. The absence of blue mussels has been specifically recorded from Heard Island (Dell 1964) and from Macquarie Island, the Australian territory and the subantarctic island closest to Antarctica (Powell 1957, Dell 1964, Powell 1965). Finding any sort of record of the presence or absence of native blue mussels on the other remote Southern Ocean islands is very difficult, and it seems likely that our knowledge of native *Mytilus* sp. biogeography in the Southern hemisphere is still incomplete, despite recent new work on the subject (e.g., Griffiths & Waller 2016). Thus, there exists the possibility of further new discovery of native blue mussels on remote Southern Ocean islands, although, on balance, we suggest that the likelihood of this appears to be low.

Examination of the biotas of the remote Southern Ocean islands presents new opportunities for hypothesis testing about the biogeography and routes of distribution of native blue mussels in the Southern hemisphere. For example, a large body of data indicate that general patterns of current flow, and therefore of colonisation route, are from west to east, following the Antarctic Circumpolar Current (ACC) (Arnaud 1974, Waters 2008, Leese et al. 2010, Zbawicka et al. 2019). For example, Powell (1965) suggests that the Kerguelen, Crozets, Marion and Prince Edward, Macquarie and possibly Heard and Bouvet islands all belong to the Kerguelenian province within the subantarctic region. Thus, the presence of native blue mussels on one island (e.g., the Kerguelen Islands) may be viewed as a likely source population for blue mussels to the east. With the application of the most recent SNP markers and new analyses testing for unidirectional gene flow (e.g., Sundqvist et al. 2016), it is now possible to test this hypothesis, both in terms of direct migration and colonisation by one mussel group, and in terms of the role of hybridisation (reticulate evolution) in the speciation process.

The use of species delimitation models

Much of biological systematics is based on phylogenetic inference and the theory of species concepts. Thus, the main objectives in systematics have usually been (1) to discover monophyletic groups (clades) and relationships within them at all hierarchical levels above species and (2) to discover lineages (i.e., species) at lower levels (Sites & Marshall 2003). While much of the discipline of systematics has been devoted to the first objective, the second, until very recently, has been largely ignored (Wiens 2007), even though species are routinely used as the basic units of analysis in biogeography, ecology and conservation biology (e.g., Agapow et al. 2004, Padial et al. 2009). However, delimiting species is difficult and is often based on qualitative assessment (Hey 2001a,b) rather than on any robust (i.e., repeatable) quantitative assessment. To help address this problem, Sites and Marshall (2003) proposed several empirical ways of delimiting species. This arises because of the need to distinguish between an ontological definition of the species (non-operational) versus what is operative, with data necessary to prove its reality (Frost & Kluge 1994). However, it was only reasonably recently that de Queiroz (2007) emphasised the distinction between a General Lineage Concept (GLC = metapopulational lineages that evolve separately, or more specifically, segments of such lineages) and the secondary biological attributes or properties of organisms that permit the empirical quantification of the status of a species. This is a crucial distinction because it clearly separates the conceptual problem from the methodological issues to delimit the species. This differentiation greatly aided the growth of the empirical species delimitation (SD) concept.

Species delimitation (SD) is a topic of growing interest in evolutionary biology (e.g., Pons et al. 2006, Knowles & Carstens 2007, Flot et al. 2010, Ence & Carstens 2011, Puillandre et al. 2012, Zhang et al. 2013, Jones et al. 2014, Yang & Rannala 2014, Leaché et al. 2014, Kapli et al. 2017). The incorporation of coalescence models to SD has been one of the most significant advances in this area (Carsten & Dewey 2010, Harrington & Near 2012). By applying probabilistic models, coalescent-based SD provides clear and objective testing of alternative hypotheses of evolutionary independence. In the last decade, several methods of coalescent-based species delimitation (CSD) have been developed, which have been adopted quickly by researchers and have facilitated the discovery and description of an important number of cryptic species (Camargo & Sites 2013), when cryptic species have long been a challenge for systematics and taxonomists (reviewed by Bickford et al. 2007). However, the increase in the findings of cryptic species has prompted further searches for them often targeted at groups where there are known taxonomic problems (e.g., bivalves of the family Pinnidae – Lemer et al. 2014; freshwater mussels – Huang et al. 2019). As such, smooth-shelled blue mussels are also a group that would benefit from the SD approach (Oyarzún et al. 2021).

Although CSD has been widely used in recent years, reproductive isolation-based species delimitation (RISD – following Mayr 1942, Dobzhansky 1970) has been the approach with which the largest number of metazoan species has been delimited (Coyne & Orr 2004). These methods focus on the quantifiable characters of reproductive isolation (i.e., success of fertilisation, viability of offspring, gametic differences, etc.). For example, in molluscs, the morphological characters of spermatozoa have been used in systematic and phylogenetic studies because the ultrastructure of the gametes is highly conserved at the species level (e.g., in the Mytiloidea (Bivalvia) – Kafanov & Drozdov 1998; differences of the sperm ultrastructure in the *Mytilus edulis* complex – Oyarzún et al. 2014). The theoretical basis is that the process of speciation involves acquiring reproductive barriers and that during this process, there are intermediate states where inter-specific hybrids may eventually emerge (Mallet 2005). So, based on information to hand today, what approach should we use for delimiting or identifying smooth-shelled blue mussels or any other group? It is probably more convenient to study the limits of species using molecular methods than by estimating the characteristics of reproductive isolation, since the generation and analysis of molecular data do not require any prior knowledge of the anatomy, ecology or behaviour of the taxa involved. Nevertheless, both approaches should be able to detect species in groups such as the *Mytilus edulis* species complex.

A species complex is a concept referring to a group of closely related species that share morphological and physiological characteristics, to the extent that the boundaries between them are unclear (Steyskal 1972). Several terms are used as synonyms to refer to a species complex, although some of them may be slightly different such as “cryptic species” or “sibling species” or “ring species” (Alcaide et al. 2014, Pereira & Wake 2015). In a phylogenetic context, a complex of species is a group that has a common ancestor (it is not always so – Steinfartz et al. 2000) and that is characterised by the fact that the time of divergence between the lineages is recent, as has happened with the *Mytilus edulis* complex (e.g., Hilbish et al. 2000, Gérard et al. 2008, Popovic et al. 2020). These species have few inter-specific differences; therefore, the lineages of these groups are located within the first speciation criterion in the so-called grey zone of the divergence representation (Figure 29) (*sensu* de Queiroz 2007). These are the characteristics that have been observed in the *Mytilus edulis* complex in the Northern and Southern hemispheres, and which have contributed to the absence of a universally accepted taxonomy of the different evolutionary lineages.

The “species” is considered one of the most important units in biology because the knowledge of a group of organisms is built on this unit (Gascon et al. 2015). As such, the empirical SD has not been exclusively of interest to evolutionary biologists and taxonomists, but is also of interest to other disciplines. For example, the species delimitation concept has direct relevance in many different areas of management. Thus, biosecurity measures are imposed by governments to protect countries from the threat of invasive species (e.g., Northern hemisphere *Mytilus galloprovincialis* – GISD 2012) linked to the high traffic caused by trade (Cook et al. 2015). In this sense, cryptic species categorised as invasive have been a problem for biosecurity authorities, particularly due to the lack of taxonomic knowledge in some groups (Armstrong & Ball 2005). As discussed elsewhere in this review, invasive blue mussels pose ecological, economic and evolutionary problems on arrival and establishment (Gardner et al. 2016 and references therein). Beyond this, there is also the question of food labelling and traceability that relies on accurate descriptions of species for production statistics, reporting and consumer protection and confidence (e.g., European Normative, Regulation (CE) No. 104/2000 and No. 2065/2001 – Ogden 2008, Muehlbauer et al. 2014) given that smooth-shelled blue mussels are the basis of the aquaculture industry in many countries (Smaal 2002, FAO 2015, Larraín et al. 2018, Zbawicka et al. 2021). Finally, from a biodiversity protection and conservation perspective the description of species contributes to the understanding of ecosystem biodiversity and relationships between communities (Gazis et al. 2011). For example, Rissler and Apodaca (2007) identified cryptic species and then developed a method to assess the ecological suitability of the contact zone between lineages to understand how appropriate a habitat is and to predict certain ecological events. It is expected that the application of SNP data to species delimitation will dramatically improve the power, cost-effectiveness and utility of the SD process (e.g., Leaché et al. 2014) across a range of disciplines. In the context of the recognition of regional species within the global *Mytilus edulis* species complex (e.g., Oyarzún et al. 2021), we anticipate that the SD approach will provide much more clarity, given its solid theoretical framework and also the objective and

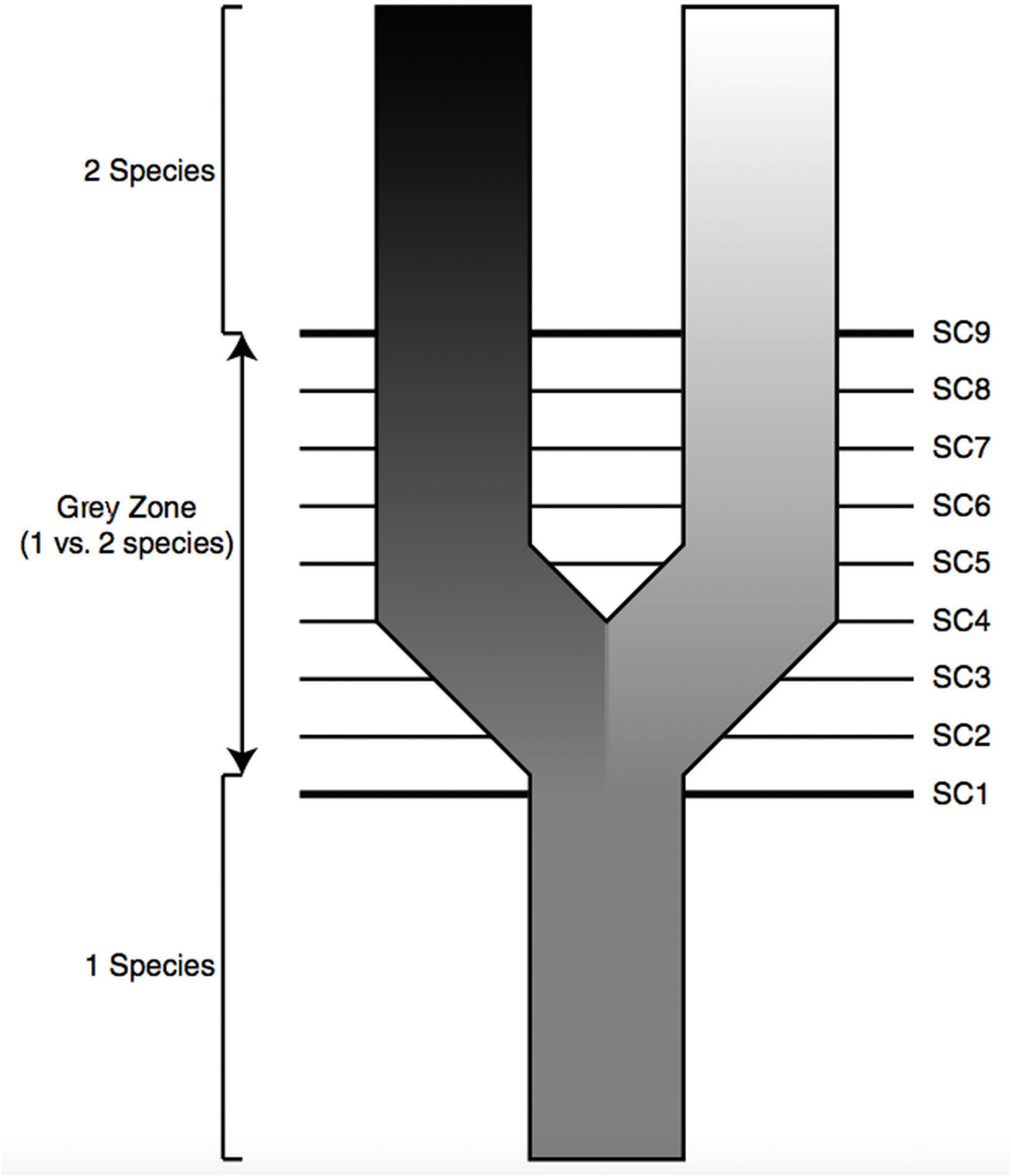

Figure 29 Graphic illustrating the concept of lineage separation and divergence (speciation). This highly simplified diagram represents a single lineage (species) splitting to form two lineages (species). The gradations in shades of grey represent the daughter lineages diverging through time, and the horizontal lines labelled SC (species criterion) 1–9 represent the times at which they acquire different properties (i.e., when they become phenetically distinguishable, diagnosable, reciprocally monophyletic, reproductively incompatible, ecologically distinct, etc.). The entire set of properties forms a grey zone within which alternative species concepts come into conflict. On either side of the grey zone, there will be unanimous agreement about the number of species. Before the acquisition of the first property, everyone will agree that there is a single species, and after the acquisition of the last property, everyone will agree that there are two. In between, however, there will be disagreement. The reason is that different contemporary species concepts adopt different properties (represented by the horizontal lines) as their species criteria – that is, as their cut offs for considering a separately evolving lineage to have become a species. Taken from de Queiroz (2007).

repeatable decision-making mechanisms that underpin its use. While it may be wishful thinking to believe that the SD approach will have all the answers or that all researchers will agree with SD outcomes, we suggest that this approach will prove to be an important next step in recognising species of the smooth-shelled blue mussel complex.

Physical oceanography explains Southern hemisphere blue mussel biogeography

The SNP analyses of native mussels from Chile (Larraín et al. 2018), Argentina (Zbawicka et al. 2018), New Zealand (Gardner et al. 2016), remote offshore islands (Zbawicka et al. 2019) and from Australia (Popovic et al. 2020, Zbawicka et al. 2021) reveal distinct native blue mussel species based on genetic differences maintained in the face of gene flow. The physical oceanography of the Southern Ocean explains these regional distributions.

As a brief recap, we note that the molecular data suggest that native Northern hemisphere blue mussels (most probably *M. edulis*) migrated into the Southern hemisphere ~1 M ybp (1.2–0.8 M ybp) via a North Atlantic route (Hilbish et al. 2000, Gérard et al. 2008). Based on geographic proximity, this strongly suggests that the first major region to be colonised in the Southern hemisphere was South America, and most likely that would have been along the Atlantic coast of modern-day Uruguay and Argentina (giving rise to *M. platensis*). Spread from this point of invasion and establishment would have occurred, most likely involving range extension into Patagonia, through the Strait of Magellan, and into modern-day Chile (giving rise to *M. chilensis*). A second major blue mussel invasion (this time of *M. galloprovincialis*), also via the North to South Atlantic Ocean route, is indicated by the molecular data, but its timing is uncertain. Popovic et al. (2020) have recently suggested that this event occurred between 0.1 and 0.6 M ybp. This gave rise to the Australasian group of mussels (*M. planulatus* in Australia and *M. aoteanus* in New Zealand), but this invasion bypassed South Africa. At some stage, offshore islands such as the Falkland Islands, the Kerguelen Islands, the Auckland Islands and the Campbell Islands were colonised, while others such as Macquarie Island and South Georgia Island were not. This hemisphere-wide pattern of distribution, as well as the natural absence of *Mytilus* mussels from South Africa, can be explained by the physical oceanography of the Southern Ocean.

In the Southern hemisphere, the predominant direction of oceanic flow is west to east (Figure 28) and numerous authors have commented on the effect that this has on biogeographic patterns across many different taxa and also on patterns of gene flow within species. This flow may promote migration directly when larvae are transported during a pelagic dispersal phase or indirectly when post-metamorphic individuals are distributed via rafting (e.g., Mortensen 1933, Fell 1962, Edgar 1987, Helmuth et al. 1994, Ó Foighil et al. 1999, Hobday 2000, Barnes 2002, Thiel & Gutow 2005a,b, Thiel & Haye 2006, Waters 2008, Leese et al. 2010). Numerous studies have described patterns of species, abundance that are consistent with a pattern of west to east flow and that these greatly outnumber examples of east to west flow (e.g., Griffiths et al. 2009, Leese et al. 2010, Griffiths & Waller 2016). Numerous authors have also noted how features such as the ACC and the Polar Front (PF) explain, at least in part, patterns of separation between regions (i.e., the ACC and the PF may often act as barriers to gene flow and connectivity). For example, Gérard et al. (2008) noted that despite the fact that the Kerguelen archipelago is isolated by the ACC and the PF, this effect is not permanent, with the result that occasional latitudinal shifts in the locations of the two features may have allowed for connection between the archipelago and South America (Hollyday and Read 1998). Thus, despite the very large area of the Southern Ocean and the remoteness of many of its islands, temporal changes to the location or the strength of the ACC or PF, or events with a low probability of success such as a raft with associated biota arriving at a new location, may be particularly important, if infrequent, occurrences that contribute to contemporary patterns of biogeography.

Most of the Southern hemisphere current flow is at the mid-latitudes – typically in the region 40–50°S – and as such it connects all major landmasses in the Southern hemisphere, except South Africa, the southern tip of which (Cape Agulhas) is located at 34°49′20″S20°1′0″E. That is, Cape Agulhas is too far north of the predominant west to east flow in the Southern Ocean to have received mussels from South America as they expanded their Southern hemisphere distributions < 1 M ybp (or if mussels did arrive in modern-day South Africa, they did not survive and left no record of their arrival).

The Southern hemisphere's only natural *Mytilus* spp. hybrid zone – the Strait of Magellan

Hybrid zones are locations of high genetic diversity and may give rise to novel genetic variants that may ultimately contribute to the process of speciation (Harrison 1990, Gardner 1997, Abbott et al. 2013). Because of the circumstances that give rise to natural hybrid zones (a zone of sympatry between two reproductively compatible species), these are of evolutionary importance as well as being a conservation management challenge.

Wherever two smooth-shelled blue mussel species co-occur, they hybridise and hybrid zones between *Mytilus* species that naturally occur and those resulting from the anthropogenic introduction of a non-native species have been described extensively in the Northern hemisphere, including from the Pacific and Atlantic coasts of North America (McDonald & Koehn 1988, Bates & Innes 1995, Comesaña et al. 1999, Rawson et al. 1999, Elliott et al. 2008, Toro et al. 2004a), from northwestern Europe and the Baltic Sea (Skibinski et al. 1978, Gardner & Skibinski 1988, Väinölä & Hvilsom 1991, Wilhelm & Hilbish 1998, Bierne et al. 2003, Gilg & Hilbish 2004, Hilbish et al. 2012, Simon et al. 2019), from Japan (Inoue et al. 1997, Brannock et al. 2009, Brannock & Hilbish 2010), and the White Sea region of Russia (Skurikhina et al. 2001).

The Magellan Region in southern Chile is characterised by a unique system of fjords and channels. Specifically, the Strait of Magellan is a complex natural channel that connects the Pacific and Atlantic Oceans. Along this Strait, molluscs of the genus *Mytilus* are the most important macroinvertebrates of the intertidal and subtidal benthic fauna (Aldea & Rosenfeld 2011). This southern region of South America has been little studied, is an area of high conservation value given the biotic differences between the Pacific and Atlantic oceans, and is one of the three recognised Antarctic provinces (Thatje & Mutschke 1999).

Using three nuclear DNA molecular markers (ITS, Glu-5′/Glu-3′ and Me15/16), Toro et al. (2005) reported the presence of what they called *M. edulis*, *M. galloprovincialis* and their hybrids from locations within the middle part of the Strait of Magellan. Larraín et al. (2012), using the Me15/16 RFLP, reported the presence of only *M. chilensis* from one site (Isla Peel) in southern Chile. More recently, Oyarzún et al. (2016) used two mitochondrial-DNA and one nuclear-DNA RFLP assays (16S, COI and Me15/16, respectively) that allowed the identification of the native Pacific Ocean blue mussel, *Mytilus chilensis*, the native Atlantic Ocean blue mussel, which they called *Mytilus edulis*, as well as invasive mussel haplotypes, *M. galloprovincialis* and *M. trossulus* to assay mussels from the Strait of Magellan. The native South American mussel of the Pacific coast, *Mytilus chilensis*, occurred at high frequency (up to 100%) at eight of nine locations, within the Strait of Magellan. The form of the hybrid zone followed a classic cline model. The percentage of *M. chilensis* decreased from 97% in the west to 0% in the most eastern location, reflecting the diminishing influence of gene (larval) flow from the Pacific towards the Atlantic. In contrast, a high percentage of *M. edulis* (now recognised to be *M. platensis*) was detected towards the Atlantic side of the Strait of Magellan, from 14% to 97% in three sampled sites within 100 km. It is hypothesised that *M. edulis* on the Atlantic coast of South America have migrated westward as larval stages, carried by the Atlantic-derived coastal currents from the east entrance into the Strait (Piola & Falabella 2009). The abiotic and topographic conditions of the east entrance of the Strait are the main factors that keep *M. edulis* at those locations. The Strait of Magellan is an inter-oceanic channel which is characterised by the presence of three micro-basins, the Atlantic water body of the eastern micro-basin penetrates through the Strait to approximately Bahía Zenteno (Valdenegro & Silva 2003, Salinas et al. 2004), which is the most westerly site in which *M. edulis* genotypes were observed (Oyarzún et al. 2016). Sampling within the Strait of Magellan indicated that the hybrid zone is ~125 km in length. Consistent with the locations of other natural *Mytilus* hybrid zones (Gardner 1996), this zone is located at an environmental ecotone between two major biogeographic regions, the southern Atlantic and the southern Pacific oceans. A unique feature of the *M. chilensis*×*M. platensis* hybrid zone is that it occurs not just between two biogeographic regions, but also within a region (the Magellan Region) that is itself recognised as being biogeographically different from the Atlantic and Pacific regions, with close affinity to the Antarctic province (Thatje & Mutschke 1999). Further assessment of this hybrid zone with SNPs may be informative, both in terms of increasing our knowledge of the spatial and temporal stability of the zone, and in terms of understanding gene flow and introgression between *M. chilensis* and *M. platensis* (which was called *M. edulis* at the time).

In this region, the importance of detailed information about sampling site location and the history of the sampling site is highlighted. For example, Oyarzún et al. (2016), Larraín et al. (2018) and Zbawicka et al. (2018) all sampled from Caleta de Pescadores which is an artisanal fishery site with a pier, and all reported finding 100% *M. chilensis* here. However, ~1 km east of Caleta de Pescadores, at Muelle Loreto, is an old and unused pier that was used to transport coal and for international commerce (it was the most important pier in Punta Arenas from 1900 to 1950). At Muelle Loreto, Oyarzún et al. (2016) reported finding 70% *M. chilensis*, 23% *M. edulis* and 7% hybrids (Figure 30). Thus, the presence of hybrids appears to be strongly linked to shipping trade

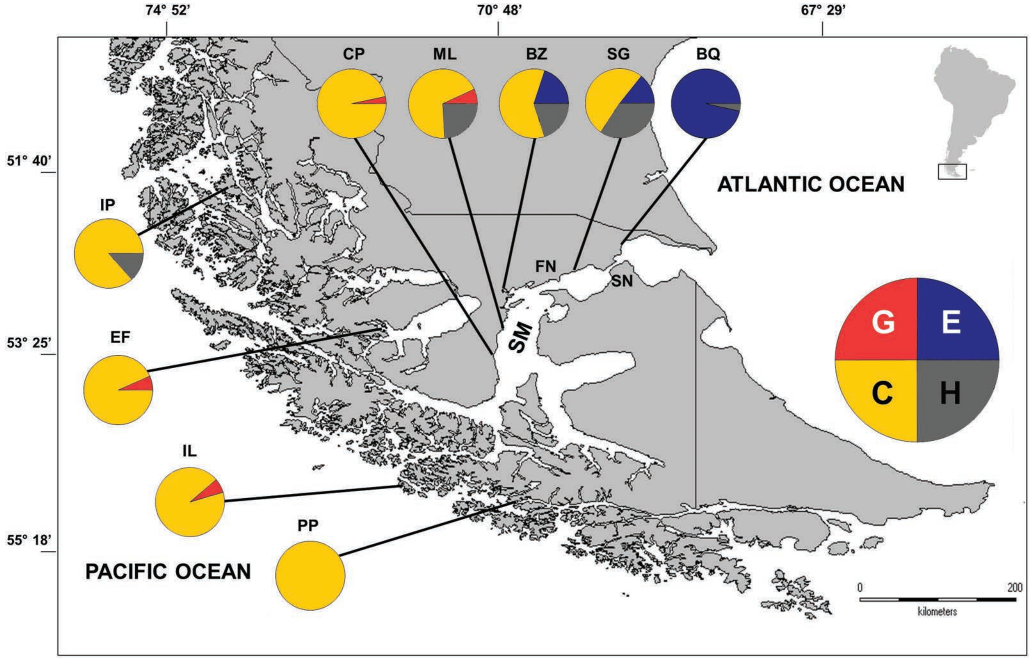

Figure 30 Location of sampling sites within the blue mussel natural hybrid zone of the Magellan Region, Chile. Allele compositions of *Mytilus* samples are shown as frequencies of alleles for the species-specific nuclear and mitochondrial DNA RFLP assays: C=*Mytilus chilensis* or Southern hemisphere *Mytilus galloprovincialis*; G=Northern hemisphere *Mytilus galloprovincialis*; E=*Mytilus edulis*; H=hybrid mussels. Sampling sites: BQ=Buque Quemado, SG=San Gregorio, BZ=Bah_ıa Zenteno, ML=Muelle Loreto (Punta Arenas), CP=Caleta Pescadores, IP=Isla Piazzi, EF=Estero Fanny, IL=Isla London, PP=Paso Pomar. Other codes – SM=Strait of Magellan, FN=First Narrow, SN=Second Narrow. Modified from Oyarzún et al. (2016).

(i.e., human-mediated bioinvasions) as well as to natural processes. During the course of their study, Oyarzún et al. (2016) also reported the presence of six individual *Mytilus galloprovincialis* (i.e., ~3% of all mussels analysed) and three *M. trossulus*×*M. galloprovincialis* hybrids (but no pure *M. trossulus*) from the Strait of Magellan. In conjunction with the native *M. chilensis* and *M. platensis*, the Strait of Magellan therefore has the highest reported genetic diversity of blue mussel species anywhere in the world. This genetic diversity results for two main reasons, one anthropogenically mediated and one natural. The Strait is a very busy shipping route with an international port at Punta Arenas that is the likely source for introduced species (e.g., Northern hemisphere *M. galloprovincialis*, *M. trossulus*) from all over the world. In addition, the Strait facilitates the exchange of waters, mostly from east to west, from the Atlantic and Pacific oceans with the result that marine organisms native to both oceans can meet and mix along the channel within the Strait of Magellan (Oyarzún et al. 2016).

In the context of hybrid zones, it may be helpful to reiterate that mussels from the Falkland Islands, the Kerguelen Islands and the New Zealand offshore islands all exhibit a hybrid background. That is, they appear to have been formed by reticulate evolution or hybrid speciation (Borsa et al. 2007, Zbawicka et al. 2019). However, the important distinction here between the situation described above for the Strait of Magellan and the situation described previously for the offshore islands is that the former involves a hybrid zone (genetic cline) between two "pure" species, whereas the latter does not involve a hybrid zone because all mussels (at least as far as we can tell) exhibit a mixed or hybrid origin. That is, outside a hybrid zone, we find "pure" parental species on either side, but "pure" species do not exist on the remote islands because over time hybridisation has produced mixed or backcrossed genotypes everywhere.

Biosecurity threats to Southern hemisphere blue mussels

Many authors have highlighted the role that anthropogenic activities such as shipping and aquaculture play in the accidental or deliberate movement of marine organisms around the world (e.g., Gardner 1997, Dias et al. 2014, Crego-Prieto et al. 2015, Grosholz et al. 2015, Gardner et al. 2016, Michalek et al. 2016, Larraín et al. 2018, Zbawicka et al. 2018, 2021, McFarlane & Pemberton 2019). Not surprisingly, human-mediated activities have resulted in the introductions of many different groups of marine organisms – algae, invertebrates and vertebrates – to many different regions of the world (Pederson 2003, Ojaveer et al. 2018). Such introductions often result in substantial ecological change to the receiving habitat, with pronounced associated ecological and economic costs (Grosholz 2002, Bax et al. 2003, Ojaveer et al. 2015).

Smooth-shelled blue mussels have been described as invasive from many different locations over, at least, the last 40 years. In the Northern hemisphere, *M. galloprovincialis* of Mediterranean origin or of Atlantic origin (usually the lineage in question is not specified) has been described as being invasive in many locations, including Japan, Hong Kong, the west coast of North America from southern California (USA) to British Columbia (Canada), Norway, Greenland, northern China, eastern Russia and possibly Hawaii (e.g., Wilkins et al. 1983, Lee & Morton 1985, McDonald et al. 1991, Geller et al. 1994, Apte et al. 2000, Anderson et al. 2002, Elliott et al. 2008, Brannock et al. 2009, Shinen & Morgan 2009, Hilbish et al. 2010, Han et al. 2014). In some instances, the invader has been so successful that it has effectively displaced the native cogener, for example, with *M. trossulus* on parts of the Pacific coast of the United States of America (Geller 1999) and in Japan (Brannock et al. 2009). In both cases, it has taken researchers a long time to identify these invasions because of the phenotypic similarity of the invader to the native mussel (this is often classed as a cryptic invasion). Because of this invasion success, Northern hemisphere *M. galloprovincialis* is listed as one of the world's most successful invasive species (Lowe et al. 2000). As far as we are aware there is no evidence for the invasion success of other smooth-shelled blue mussels in the Northern hemisphere, although Beaumont et al. (2006) note that there is anecdotal evidence that *M. edulis* from the North

Atlantic region have been introduced to the Mediterranean coast of France for aquaculture. In contrast to invasion success, Crocetta (2012) lists *M. edulis* in Italy as a possible introduction, but this is impossible to verify for sure, and Casoli et al. (2016) report the failed establishment of *M. edulis* in the Mediterranean Sea after the wreck of the *Costa Concordia* on Italian shores. It seems more than likely that successful invasions or ingressions have occurred elsewhere, but they have not been noticed or cannot be verified.

In the Southern hemisphere, it is again Northern hemisphere *M. galloprovincialis* that has been most often described as the invader. Using a range of different genetic markers, sometimes supported by shell morphological analyses, invasive Northern hemisphere *M. galloprovincialis* has been described from South Africa (Grant & Cherry 1985, Robinson et al. 2007a, Hanekom 2008, Pickett & David 2018, Zardi et al. 2018), southern Namibia (Branch & Steffani 2004, Zardi et al. 2018), from locations in central and southern Chile and from locations in central and southern Argentina (Daguin & Borsa 2000, Toro et al. 2005, Westfall & Gardner 2010, Borsa et al. 2012, Larraín et al. 2012, Tarifeño et al. 2012, Oyarzún et al. 2016, Larraín et al. 2018, Pickett & David 2018, Zbawicka et al. 2018), in much of Australia including Tasmania and also eastern and western mainland sites (Hilbish et al. 2000, Borsa et al. 2007, Gérard et al. 2008, Westfall & Gardner 2010, Colgan & Middelfart 2011, Dias et al. 2014, Ab Rahim et al. 2016, Pickett & David 2018, Popovic et al. 2020, Zbawicka et al. 2021), and in much of New Zealand, particularly in the north (Hilbish et al. 2000, Gérard et al. 2008, Westfall & Gardner 2010, Gardner & Westfall 2012, Gardner et al. 2016). In addition to this, the presence of Northern hemisphere shell types, taxon-specific alleles or haplotypes has also been reported in Southern hemisphere populations. For example, based on morphometric analysis of shells from middens, Gardner (2004) highlighted the similarity of some shells from northern New Zealand to Northern hemisphere *M. edulis*, but was careful not to state that such mussels are (or were) *M. edulis*. Westfall & Gardner (2010) reported the occurrence of two *M. edulis*×*M. galloprovincialis* hybrids from the subantarctic Auckland Islands and noted that although this particular hybrid combination was rare in New Zealand (a total of 484 mussels were examined), it was quite common at this site (two of 34 mussels examined). As noted previously, the presence of *Mytilus trossulus*-like alleles in wild mussel populations of the Southern hemisphere has also been reported by Larraín et al. (2012) at four sites in central Chile and from the Strait of Magellan region by Oyarzún et al. (2016). Larraín et al. (2018), using SNPs, found no evidence of *M. edulis* or *M. trossulus* alleles in Chile. Thus, the status of *M. trossulus* in the Southern hemisphere remains unclear. It requires further research to determine whether these reports of its presence are actually cases of ancestral polymorphisms, or whether it is a natural arrival, or whether it has been spread via anthropogenic activity.

The threat of introduction of non-native mussels to remote Southern hemisphere islands and even to Antarctica has long been recognised (Lewis et al. 2003, Lee & Chown 2007, Shaw et al. 2014, Gardner et al. 2016, Oyarzún et al. 2016), but at the moment, there are still few documented examples of invasion. Ralph et al. (1976) reported the presence of a single, very large (shell length = 83 mm, shell height = 49 mm) blue mussel collected from jetty piles at King Edward Point, South Georgia Island, a region from which blue mussels are naturally absent (Knox 1960, Dell 1964, Powell 1965). Ralph et al. (1976) noted that the nearest population of *M. edulis* (they state that the actual species designation of the mussel remains unclear, but that it is definitely a smooth-shelled *Mytilus* species) is the Falkland Islands, and they go on to discuss the possible ship-borne routes that such an introduction might take, given the history of the South Georgia Islands as both a whaling station and then, more recently, as a science station and stop-over point. Ralph et al. (1976) conclude by stating that it is surprising that this species has not established itself at South Georgia. The fate of this single mussel is unknown (presumably it died a lonely death!), but the threat of future invasion remains. Following on from this, Cárdenas et al. (2020) have recently reported the successful settlement of a newly arrived cohort of *Mytilus* cf. *platensis* (mean shell length 2.0 mm ± 0.1 [mean ± SD]) in a shallow subtidal habitat of the South Shetland Islands in 2019. This is the first report of smooth-shelled blue mussels from the Antarctic region, and while these mussels may not yet have reached the mainland of Antarctica, it appears that they will do so very soon. Cárdenas et al. (2020) note that their genetic analyses, in conjunction with the available shipping records, indicate that the presence of the mussel is consistent with the dominant vectors and pathways linking southern Patagonia with the Antarctic Peninsula, exactly as predicted previously by Oyarzún et al. (2016).

It is now very clear that the Southern hemisphere has been extensively invaded by Northern hemisphere mussels (we do not know of an invasion event in the other direction, but this may well be related more to the fact that no one has looked for it than that it has not occurred). Of the Southern hemisphere invasions, all major land masses have now been colonised. The invasion of South Africa and subsequently southern Namibia is particularly interesting because this is the only Southern hemisphere location where *Mytilus* sp. does not naturally exist (Grant & Cherry 1985) but where other mussels are abundant and an important component of the local system. In all other locations, as far as we can tell, naturally occurring blue mussel populations have been invaded by one or perhaps both lineages of Northern hemisphere *M. galloprovincialis*, and, as noted above, there is some evidence of the presence of other Northern hemisphere taxa such as *M. trossulus* and *M. edulis* in the Southern hemisphere based on RFLP and SNP markers, but these refer to alleles only (i.e., introgression), not to actual mussels. As noted by Gardner et al. (2016), the occurrence of such alleles does not necessarily reflect the occurrence of invasive mussels, it may simply reflect co-ancestry of the marker in question. The very recent description of blue mussels from islands off Antarctica (Cárdenas et al. 2020) is both worrying and fascinating. Antarctica has been described as the “final frontier for marine biological invasions” (McCarthy et al. 2019), and with it having no native intertidal or shallow subtidal mussels, the spread of invasive blue mussels is likely to be rapid and extensive, once established on the mainland.

The usual explanation for the occurrence of Northern hemisphere mussels at Southern hemisphere sites is that they have arrived accidentally via maritime vectors, either as hull fouling or in ballast water (e.g., Apte et al. 2000, Williams et al. 2013, Bailey 2015). Dating introductions can be very difficult, given the reasonably long history of shipping connections across many parts of the globe (e.g., Carlton & Hodder 1995, Gardner 2004, Svane 2011), although we note that it is possible to use the software Structure to estimate the time (number of generations) since admixture between two taxa (Falush et al. 2003). The occurrence of two *M. edulis*×*M. galloprovincialis* hybrid mussels from the remote New Zealand subantarctic Auckland Islands in the Southern Ocean may be attributable to historic attempts at colonisation of this inhospitable islands at least 100 years ago and/or the islands’ use as a base for whaling (with numerous associated ship wrecks) dating back 200 years (O’Connor 1999, Westfall & Gardner 2010). Not surprisingly, many different authors have noted that invasions are associated with the presence of ports or harbours, suggesting a significant role for hull fouling (and ballast water to a lesser extent) as the vector of introduction (e.g., Branch & Steffani 2004, Westfall & Gardner 2010, Gardner & Westfall 2012, Oyarzún et al. 2016, McCarthy et al. 2019, Simon et al. 2019, Cárdenas et al. 2020). In addition, deliberate introductions for aquaculture have also been reported (e.g., Crego-Prieto et al. 2015, Michalek et al. 2016, Gurney-Smith et al. 2017), sometimes after the arrival and establishment of *M. galloprovincialis*, for example in South Africa (Branch & Steffani 2004). There is also anecdotal information that *M. galloprovincialis* from NW Spain was transferred to Chile for aquaculture purposes, after the first report of *M. galloprovincialis* in Chile.

What this record shows is that Northern hemisphere *M. galloprovincialis* is a particularly successful invader, in both the Northern and Southern hemispheres. It is very competitive and can increase its invasive distribution in the face of competition from native mussels and also against the predominant oceanographic flow (e.g., McQuaid & Phillips 2000). It is, however, worth noting that in line with problems of recording invasions generally, it is the successful invasion events that we know about, while unsuccessful invasion events are usually unknown and therefore unrecorded. While *M. galloprovincialis* is undoubtedly a very successful invader, there are cases of invasion collapse. For example, Robinson et al. (2007b) report the complete die-off of invasive *M. galloprovincialis* from the sand banks of Langebaan Lagoon on the west coast of South Africa. This report is unusual given that there are, to the best of our knowledge, no other reports of invasion die off for *M. galloprovincialis* (but as noted above there is one for *M. edulis* in the Mediterranean Sea – Casoli et al. 2016), but this was a small spatial scale event in the context of a much larger, ongoing and successful, invasion of southern Africa. Nonetheless, the report highlights the importance and difficulty of understanding invasion events and invasion collapses. The global connectivity patterns of invasive *M. galloprovincialis* based on COI variation have recently been reviewed by Pickett & David (2018). Their results (Figure 31) highlight the complex and multi-directional routes of invasion as documented by 360 bp of the COI region from a large central group of haplotypes to numerous regions in the world.

The biosecurity and management implications of invasive blue mussels have been discussed extensively. There are two main concerns associated with a blue mussel invasion (e.g., Geller et al. 2010, Gardner & Westfall 2012, Gardner et al. 2016, Bourne et al. 2018, Larraín et al. 2018). The first relates to the ecological and environmental outcomes of the bioinvasions, in particular to the displacement of native biota and the subsequent change in ecosystem structure and function (Wilkins et al. 1983, Grant & Cherry 1985, Lee & Morton 1985, Geller, Carlton & Power 1994, Geller 1999, Schneider & Helmuth 2007, Elliott et al. 2008, Hanekom 2008, Shinen & Morgan

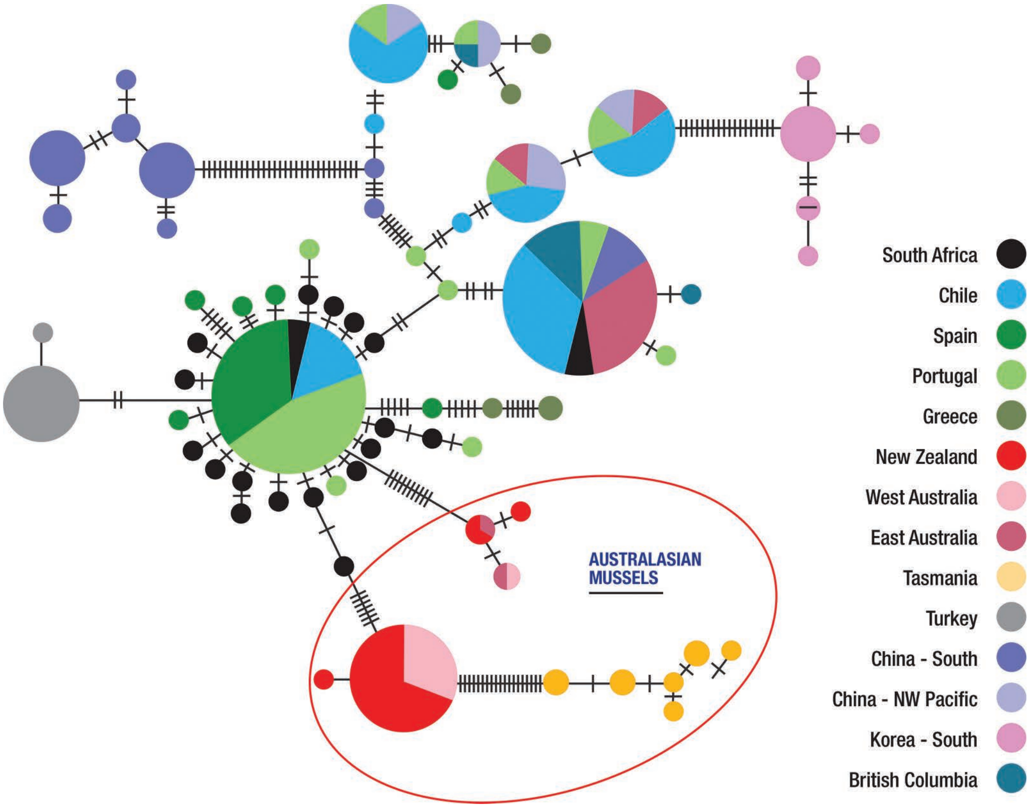

Figure 31 Haplotype network for *Mytilus galloprovincialis* based on mtDNA COI sequence data. Size of circles is representative of individuals with that haplotype. The smallest circles represent a haplotype frequency of one. Each connecting line between haplotypes represents one mutational step and perpendicular lines represent an additional mutational change. Dashed circles indicate distinct haplogroups. Modified from Pickett & David (2018).

2009, Gardner & Westfall 2012, Gardner et al. 2016, Cárdenas et al. 2020). The second relates to the extensive hybridisation that may occur when two or more taxa co-exist and the subsequent introgression that may occur (e.g., Skibinski 1983, McDonald & Koehn 1988, Gardner & Skibinski 1990a, McDonald et al. 1991, Väinölä & Hvilsom 1991, Hilbish et al. 1994, Gardner 1996, Suchanek et al. 1997, Rawson et al. 1999, Bierne et al. 2002, Brannock et al. 2009, Simon et al. 2020, Wenne et al. 2020). The fear of the loss of the genetic integrity of the native taxon in the face of gene flow from the invader, mostly usually Northern hemisphere *M. galloprovincialis*, has been highlighted several times (e.g., Gardner & Westfall 2012, Gardner et al. 2016, Oyarzún et al. 2016, Larraín et al. 2018; Zbawicka et al. 2018, 2019, 2021, Popovic et al. 2020). How this hybridisation and any associated introgression may translate into fitness differences among individuals (pure native taxon, F_N hybrids, backcrosses and pure invasive taxon) remains largely unexplored, in particular in the context of field-based and laboratory-based comparisons of fitness among naturally occurring mussels that have been made in an evolutionary perspective (e.g., Gardner & Skibinski 1988, Gardner & Skibinski 1990a,b, 1991, Wilhelm & Hilbish 1998, Toro et al. 2006, Schneider & Helmuth 2007, Dutton & Hofmann 2009, Elliott et al. 2008, Shields et al. 2010, Dias et al. 2009, Shinen & Morgan 2009). Fitness comparisons and genomic interactions may be key to better understanding the ecological consequences of mussel invasions and the interactions of native and invasive mussels.

Dealing with a mussel invasion most usually means recognising that it has occurred and then accepting that there is little or nothing that can be done about it. Most authorities seem to believe that the relatively rapid growth rate, young age at first reproduction, the production of huge numbers of gametes, considerable larval dispersal ability and tolerance of environmental variation are likely to mean that once established, a mussel invasion cannot not be wound back (Coutts & Forrest 2007, Forrest et al. 2009, Gardner & Westfall 2012). Whether this is true or not, will depend to some extent on how soon after its establishment the invasion is found, the specific context (geographic location) of the invasion and the will of the government of the day to spend money on eradication. Successful invasive mussel eradication programmes have occurred. For example, the black striped mussel, *Mytilopsis sallei*, was successfully eradicated from Darwin Harbour in northern Australia in 1999 (https://nt.gov.au/marine/for-all-harbour-and-boat-users/biosecurity/aquatic-pests-marine-and-freshwater/black-striped-mussel; Ferguson 2000), the invasive *M. galloprovincialis* was prevented from establishing in Pearl Harbor, Hawaii, following its arrival there (Apte et al. 2000), and the brown mussel, *Perna perna*, was eradicated from Tasman Bay, New Zealand, in 2007 (Hopkins et al. 2011). However, the two non-*Mytilus* examples are, of course, very different from the invasion of a blue mussel taxon, in particular if that invasion occurs into a region already home to a blue mussel where it will be difficult to detect and eradicate.

Biosecurity – future threats

In the modern world, where nearly everything is interconnected (Williams et al. 2013), geographic isolation does not guarantee the protection from invasion that it was, until fairly recently, assumed to provide (McCarthy et al. 2019). Even small and remote Southern Ocean islands are not now immune to unwelcome visitors. The two main threats to Southern Ocean biodiversity as posed by an invasive species have been identified as maritime traffic and rafting, either naturally on substrata such as kelp rafts or on anthropogenic substrata such as plastics. In an area as large as the Southern Ocean, the concept of island hopping is important (Leese et al. 2010) because an invader may arrive from its natal region and then proceed to expand its new, invasive range in a series of steps, consistent with patterns of colonisation already recorded for native Southern Ocean species with a benthic life style and no pelagic larval stage (Leese et al. 2010). With an increasing number of reports of the northward expansion towards the Arctic region of the invasive *M. galloprovincialis* in the Northern hemisphere, a spread that may be aided by global climate change and warming temperatures (e.g., Berge et al. 2005, Wenne et al. 2016), there is a similar and related fear that *M. galloprovincialis* or one of its congeners may soon reach the mainland of Antarctica, from where it (and all other *Mytilus* species) is presently and historically absent (e.g., Clark 1996, Lee & Chown 2007, Griffiths et al. 2009, Gardner et al. 2016, Oyarzún et al. 2016, Cárdenas et al. 2020).

Maritime traffic

Lewis et al. (2003) and Lee & Chown (2007) have suggested that hull and sea chest fouling assemblages are of particular concern for the antarctic region because of long winter port layover times, slower cruising speeds and the lack of antifouling agents used on ship hulls breaking through sea-ice in the Southern Ocean and polar seas. Lewis et al. (2003) and Lee & Chown (2007) also cite future increases in the numbers of ships for tourism, fisheries and science as possible vectors for introduction of non-native species to Southern Ocean islands and even Antarctica itself.

Natural rafting

Numerous authors have highlighted the importance of natural rafting, most usually of biota on kelp raft holdfasts, for the dispersal of species around the Southern hemisphere, both among the major continental landmasses and also to/from Antarctica. The earliest report of kelp rafting that we are aware of dates back almost 90 years (Mortensen 1933 cited in Leese et al. 2010), and this has been followed by multiple reports or reviews (e.g., Fell 1962, Edgar 1987, Hobday 2000, Thiel & Gutow 2005a,b, Thiel & Haye 2006, Waters 2008, Leese et al. 2010, Nikula et al. 2010, Fraser et al. 2011). The importance of kelp rafting to dispersal and long-range expansion is highlighted by Ó Foighil et al. (1999) for the brooding oyster *Ostrea chilensis* (from New Zealand to Chile) and by Griffiths & Waller (2016) who note that patterns of kelp rafting are likely to explain many of the biogeographic patterns of different groups in the Southern Ocean. Based on ship-board transect counts, Smith (2002) estimated that at any one time, there may be ~70 million kelp rafts in the Southern Ocean (mostly *Durvillaea antarctica*), of which ~20 million had a holdfast with associated fauna. Tala et al. (2019) note that more rafting kelps occur at higher latitudes (50–60°S) than at lower latitudes (30–40°S), another factor that will facilitate transport of species such as blue mussels to/from Southern Ocean islands and Antarctica. Given that even if only a very small proportion of these kelp rafts are derived from a location with invasive blue mussels, it is still possible that such invaders may be moved around the Southern hemisphere on natural kelp rafts and will tend to go with the flow, mostly travelling west to east on the Antarctic Circumpolar Current and dispersal through West Wind Drift (Arnaud 1974, Waters 2008, Leese et al. 2010, Zbawicka et al. 2019). While there is a low probability that any given raft will make landfall at a location with suitable conditions for the establishment of its hitch-hikers (Griffiths & Waller 2016), once established the early colonisers are likely to experience little competition for space and resources, and may therefore thrive (Waters et al. 2013, Cárdenas et al. 2020). In their description of the biodiversity and biogeography of Antarctic and sub-Antarctic intertidal communities, Griffiths & Waller (2016) note that all of the significant pattern-driving species of the Antarctic and sub-Antarctic are molluscs or macroalgae. Specifically, they report that distributions of several of the key animal species (*Laevilitorina caliginosa*, *Kerguelenella lateralis* and the genera *Nacella* and *Mytilus*) correspond to the distribution of large kelps (mostly *Durvillaea antarctica* but also *Macrocystis pyrifera*). Interestingly, while both *D. antarctica* and *M. pyrifera* are absent from the Antarctic region, another species, *Himantothallus grandifolius*, is circumpolar and may play a role in transporting shallow water species around the continent. From a management perspective, it is, of course, impossible to protect against rafting as a vector of transport, not only because of the sheer number of such rafts that are on the move at any given time, but also because many of the island locations where the rafts may arrive are simply not staffed to deal with this sort of potential incursion. What this suggests is that in the near future, we must expect a number of range expansions of native and non-native mussels in the Southern Ocean.

Rafting on manmade substrata

Many species, including mussels of the genus *Mytilus*, have a prodigious ability to settle and then grow rapidly on a wide range of manmade substrata. This is one reason why blue mussels are such a problem in terms of fouling of wharf piling, ships, power station cooling water intake pipes, and indeed just about any substratum in the water column. With the rapid increase in the amount of plastics in the oceans over the last 50 or 60 years, and the general tendency of this material to float near the surface and to degrade very slowly, multiple different taxa have been recorded on manmade debris found in the oceans, in particular on plastics (Barnes 2002, Barnes & Fraser 2003, do Sul et al. 2011, Griffiths & Waller 2016). Do Sul et al. (2011) report that fishing operations in the Southern Ocean are the main source of manmade marine debris and that plastics from lower latitudes have the ability to cross the PF. They suggest that the most likely route of invasion of Antarctica by fouled plastic debris is from South America, given its proximity to Antarctica. The authors highlight an alarming lack of knowledge about the problem of marine debris and call for more research. In contrast to this view, Griffiths & Waller (2016) suggest that because rafting on debris, like kelp rafting, is a passive process under the control of ocean currents, it is unlikely to promote a wider range of species to colonise Antarctica or the sub-Antarctic region.

The role of anthropogenic debris in the spread of many species has recently been discussed by Carlton et al. (2017) in the context of the huge volume and very large number of individual pieces of debris resulting from the 2011 East Japan tsunami. The authors documented 289 living Japanese coastal marine species from 16 phyla, transported over six years from Japan to Hawaii and the Pacific coast of the USA. *M. galloprovincialis* (itself originally invasive in Japan) was recorded as being a long-term survivor of this trans-ocean dispersal event. Most of the dispersal occurred on manmade non-biodegradable objects, highlighting the role that manmade materials may play in future marine invasions. More recently, Miller et al. (2018) reported that *M. galloprovincialis* was present on >50% of the pieces of biofouled debris (*M. trossulus* at 2.7% and *M. coruscus* at 0.2% occurrence were also reported) and that the majority of mussels (79%) had developing or mature gametes. That is, the mussels were not only viable but ready to reproduce. While we cannot protect in a management sense against natural events such as earthquakes, submarine slumps and tsunamis, it is now apparent that we need to be thinking in terms of manmade debris from such events as a vector for invasive species, in particular for blue mussels given their tolerances of environmental variation.

Climate change and possible new invasions or range expansions

With global climate change and in particular with increasing sea surface temperatures, many intertidal and shallow water species are expected to move poleward, in both hemispheres. Sea water temperate has, of course, long been known to influence species' distributions and to (partially) explain many biogeographic patterns. For example, Ekman (1953) noted that sea water temperature during the post-glacial warm period (approx. 7000–4000 ybp) was ~2°C warmer than at the time of his writing and that *M. edulis* had at that time lived near Spitsbergen and other Arctic localities outside its (then) present distribution. More recently, *M. edulis* has again been reported from Svalbard after 1000 years of absence (Berge et al. 2005). Thus, sea surface temperature changes, in particular in polar regions, are expected to result in range shifts for many species over the next few decades (e.g., Diez et al. 2012, Poloczanska et al. 2013, Early et al. 2016, McCarthy et al. 2019) and have already done so in the Northern hemisphere for species such as *M. edulis* (Berge et al. 2005), *M. galloprovincialis* (Beaumont et al. 2006, Mathiesen et al. 2017) and *M. trossulus* (Feder et al. 2003, Mathiesen et al. 2017). It is interesting to note that this poleward expansion of blue mussels may, in some cases, be matched by catastrophic mortality at the southern (equatorward) limit of distribution associated with increased summer warming above a species' thermal limit (Jones et al. 2010).

Based on fairly extensive, but still incomplete, surveys of many Southern hemisphere regions, smooth-shelled blue mussels are known to be absent from many subantarctic islands including Heard Island (Dell 1964) and Macquarie Island (Powell 1965), and also from the Antarctic mainland (Clark 1996, Griffiths et al. 2009, McCarthy et al. 2019 but see Cárdenas et al. (2020) for a report of introduced mussels on Antarctic offshore islands). They are, however, naturally present in regions such as southern South America (e.g., Oyarzún et al. 2016) and offshore islands in the Southern Ocean (e.g., Gardner et al. 2016, Zbawicka et al. 2019) that are either in immediate proximity to Antarctica (e.g., the Antarctic Peninsula and South America) or are relatively close to Antarctica. As such, both Antarctica itself and the most southern islands that do not have native mussels are likely to be subject at some stage to climate-change-mediated range expansion of smooth-shelled blue mussels and numerous other taxa (e.g., Aronson et al. 2007). As noted by Leese et al. (2010), changing temperatures and associated shifts in the Polar Frontal Zone are likely to mean that higher latitude marine habitats become suitable for invading species. The remote Antarctic and sub-Antarctic islands are therefore expected to act as stepping stones that promote entry of species into Antarctica's coastal systems. The question then may well be what can be done to minimise or perhaps even prevent this, given that many countries have limited capacity to respond to invasions (Early et al. 2016). Antarctica's independent political status may, in fact, hinder the likelihood of invasion identification and subsequent eradication given that no one country has legal responsibility for the continent. While several authorities have advocated for increased monitoring and surveillance (e.g., Gardner et al. 2016, Carlton & Fowler 2018, Ojaveer et al. 2018), others have taken a completely different approach. For example, Beaumont et al. (2006) make the point that short-term (5–10 years) crisis management may well not be worth the effort in the face of longer term (50–100 years) climate change factors. Both views may be correct depending on the geography and the spatial context. Identification of an invasion on, for example, Macquarie Island may be possible and may even be followed up by a successful eradication programme, given the comparatively small scale of the island and the commitment of the Australian Government to prevent bioincursions. However, once established on Antarctica a blue mussel invasion is unlikely to be eradicated successfully given the lack of individual governmental responsibility (with associated cost implications), the remoteness of the location and also the scale of the invasion once established and its potential for subsequent spread.

Management – the need for monitoring and rapid decision-making

As noted, invasive blue mussels are difficult to identify quickly (e.g., when they first arrive at a new destination – but see Ralph et al. 1976, Cárdenas et al. 2020) and are therefore difficult to eradicate (we are unaware of any successful attempts to eradicate invasive blue mussels). Once established, a new invader is likely to spread relatively rapidly and its spread may be aided, at least in part, by its ability to hybridise and interbreed with the native taxon. Alternatively, if an invader arrives at a location where mussels are not native, it may be able to spread rapidly in the absence of biotic resistance. Generally speaking, once an invader is established it will be impossible to eradicate it (Coutts & Forrest 2007, Forrest et al. 2009, Gardner & Westfall 2012). Many authors over the years have highlighted these and other problems associated with bioinvasions, the risks associated with various forms of vectors, and have also suggested a range of different management options aimed at minimising the establishment potential and/or the impact of an invader (e.g., Lewis et al. 2003, Lee & Chown 2007, Gardner & Westfall 2012, Gardner et al. 2016). Not surprisingly, blue mussel bioinvasions are often associated with aquaculture operations (Beaumont et al. 2006, McKindsey et al. 2007, Dias et al. 2014, Grosholz et al. 2015, Crego-Prieto et al. 2016, Michalek et al. 2016. Gurney-Smith et al. 2017), with working ports (e.g., Gardner et al. 2016, Oyarzún et al. 2016, Larraín et al. 2018, Simon et al. 2020), and it has been suggested that many introductions may be relatively old and associated with seventeenth- or eighteenth-century sailing vessels (e.g., Carlton & Hodder 1995, Gardner 2004, Svane 2011). Recent work has highlighted that geographic remoteness is no longer a protection from bioinvasions (e.g., Larraín et al. 2012, Gardner et al. 2016, Oyarzún et al. 2016, Wenne et al. 2016, McCarthy et al. 2019, Cárdenas et al. 2020).

The need for ongoing monitoring is clearly an important step in protecting native biodiversity and identifying an invader (Ojvaeer et al. 2015, 2018, Gardner et al. 2016). Monitoring may be time-consuming and is expensive, in particular if molecular tools are needed to identify an invader and if many samples need to be processed. Typically, existing monitoring is focussed on high-risk areas such as primary ports (e.g., routine surveys in Australia and New Zealand), but is not routinely carried out by all countries (e.g., not in Chile, Argentina and Uruguay). However, specific monitoring of mussel settlement is sometimes carried out. For example, in Chile, from Tongoy (IV Region) in the north to Porvenir (XII Region) in the south, across a latitudinal range of ~3200 km, nine sites are presently being monitored using spat collectors that are replaced every month, over a three-year period (Jorge Toro, pers. obs.). Regardless of which country we are talking about, because routine monitoring cannot be carried out at all locations (e.g., smaller ports, marinas and remote offshore islands), it is easy to miss an invasion, in particular one that does not originate at a primary port. Furthermore, because of the difficulty of differentiating between or among blue mussel taxa based on morphometric criteria alone (Geller 1999, Krapivka et al. 2007, Gardner & Thompson 2009, Illesca et al. 2018), many invasions will not be identified at all because molecular testing for Northern hemisphere blue mussels is not routinely carried out by biosecurity agencies in the Southern hemisphere.

The need for baseline monitoring to establish the present situation for native blue mussel presence/absence and also for native blue mussel genetic identity and integrity has been highlighted by Ovajeer et al. (2015, 2018), Gardner et al. (2016), Oyarzún et al. (2016) and Larraín et al. (2018). The rationale for the Southern hemisphere is clear – until we know what we have and where it is, it is going to be very difficult to protect native biodiversity, native ecosystem structure and function, and native genetic variation.

Given the financial and logistical difficulties associated with monitoring, this activity will, at best, only be targeted to certain areas or events. For example, towing of the *USS Missouri* from Bremerton, Washington State on the Pacific coast of the USA, approximately 4200 km to the state of Hawai'i was known to carry with it some risk of movement of marine invaders. Because of this, an extensive programme was set in place to monitor the vessel and any associated biofouling on arrival in June 1998 into Pearl Harbor (Apte et al. 2000 and references therein). Blue mussels were noted to initiate spawning activity almost immediately upon arrival in Pearl Harbor, and subsequently, mussels were collected from the ballast tanks of a US Navy submarine in the port. Molecular analysis identified these mussels as invasive *M. galloprovincialis* (Apte et al. 2000). While this series of events may be unusual, they highlight the need for targeted monitoring and how management actions may reduce or prevent the likely spread of an invader, even when via an apparently unsuitable habitat or region.

Gardner & Westfall (2012) note that following the identification of non-native blue mussels, it may be possible to model the likely spread of the invader (providing, of course, that sufficient environmental, habitat distribution and physical oceanography data exist) to help predict the spread and the taxon's likely distributional pattern. Such information might then be used in the context of designing a targeted monitoring or eradication programme at sites of particular interest, for example, of high conservation value or of high economic value (e.g., aquaculture production sites). Such an approach may be based on the concept of internal borders (Forrest et al. 2009), which are loosely defined as natural barriers within a country or region that may prevent or slow the spread of the invader. For blue mussels, examples include deep water between islands, long stretches of unsuitable habitat type (e.g., long sandy beaches that separate rocky reef environments) or river outflow that creates a freshwater barrier to dispersal. Identification of such natural barriers to dispersal and range expansion by the invader and the subsequent management planning around such barriers is a well-developed concept in biosecurity, but has not been that widely applied in marine environmental science (Forrest et al. 2009). The concept is rather like a military plan in which it is acknowledged that certain territory has been lost to the invader but that a line exists at a given point, past which the invader will not cross. But for this strategy to be successful, there is a need for ongoing monitoring and the capacity for a rapid incursion response.

In conclusion, it seems likely that there are a number of steps that are required to protect native Southern hemisphere ecosystems and also to protect the integrity and uniqueness of Southern hemisphere genetic lineages of mussels. In particular, we are thinking here of the island-specific lineages, e.g., Borsa et al. (2007), Gardner et al. (2016) and Zbawicka et al. (2019). Gardner et al. (2016, p. 3193) state that "… there is a need for (i) a greater understanding of biosecurity threats, (ii) more baseline information about native (endemic) species plus their genetic uniqueness, (iii) an increased understanding of the likely extents and effects of hybridization and introgression and what has been called 'the invasion of the genome' (Mallet 2005), and (iv) ongoing monitoring and surveillance, plus the political will to act in the event of an incursion".

Aquaculture

Marine mussels of the genus *Mytilus* are one of the most widely cultivated and sold molluscs in the world (FAO 2016, Ferreira & Bricker 2016). In the Southern hemisphere, the major blue mussel producer is Chile, with Australia and to a much lesser extent both Argentina and South Africa also farming *Mytilus* species. Understanding which species is being cultivated is important to growers, processers and marketers alike given that correct labelling of food products is now a legal requirement in many parts of the world and as a point of commercial difference among the many countries around the world that grow and sell blue mussels.

Blue mussel aquaculture is associated with several problems that contribute to production issues (e.g., more fragile shells of *M. trossulus* in comparison to other species in North America – Penney et al. 2007 and also in Europe – Beaumont et al. 2008) and also to biosecurity issues (e.g., accidental and deliberate introductions of species – Branch & Steffani 2004, McKindsey et al. 2007, Crego-Prieto et al. 2015, Grosholz et al. 2015). Associated with this latter point, there may be subsequent issues in terms of inter-specific hybridisation and introgression of non-native genes into the local, native stock (reviewed by Michalek et al. 2016), with concomitant problems in terms of reduced fitness of aquaculture mussels when compared to locally adapted stocks (e.g., Perez et al. 2003, Beaumont et al. 2006, Penney et al. 2006, Toro et al. 2006, Oyarzún et al. 2013). As a consequence, in many parts of the world, legislation now exists that governs aquaculture transfers to help safeguard the consumer, the local industry, the genetic integrity of locally adapted stocks and also the local environment (e.g., Dias et al. 2014, Muehlbauer et al. 2014, Larraín et al. 2018). Despite this, invasive blue mussels in countries like Australia, Canada and Chile may now pose a threat to the well-being of the local industry, even if only in certain regions (Dias et al. 2014, Crego-Prieto et al. 2015, Ab Rahim et al. 2016, Gurney-Smith et al. 2017, Larraín et al. 2018). Zbawicka et al. (2021) have recently suggested that mussel aquaculture (e.g., based on hatchery production) in the Australian island state of Tasmania for the native mussel, *M. planulatus*, could help enhance the status of threatened native mussel in the wild, as well as providing a sales point of difference for the state's mussel farmers.

The importance and difficulty of differentiating among mussel species in an aquaculture context are particularly well highlighted by a recent example from Chile. Coelho-Caro et al. (2018) note that the classification, counting and sorting of mussel seed for aquaculture production is currently performed by human experts (this is time-consuming and labour-intensive). They described the development of an automatic mussel classifier system that uses machine learning to differentiate with ~95% success among five mussel species of four genera, including the native *M. chilensis* and the introduced Northern hemisphere *M. galloprovincialis*. The aquaculture industry's move towards the use of such technology, in particular to differentiate among different species at the spat/seed stage that are derived from wild settlements, illustrates how important it now is to industry to know which species is being cultivated to maximise the economic return. The use of this sort of technology, which is cost-effective to develop and deploy, may help mitigate some of the problems that the mussel aquaculture industry faces in certain regions in terms of differentiating between a native and an introduced species or between a strong shell shape and a weak shell shape, something that is particularly important at the post-harvest processing stage.

Chile

Chile is now the world's second largest mussel (*Mytilus* spp.) aquaculture producer at 365,595 tonnes, behind only China at 880,000 tonnes (FAO 2006–2019, FAO 2017, FAO 2018c). Production is concentrated in the Gulf of Reloncaví and along the coastline of Chiloé Island (Los Lagos region) and is based on the native blue mussel, *Mytilus chilensis* (Larraín et al. 2018). There has been a steady pattern of industry growth since 1993 from 3,864 tonnes production to 338,847 tonnes production in 2017 (SERNAPESCA 2017), rising to 365,595 tonnes in 2018 (FAO 2018c). The contribution of mussel production to total Chilean aquaculture increased from 6.1% in 2001 to 27.8% in 2017, and mussel (*M. chilensis*) production was 97.5% of total mollusc production in Chile (SERNAPESCA 2017). While China is producing mainly for its domestic market, Chile exports almost all of its production, with most going to the EU (Fernández-Tajes et al. 2011), such that Chile is rapidly becoming the top mussel exporter in the world (FAO 2018a,b).

The industry is almost totally dependent on the supply of seed from natural (wild) populations (Uriarte 2008). Therefore, for the ongoing sustainable exploitation of *M. chilensis* it is important to recognise native from introduced (*M. galloprovincialis*) mussels and to understand regional population dynamics of the species (Astorga et al. 2015). Aquaculture activity in Chile has an enormous impact on anthropogenic-mediated gene flow via the transfer of juveniles from two or three major spat collection sites to a broad number of sites for grow-out to commercial size (Holmberg 2012). As noted above, Chile is a world leader in the development of image analysis technology and machine learning to differentiate among wild-caught seed (Coelho-Caro et al. 2018), and as noted below, it is also a world leader in terms of mussel food forensics (Fernández-Tajes et al. 2011, Larraín et al. 2014, Jilberto et al. 2017).

Argentina

Despite its very long coastline and the presence of two native mussel species (*M. platensis* in the north and *M. chilensis* in the south), Argentina is not a major player in world mussel aquaculture terms. Bivalve molluscs occupy the third place in aquaculture production statistics in Argentina. *Mytilus platensis* is produced at Río Negro and Chubut, while *Mytilus chilensis* is produced in Tierra del Fuego. All of this production is based on the suspended culture techniques. Commercial production for the domestic market commenced in 1996. By 2014, a total of 11.2 tonnes were produced, which is equivalent to 0.33% of total aquaculture production in Argentina (Dirección de Acuicultura, Ministerio de Agroindustria 2016).

Uruguay

Mytilus platensis, the native mussel in Uruguay, inhabits the intertidal and subtidal rocky shore of the Atlantic coast (Riestra & Defeo 2000). This species is the dominant organism in these coastal systems, and the natural mussel beds have been exploited for over 40 years by artisanal fishers. No mussel aquaculture exists so far in Uruguay, although there are moves to develop a new industry.

Falkland Islands

There is a small local aquaculture industry based on the production of *M. platensis* in the Falkland Islands, and all of this production is used for domestic consumption. The FAO does not yet report annual production values for the islands (FAO 2018c). The coastal topography of the Falkland Islands with its many sheltered bays and its clean water is ideal for mussel aquaculture.

Low human population density is, however, a problem that will limit further development of the industry. Nonetheless, the feasibility of developing an export industry has been explored – https://en.mercopress.com/2004/11/16/prospects-for-falklands-mussel-industry-examined

South Africa

Mussel aquaculture of two species – the native *Choromytilus meridionalis* and the introduced *M. galloprovincialis* – occurs on a limited scale in Saldanha Bay, Western Cape, where four farms exist (Louw 2020). The FAO reports production of 2182 tonnes in 2018 for *M. galloprovincialis*, up from 682 tonnes in 2009 (FAO 2018c). Mussel culture method is based on ropes suspended from longlines in the cool and highly productive waters of Saldanha Bay (e.g., https://blueocean-mussels.com/; https://www.vikingaquaculture.co.za/mussels/) that are well known for periods of wind-driven upwelling that bring cooler, nutrient-rich waters from deep to the surface, a regular phenomenon that enhances mussel growth.

New Zealand

New Zealand is unique among the larger Southern hemisphere countries with a native blue mussel because at present it does not have an aquaculture industry for *Mytilus* sp., in this case *M. aoteanus*. New Zealand's mussel aquaculture industry is very well developed, but is entirely focussed on another native species, the greenshell mussel *Perna canaliculus* (Hickman 1991, Jeffs et al. 1999, Alfaro et al. 2011). Native (*M. aoteanus*) and introduced (Northern hemisphere *M. galloprovincialis*) blue mussels settle and grow on the suspended culture (long line) system that is employed to grow *P. canaliculus*. These blue mussels, which tend to settle on the tops of the ropes and can outcompete the native greenshell mussels for space and access to particulate food, are more resilient to salinity fluctuations than are the green mussels (Forrest & Atalah 2017). At harvest, the blue mussels are collected at the same time as the greenshell mussels, but they are separated from the greenshells, and are treated as fouling and a waste product. Historically, blue mussels have been sent to landfill sites or used as pig food. For the last 40 years or so, the New Zealand mussel aquaculture industry has been solely focussed on the production of *P. canaliculus* (2018 production was 86,176 tonnes – FAO 2018c) because this is a major point of difference for New Zealand from all other producers, and because the New Zealand greenshell mussel often sells for twice the price per kg of blue mussels on international markets (mostly Europe and North America, but SE Asia as well). However, over the last few years, there has been recognition within New Zealand that these non-target blue mussels can be used in soups and chowders, and it seems likely that a new, but small value, blue mussel aquaculture industry will develop in New Zealand. In taste tests, international consumers often prefer blue to green mussels, and international chefs have commented that they are not used to working with big mussels (often 7 cm shell length and larger for *P. canaliculus*) but prefer smaller blue mussels (5–7 cm shell length). Much of the information above is taken from Aquaculture New Zealand, which is the industry trade magazine (https://www.aquaculture.org.nz/).

One final point relates to monitoring of the occurrence of the invasive Northern hemisphere *M. galloprovincialis* (e.g., Gardner et al. 2016) on New Zealand greenshell mussel farms, and whether or not aquaculture farms are important manmade surfaces that inadvertently promote the further spread of this invader. A preliminary study is presently underway testing this idea at five sites within the Marlborough Sounds, New Zealand's major centre for mussel aquaculture.

Australia

Blue mussels in Australia are naturally distributed from approximately Cape Hawke, in New South Wales on the east (Pacific Ocean) coast, along the southern coastline including the island state of

Tasmania, to Perth in Western Australia on the west (Indian Ocean) coast (Love & Langenkamp 2003, Dias et al. 2014). The biggest producer is the state of Victoria followed by Western Australia (Dias et al. 2014, Ab Rahim et al. 2016), but all regions except Queensland and Northern Territory have an industry (Dias et al. 2014). According to Dias et al. (2014), Western Australia produced 365 tonnes of mussels in 2011. By world standards, the Australian mussel industry is small, but it is growing rapidly: the FAO lists production of *M. planulatus* as 3781 tonnes in 2018 (FAO 2018c). Until recently, all seed were wild caught, but the unpredictable supply of spat and the requirement to develop the industry has seen the advent of hatchery seed production, with particular emphasis in the states of South Australia and Victoria (Hickman et al. 2005; Jahangard et al. 2010; Nguyen et al. 2011).

In Australia, the native mussel is recognised as *M. planulatus* following recent SNP-based work (Popovic et al. 2020, Zbawicka et al. 2021), which until recently was widely recognised as a native Southern hemisphere lineage of *M. galloprovincialis* (e.g., Westfall & Gardner 2010, Dias et al. 2014, Ab Rahim et al. 2016). In addition, several authors have recorded the presence of the invasive Northern hemisphere *M. galloprovincialis*, in particular in Western Australia, but also at lesser frequencies elsewhere (e.g., Gérard et al. 2008, Westfall & Gardner 2010, Colgan & Middelfart 2011, Dias et al. 2014. Ab Rahim et al. 2016). In a broad survey across Australia, Ab Rahim et al. (2016) reported that 56.2% of all mussels were native Southern hemisphere haplotype, 10.3% were putatively introduced Northern hemisphere mussels, and 32% of all mussels had genotypes consistent with either Northern or Southern hemisphere lineages. In the context of seed supplied from hatcheries by the states of South Australia, Victoria and Tasmania, Dias et al. (2014) reported that most mussels were native Southern hemisphere lineage mussels (i.e., *M. planulatus*), but also noted that a significant proportion of the seed supply was of Northern hemisphere *M. galloprovincialis* stock (South Australia = 43%, Victoria = 48% and Tasmania = 30%). Consistent with earlier reports of very high frequencies of Northern hemisphere *M. galloprovincialis* in Western Australian populations, Dias et al. (2014) reported frequencies of 65%, 88%, 60% and 24% of this non-native mussel at four separate aquaculture sites in Western Australia. Thus, blue mussel aquaculture in the state of Western Australia is largely, but not exclusively, based on the production of the introduced Northern hemisphere *M. galloprovincialis*, whereas blue mussel aquaculture in the eastern and southern states is largely, but not exclusively, based on the production of the native Southern hemisphere *M. planulatus*. However, subsequent movement of stocks and hatchery-produced spat around the country will contribute to further mixing, as will hybridisation and introgression between the two species.

Importance of correct taxonomy for food labelling, marketing, traceability and production statistics

Taxonomy has a key role to play in the protection and sustainable exploitation of species (Mace 2004, Larraín et al. 2018). Correct product identification (taxonomy) underpins a lot of aquaculture at the post-harvest stage of production (Beaumont et al. 2008). This is more than just getting the species name correct on the can: this is about differentiating the product of one country or one region from others, protecting the consumer, preventing commercial fraud by substitution, recognising biosecurity concerns when the product is grown in one country but processed in another, understanding regional production statistics, monitoring temporal change in production dynamics and the effective use of marketing to sell more product. While this aspect of mussel taxonomy has not been a major focus of global efforts to better understand the taxonomy and phylogeography of the world's blue mussels, its relevance to aquaculture and to national economies has long been recognised. In the Southern hemisphere, this is most applicable to major mussel producing countries such as Chile, and to a lesser extent to Australia and Argentina, but not presently applicable to New Zealand.

Identification of mussel species and their hybrids is of economic importance for different reasons, some of which are not immediately obvious. For example, while mixed species can be sold in some regions of the world (e.g., Canada – Penney et al. 2002) the more fragile-shelled *M. trossulus* can cause problems at the sorting and processing stage in the factory that may render rope growth of *M. edulis* and *M. trossulus* uneconomical for some farmers. In another example, Beaumont et al. (2008) describe how biosecurity fears may directly impinge on aquaculture production. They note that most bottom-cultured mussels in the United Kingdom are sent to the Netherlands for processing, but the identification of *M. edulis*, *M. galloprovincialis* and *M. trossulus*, as well as their hybrids, at the main growing site in Loch Etive, Scotland, raised concerns from the Dutch Government who lodged legal challenges against the importation of Scottish mussels on biosecurity grounds. In this case, correct mussel taxonomy may have helped protect the Netherlands (its mussel growers and its native ecosystem), but at the time it cost Scottish growers, at least in the short term, until the problem was resolved.

Seafood traceability has three levels: species identification, geographic location of origin, and supply chain tracking and tracing (Ogden 2008, Larraín et al. 2014). Numerous authors have pointed out the difficulties of identifying aquaculture-produced mussels by species or even by genera, most often because of the absence of shells and/or because mussel flesh is in some processed (unrecognisable) form. As a consequence, several studies have either applied existing molecular markers or developed new markers to test species identity and/or the provenance of mussels (Santaclara et al. 2006, Fernández-Tajes et al. 2011, Larraín et al. 2014). Because these sorts of approaches are informative about mussel species identity and perhaps provenance, they may contribute to supply chain tracking. Compared to other industries (e.g., beef), the seafood tracking component of the aquaculture industry is still young, poorly developed and not that widely applied, but it is increasing and contributes to meeting labelling obligations (e.g., the European decision concerning labelling, Regulation [CE] 104/2000 (Santaclara et al. 2006), the more recent Regulation (EU) n. 1379/2013 (D'Amico et al. 2016) and the *Codex Alimentarius* regulations CE.Nº104/2000 and CE.Nº178/2002 (Larraín et al. 2014)).

In the Southern hemisphere, Chile is by far the largest blue mussel producer, and much of this product is exported to the European Union (EU) in frozen or canned form (Fernández-Tajes et al. 2011). Perhaps not surprisingly then, all blue mussel traceability studies from the Southern hemisphere are from Chilean laboratories. DNA-based methods to assess canned (heat-treated) and frozen products have been developed to identify different mussel species and also different genera (Fernández-Tajes et al. 2011). Examination of four cans of mussels from Galicia (northwest Spain) that were supposed to be Northern hemisphere *M. galloprovincialis* revealed that three cans were correctly labelled and that one can contained *M. chilensis* from Chile, as well as the fact that two mussels were hybrids of *M. chilensis*×*M. trossulus*. This study highlights the value of molecular assays designed for taxonomic (species delimitation) purposes that are applied to food testing with outcomes directly relevant to labelling, fraud by substitution and to consumer protection. Subsequently, Larraín et al. (2014) used microsatellite markers to test the assignment success of blue mussels to populations from southern Chile. Their different assignment approaches showed varying levels of success, up to only ~50%, highlighting the difficulty of identifying the correct production site when population-level genetic differentiation is not pronounced because of the relatively close proximity of the sites and the apparently high levels of gene flow among them (and the possibility of human-mediated transfers). Additionally, the high frequency of occurrence of null alleles in most/all shellfish is likely to hinder the use of microsatellites in the field of food forensics (e.g., Vera et al. 2010). Most recently, in an attempt to move beyond traditional DNA-based PCR methods that are laborious and time-consuming, Jilberto et al. (2017) and more recently Quintrel et al. (2021) have developed a high-resolution melting point analysis that can differentiate among *M. chilensis*, *M. galloprovincialis*, *M. edulis* and their hybrids with high sensitivity, specificity and precision. Increasingly, we will see these sorts of approaches applied to seafood generally, as countries seek to protect their industries and products.

Reference to the results of many different population genetics studies of Southern hemisphere blue mussel species based on nuclear or mitochondrial DNA markers (e.g., Inoue et al. 1995, Santaclara et al. 2006, Westfall et al. 2010, Fernández-Tajes et al. 2011, Larraín et al. 2014) suggests that in terms of aquaculture traceability and species identifications, these markers are powerful enough to differentiate among species and to identify hybrids, but are unlikely to be powerful enough to pinpoint a specific production site when samples from a single species are analysed with samples from other nearby sites within a single region. The application of new SNP markers, as applied to mussels in both the Northern and Southern hemispheres, is expected to substantially increase diagnostic power for traceability and provenance testing. One caveat is that generally speaking SNP analysis requires high-quality DNA, something that may usually be obtained from frozen samples, but may not be so easily obtained from heat-treated (e.g., canned) product and/or product that is sold in wine vinegar (acetic acid) or tomato-based sauce (e.g., Quintrel et al. 2021). Application of the SNP markers to mussels as a food product is an exciting new step forward, and one that may substantially increase traceability and provenance analyses (Vera et al. 2010, Larraín et al. 2014, 2018, Jilberto et al. 2017).

Future research directions

The application of SNPs to Southern hemisphere smooth-shelled mussels has provided a new insight into the evolutionary history and biogeography of this important model group. Some of the results provide a new verification of the specific status of native mussels (e.g., Chile, Argentina/Uruguay, Australia, New Zealand), a subject that has been hotly debated for many years, other results confirm the findings of several different studies that have pointed to the distinct status of native mussels between regions (e.g., South America versus Australasia) and also within regions (e.g., the Falkland Islands, the Kerguelen Islands), while still other findings suggest the existence of new, previously unrecognised lineages (e.g., the New Zealand offshore islands). Below, we highlight in bullet points some areas of research that new generations of molecular markers and also new generations of analytical tools and software may be able to shed light on. This is by no means an exhaustive list. Examples include an improved understanding of

- Species and evolutionary lineages present in the Southern hemisphere and their evolutionary relationships with Northern hemisphere congeners
- The extent of co-ancestry of SNP alleles across all species to clarify the situation for *M. trossulus* in the Southern hemisphere
- The genetic basis of selection to environmental variation, for example at the Kerguelen Islands or at the New Zealand offshore islands compared to the New Zealand mainland
- The genetic architecture of hybridisation between two taxa, whether they are naturally occurring or introduced
- The role that hybridisation may play in the speciation process (i.e., reticulate evolution)
- Karyotype differences between the taxa and lineages and the role that chromosomal differences play in promoting or retarding interbreeding
- The role of cytonuclear incompatibilities in promoting or retarding hybridisation and speciation
- The detection of non-native mussels in the context of biosecurity management and biodiversity protection
- Range expansions and how genetic processes promote or retard these as new areas are colonised by blue mussels in the Southern hemisphere
- The timing of natural range expansions and also invasions by non-natives
- The extent of introgression following hybridisation and which genes or gene complexes are involved

- Species delimitation as quantitative analytical approaches are developed and applied to complex “problem” groups such as smooth-shelled blue mussel
- Population genetic diversity and gene flow, and how connectivity is mediated by, for example, patterns of coastal and oceanic flow and/or rafting on natural and manmade substrata
- How best to apply new markers such as SNPs to food products (frozen, canned, vacuum-packed) and how best to protect producers and consumers via the process of labelling
- How best to apply new markers such as SNPs to counter food substitution (counter-feiting) and to demonstrate and guarantee provenance.

Concluding remarks

Smooth-shelled blue mussels of the genus *Mytilus* have long been a favourite model group, in large part because of their almost cosmopolitan distribution (e.g., the Mussel Watch Program established in 1986 by NOAA as part of the National Status and Trends monitoring programme), their ecological and economic importance, and their intriguing evolutionary history. As a group, these mussels provide new insights into the process of speciation (often in the face of gene flow), into hybridisation and introgression (including speciation by hybridisation), and also into one of the biggest single threats to global biodiversity – bioinvasions. Recent SNP-based work on Southern hemisphere blue mussels has provided a new layer of detail and a new level of confidence to our understanding of this group’s evolutionary origin, phylogeography and their taxonomy and systematics. The SNP markers have helped provide clarity among the many different interpretations provided in earlier times by researchers who did not have the benefit of working with such high-definition markers, as well as providing new insights that simply were not previously possible. SNP markers have not, of course, answered all the questions or resolved all the uncertainties, but coupled with further developments and new applications (e.g., species delimitation models, whole-genome sequencing), smooth-shelled blue mussels will doubtless continue to be an excellent study group to help us better understand the process of speciation in the sea, with all that this entails for global aquaculture, biosecurity and conservation.

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PREDICTING RESPONSES OF GEO-ECOLOGICAL CARBONATE REEF SYSTEMS TO CLIMATE CHANGE: A CONCEPTUAL MODEL AND REVIEW

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Abstract Coral reefs provide critical ecological and geomorphic (e.g. sediment production for reef-fronted shoreline maintenance) services, which interact in complex and dynamic ways. These services are under threat from climate change, requiring dynamic modelling approaches that predict how reef systems will respond to different future climate scenarios. Carbonate budgets, which estimate net reef calcium carbonate production, provide a comprehensive 'snap-shot' assessment of reef accretionary potential and reef stability. These budgets, however, were not intended to account for the full suite of processes that maintain coral reef services or to provide predictive capacity on longer timescales (decadal to centennial). To respond to the dual challenges of enhancing carbonate budget assessments and advancing their predictive capacity, we applied a novel model elicitation and review method to create a qualitative geo-ecological carbonate reef system model that links geomorphic, ecological and physical processes. Our approach conceptualizes relationships between net carbonate production, sediment transport and landform stability, and rates knowledge confidence to reveal major knowledge gaps and critical future research pathways. The model provides a blueprint for future coral reef research that aims to quantify net carbonate production and sediment dynamics, improving our capacity to predict responses of reefs and reef-fronted shorelines to future climate change.

Keywords: Carbonate Budgets; Ecological Modelling; Mental Model Elicitation; Coral Reefs; Reef Islands; Climate Change

Introduction

Coral reefs provide a number of critical ecosystem services. They offer complex habitats for a multitude of marine organisms (Darling et al. 2017) and are critical for maintaining biodiversity that supports economically valuable tourism and fisheries (Spalding et al. 2017). These systems also provide an essential supply of sediment to reef-fronted shorelines and islands (Ogden 1977, Harney & Fletcher 2003, Dawson & Smithers 2014, Cuttler et al. 2019) and act as physical structures that buffer wave energy to protect coastlines (Ferrario et al. 2014, van Zanten et al. 2014). Reef systems rely on the net accumulation of biologically produced calcium carbonate ($CaCO_3$) by reef communities (e.g. corals, crustose coralline algae or CCA), to maintain these ecosystem services. The three-dimensional structure of the reef framework is the result of organisms that produce carbonate (and construct reefs) and the biological, physical and chemical processes that remove carbonate (and deconstruct reefs). Calcifying organisms on reefs include corals, which contribute to the development of the reef structure (Stearn et al. 1977, Hubbard et al. 1990, Perry & Larcombe 2003); CCA, which cement and stabilize the reef framework (Martindale 1992, Rasser & Riegl 2002, Tierney & Johnson 2012); and foraminifera (Hallock 1981), molluscs (Kay & Kawamoto 1983) and algae such as *Halimeda* spp., (Perry et al. 2016; termed direct sediment producers), which contribute to reef sediment sinks upon death (Hallock 2001, Hart & Kench 2007, Browne et al. 2013). Erosion of the reef framework can occur through biological removal by grazing and boring organisms (e.g. parrotfish and molluscs; Frydl & Stearn 1978, Bellwood & Choat 1990, Glynn & Manzello 2015), physical removal by strong wave action and current velocities (e.g. during cyclones; Harmelin-Vivien 1994, Perry et al. 2014) and chemical dissolution (Cyronak & Eyre 2016).

Over time, the balance between reef framework construction and removal (i.e. net carbonate accumulation) results in negative (eroding), limited (static) or positive reef growth (accretionary) potential, also termed the budgetary state of the reef (Chave et al. 1972, Stearn et al. 1977, Scoffin et al. 1980, Hubbard et al. 1990, Perry et al. 2008, Perry et al. 2013b). Both biological and physical processes that erode the reef framework, together with direct sediment producers, generate sediments that are either lost from the reef system (e.g. dissolved or transported off-reef), or incorporated into the reef framework and/or depositional sinks (Kennedy & Woodroffe 2002, Mallela & Perry 2007, Morgan & Kench 2014). Knowledge of these processes can be actualized through the use of a reef carbonate budget, which provides a conceptual approach to capture the geological and ecological processes that drive reef accretion and erosion (Chave et al. 1972, Stearn et al. 1977, Perry et al. 2012, Lange et al. 2020).

A carbonate budget is typically estimated using either (1) the biological census-budget technique (e.g. Browne et al. 2013), (2) the hydro-chemical estimate (e.g. Muehllehner et al. 2016) or (3) from reef cores that are used to determine geological estimates of net carbonate accumulation rates (e.g. Ryan et al. 2001). The census-based approach calculates net carbonate production directly by (1) quantifying biologically produced calcium carbonate based on organism relative abundance and calcification rate (e.g. corals, CCA), and (2) subtracting rates of carbonate removal based on the biomass and/or feeding rates of grazing organisms (e.g. parrotfish and urchins), and abundance and boring rates of internal bioeroding organisms (e.g. bioeroding sponges; Table 1; Stearn et al. 1977, Eakin 2001, Perry et al. 2008). In contrast, the hydro-chemical approach provides an indirect estimate by assessing changes in seawater carbonate chemistry over the reef as a proxy for net calcification, and reef cores estimate historical net carbonate accumulation based upon reef accretion rates (see Lange et al. 2020 for detailed review of carbonate budget methods). Census-based approaches provide a detailed estimate of the net carbonate production over ecological scales (days to years), whereas hydro-chemical estimates provide indirect estimates of net calcification flux over short timeframes (hours to days). Although reef cores provide long-term insight into past reef accretion on geological timescales (centuries to millennia), these *in situ* records of net accretion only provide the cumulative result of constructive and destructive processes rather than a delineation between these processes. Of the >300 reefs globally that have been studied using carbonate budgets, the census-based approach has been applied in 64% of Indo-Pacific and 87% of Atlantic carbonate budget studies (Lange et al. 2020).

Census-based carbonate budgets were primarily designed to provide ‘snap-shot’ estimates of ecological processes, but interest is growing in the potential application of carbonate budgets as a predictive tool for both long-term reef accretion and associated shoreline responses (i.e. accretion/erosion), particularly in relation to climate change (e.g. Morgan & Kench 2016b, Perry et al. 2018b). Understanding how environmental processes interact to enhance or limit carbonate budgets is critical to developing predictive dynamic models of reef accretion, sediment production and landform stability under future climate change. By coupling ecological models and carbonate budgets with future climate scenarios, Kennedy et al. (2013) identified impacts of climate change on the carbonate balance on Caribbean reefs and demonstrated the importance of managing water quality and herbivore fisheries in maintaining carbonate production and reef growth under future climate change. Quantitative dynamic models of carbonate budgets have also been used to assess reef budgetary state at global scales by coupling calcification and bioerosion rates with predicted changes in coral cover under future climate change scenarios (Cornwall et al. 2021). These models quantitatively link ecological processes to environmental drivers to predict responses of constructive and destructive processes on a reef, but how these predicted changes in net carbonate accumulation (based on ecological data from limited temporal and spatial scales) translate to longer-term changes in reef accretion and associated landform stability has yet to be resolved.

The capacity to predict the future trajectory of reefs and associated landforms in the Anthropocene will be of considerable value for future ecosystem conservation and coastal management. To illustrate, thermal coral bleaching events associated with climate change have reduced the abundance and function of carbonate producing organisms globally, resulting in reef degradation, declines in structural complexity and biodiversity, and reduced reef growth (Hoegh-Guldberg et al. 2007, Graham & Nash 2013, Hoegh-Guldberg et al. 2017, Perry & Morgan 2017). These ecological

Table 1 All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
1977 and 1980	Bellairs Reef, Barbados	A detailed survey of carbonate production and loss within ecological zones together with a comprehensive assessment of habitat complexity	Living and dead coral cover, CCA cover, sand and rubble cover, rugosity, coral growth rates and skeletal density, coral composition and community size distributions, CCA growth rates (Stearn et al. 1977), fish species, size and abundance, parrotfish gut content analysis and feeding activity, urchin abundance, test size and gut content analysis, macroboring rates, sediment particle size and composition, sediment accumulation rates, dead reef erosion/lowering rate, diagenetic constituents and reef cementation rates (Scoffin et al. 1980; 26 variables across two papers)	• No assessment of carbonate sediment production as it assumes that the contribution of direct sediment producers was so low to have no effect on gross carbonate production rates • Focuses on five coral species for coral gross carbonate productivity rates and ignores other coral species contributions to the budget • Suggests that mechanical erosion is not important based on *in situ* observations	Stearn et al. (1977) and Scoffin et al. (1980)
1979	Discovery Bay, Jamaica	This study provides an assessment of coral carbonate production with detailed sediment accumulation profiles from seismic scanners and sediment cores	Living coral cover and composition, coral growth rates, sand cover, sediment carbonate content, sediment loss and accumulation rates, sediment size fraction, sediment depth layer, mass of reef-derived sediment (ten variables)	• Limited benthic cover data and no site-specific coral growth data • No data on other carbonate producers, e.g. encrusters or direct sediment producers • No data on biological, physical or chemical erosional rates • Several assumptions made regarding sediment compositional links to gross reef carbonate productivity and coral carbonate productivity rates • No assessment of how carbonate production varies among reef zones	Land (1979)

(*Continued*)

Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
1979	Onslow Island, Galapagos	This study provides an assessment of coral cover and urchin activity to estimate a net carbonate budget	Live and dead coral cover, CCA cover, coral composition, urchin species, abundance, size and grazing rates, urchin gut content analysis, sediment composition and particle size (11 variables)	• Coral gross carbonate production is a function of live coral cover as opposed to growth rates • Carbonate production from other carbonate producing organisms is not included • No assessment of other bioeroding species (fish, macro- and microborers) • No assessment of physical and chemical erosion	Glynn et al. (1979)
1982	Hawaii to Kure atoll, Hawaiian archipelago	This study uses coral cover data from 14 major islands with detailed coral growth assessments for *Porites lobata*	Live coral cover and composition, coral growth rate and skeletal density (four variables)	• Uses *Porites lobata* to represent all coral species growth rates • Suggests that rates of accretion are equal to maximum rates of gross carbonate production due to site selection characteristics • Assumes that rates of chemical and mechanical erosion are negligible • Assumes that gross production rates are equal to net production rates; hence, there is no assessment of rates of carbonate removal • No assessment of carbonate production from other carbonate producing organisms	Grigg (1982)
1984	Cane Bay, St. Croix	This study uses transects and sediment tagging to assess gross carbonate production and sediment dynamics, respectively	Living and dead coral cover, sand cover, CCA cover, rugosity, coral composition, skeletal growth and density, sediment transport loss and accumulation rates, sediment carbonate content (11 variables)	• Uses previously published skeletal growth and density rates • Uses a depth correction factor to include differences in growth rates with depth • Rare coral growth rates are assumed and grouped as ‘other corals’ • There is no measure of the calcification rate of other calcifiers even though the coral sediment fraction is only 45%. Instead, this is estimated from reef cores • No data on physiochemical erosional rates due to the assumption that these elements are captured by changes in sediment accumulation and loss	Sadd (1984)

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Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
1988	Uva Island and Onslow Reef, Eastern Pacific	A detailed study of urchin bioerosion and sediment production pre and post an El Nino warming event	Living coral cover, coral colony size and shape, rugosity, urchin species, abundance, size and grazing rates, damselfish territories, macroboring rates, bioeroder sediment production, sediment composition (12 variables)	• Net carbonate production values are provided but unclear how they were determined, most likely from percentage of living coral cover • Carbonate production from other carbonate producing organisms likely not included • Data on cumulative bioerosion from non-echinoid organisms (mostly macroborers) are provided, but not details on parrotfish • No assessment of physical and chemical erosion	Glynn (1988)
1990	Tiahura, Moorea	A detailed study on urchin densities and size distributions with changing substrate	Living and dead coral cover, coral composition and condition, rubble and sand cover, urchin species, size and abundance, urchin gut content (ten variables)	• Rates of carbonate consumption were based of published exponential relationships between test size and gut content • Uses published coral growth rates and skeletal density to estimate gross carbonate production • Does not account for other carbonate producing organisms • Does not account for other bioeroding organisms and physiochemical processes that remove carbonates	Bak (1990)
1990	St Croix, US Virgin Islands	This study provides an assessment of carbonate production with an estimation of sediment import, export and accumulation rates	Living coral cover, CCA cover, coral composition, growth rates and bulk density, sediment composition, rugosity, sediment import, export and accumulation rate, reef accretion rates (11 variables)	• Some measured and some published coral growth rates used • No *in situ* measures of coralline algae production rates or other encrusting organisms • Several assumptions made around sediment production from bioerosion (based off the Land 1979 study) • No direct estimates of bioerosion from key bioeroding species	Hubbard (1990)

(*Continued*)

Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
1996	Uva Island, Eastern Pacific	This study uses *in situ* census-based data together with published carbonate production rates to develop a carbonate budget model	Live and dead coral cover, CCA cover, damselfish lawn cover, coral composition, rugosity, urchin density, sediment size distribution and hydrodynamic properties (nine variables)	• Uses published growth rates for coral and coralline algae as well as erosion rates from urchins, fish and other non-echinoid grazers • Makes assumptions regarding coral skeletal density • Uses published data on net erosion rates of the reef framework • Assumes that direct sediment producers are not important for the budget • Assumes that rates of chemical erosion are comparatively low compared to physical and biological erosion • Estimates rates of sediment retention based on a comparison between size of sediments produced by bioeroders versus those retained on the reef	Eakin (1996)
2000	13 reefs in three regions (Java Sea, Ambon and South Sulawesi) in Indonesia	This study provides an assessment of benthic cover and carbonate production and removal across several reef sites along a water quality gradient	Live and dead coral cover, algal cover, sand and rubble, sponges, coral composition, growth rate and skeletal density, macroboring rates, water clarity, maximum depth of coral growth, temperature, salinity, chlorophyll-a, nitrate and phosphate concentrations, SPM, sediment accumulation and light intensity (20 variables)	• Applies measured growth (and bioerosion rates) from *Porites* spp. for all corals, thereby assuming approximately equal calcification rates • Assumes approximately equal rates of bioerosion for live and dead standing corals • Uses live corals to estimate bioerosion rates • No estimation of direct sediment producers • No estimation of physiochemical rates of erosion	Edinger et al. (2000)
2000	Green Island, Australia	This study focuses on the contribution of foraminifera to the carbonate budget using a census-based approach	Living coral cover, algal and turf cover, *Halimeda* cover, calcareous algal cover, sand cover, coral composition, sediment trap content weight, sediment composition and particle size, foraminifera density and species composition, wind and current data (14 variables)	• Focuses only on gross carbonate production from corals, foraminifera and *Halimeda*, which were used to calculate total carbonate production. Therefore, no assessment of other encrusters or other direct sediment producers • Does not apply a rugosity factor, so coral production estimates likely underestimated • Uses published carbonate production rates for corals, calcareous algae and foraminifera	Yamano et al. (2000)

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Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2001	Uva Island, Eastern Pacific	Study combines *in situ* census-based data with published carbonate production rates to develop a carbonate budget model	Same as Eakin et al. (1996)	• Same as Eakin et al. (1996)	Eakin (2001)
2003	Kailua Bay, Oahu, Hawaii	An assessment of carbonate production and removal that also considers variable production between zones and includes direct sediment production rates	Live and dead coral cover, macro and turf algal cover, CCA cover and growth rates, sand and reef framework cover, rugosity, coral composition, growth rates and skeletal density, urchin abundance and size, macroboring rates, sediment depth layers, sediment carbonate content and composition, mechanical erosion rate (19 variables)	• Coral growth rates sourced from the literature except for three key coral species • Assumes that timeframe of coral rubble availability for macroboring rates related to coral vertical height and growth rates • Estimates of urchin bioerosion rates taken from previous studies • Uses published turnover rates to estimate direct sediment production rates • Physical erosion on *in situ* framework included but based on previously published estimates • No estimates of chemical erosion	Harney & Fletcher (2003)
2007	Rio Bueno, Jamaica	A comprehensive carbonate budget using transects and *in situ* experiments together with environmental data collection	Living and dead coral cover, algal cover, rubble, reef framework and sand cover, rugosity, coral composition, growth and skeletal density, encrusting community composition, cover and growth, fish species, numbers and size, urchin density and size, macroboring and micro-boring rates, sediment accumulation rates, rates of framework infilling, sediment carbonate content and composition, temperature, salinity, DIN, phosphorus, ammonia, light, suspended sediments (31 variables)	• Uses previously published coral growth and density rates • Uses a depth correction factor to include differences in growth rates with depth • Rates of bioerosion from dead coral colonies are based on the assumption that corals were recently dead • Estimates of urchin bioerosion rates taken from previous studies and applies a correction factor to consider reworked sediments • Calculation of fish erosion rates also uses off site data, a correction factor and no assessment of fish behaviour • No assessment of direct sediment production rates • No estimates of physical erosion on both sediments or *in situ* carbonate framework	Mallela & Perry (2007)

(*Continued*)

Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2007	Warraber Island, Torres Strait, Australia	This study assesses gross carbonate production using quadrates and transects within ecological zones	Living coral cover and composition, CCA cover, *Halimeda* cover, sponge and brown algal cover, seagrass cover, sand and reef framework cover, rugosity, sediment depth and type, foraminifera and mollusc abundance (14 variables)	• Uses previously published rates for all calcifying organisms and applies an adjustment factor based on organism abundance • Focuses on gross carbonate production so not a full budget	Hart & Kench (2007)
2012	Bonaire	This study provides the method of a rapid census-based approach termed 'ReefBudget', which focuses on quantifying the relative contributions of key calcifying organisms	Living coral cover, CCA cover, turf and macroalgal cover, *Halimeda* cover, sand, rubble and reef framework cover, rugosity, coral composition, growth rates and skeletal density, encrusting cover and growth rates, parrotfish species, size and abundance, parrotfish bite rates, scars and mass eroded, urchin abundance, size and species, clionid sponge cover, microbioerosion rates (25 variables)	• Uses previously published coral growth and skeletal rates • Uses the average calcification rate for the encrusting carbonate producers • Fish, urchin, sponge and microbioerosion rates based on previously published (off site) data that takes limited account of differences in depth, reef habitat and other environmental drivers of these processes • No assessment of direct sediment production rates • No assessment of physical or chemical erosion rates	Perry et al. (2012)
2013	19 reefs in the Caribbean	This study uses the ReefBudget method to assess carbonate production on several reefs	Same as Perry et al. (2012)	• Same as Perry et al. (2012)	Perry et al. (2013b)

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Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2013	Middle Reef and Paluma Shoals, Great Barrier Reef, Australia	A comprehensive study of carbonate production and removal in ecological zones with a detailed assessment of sediment dynamics and direct sediment production	Live and dead coral cover, macro- and turf algal cover, CCA cover, encrusting community cover, composition and growth rates, sand, rubble and reef framework cover, rugosity, coral composition, growth rates and skeletal density, fish species, abundance and size, urchin abundance and size, macroboring rates, light, suspended sediments, direct sediment producers, net sediment accumulation rates, sediment export rates, sediment depth layers, sediment particle size, carbonate content and composition (30 variables)	• Coral growth rates of the three most abundant corals measured on site, but the remaining coral growth rates sourced from the literature • Assumes coral rubble samples for macroboring rates have been available for <1 year on the reef • Estimates of urchin bioerosion rates from previous studies • Uses published turnover rates to estimate direct sediment production • No estimates of physical erosion on *in situ* carbonate framework • No estimates of chemical erosion/dissolution	Browne et al. (2013)
2013	Warrabar Reef and Bet Reef, Torres strait	Study combines published census-based data with remote sensing data to provide an estimate of carbonate production for a number of reef habitats	Living coral cover and composition, CCA and *Halimeda* cover, seagrass, sand and reef framework cover, rugosity, sediment depth and type, foraminifera and mollusc abundance, wave exposure (13 variables)	• For Warraber reef, uses site-specific carbonate production rates from Hart & Kench (2007) • For Bet reef, uses published substrate data together with non-site-specific data on carbonate production • Includes additional limitations as outlined for Hart & Kench (2007)	Leon & Woodroffe (2013)

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Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2013	One Tree Island, Australia	Study compares rates of gross carbonate production from a census-based approach with hydro-chemically derived estimates, and uses remote sensing to classify reef habitat types over broad areas	Live and dead coral cover, macroalgal cover and algal mat, sand, rubble and consolidated rubble cover, reef platform (eight variables)	• Study focuses on gross carbonate production so does not include estimates of carbonate removal • Uses off-site published carbonate production rates for corals, coralline algae and direct sediment producers	Hamylton et al. (2013b)
2014	Vabbinfaru Reef, North Malé Atoll, Maldives	This study provides a detailed census-based carbonate budget of different reef eco-geomorphic zones, which also includes an assessment of sediment flux and a sediment budget	Live and dead coral cover, CCA and Halimeda cover, sand, rubble and reef framework cover, rugosity, coral composition, growth rates and skeletal density, encruster community composition and calcification rate, CCA carbonate production, fish species, abundance and size, urchin abundance and size, macroboring rates, light, suspended sediments, net sediment accumulation rates, sediment export rates, sediment depth layers, sediment particle size, carbonate content and composition, reef island planform morphology, wave energy (30 variables)	• Coral growth and calcification rates calculated for a selection of dominant hard corals • Does not account for chemical dissolution of reef framework • Internal bioerosion rates of lagoon rubble assumed available for 10 years (since 1998 bleaching event) • Uses published rates of urchin bioerosion • Calculates parrotfish erosion rates for dominant initial and terminal phase excavating species (not scrapers) • Microbioerosion rates from published literature and applied uniformly to reef substrates	Morgan (2014)

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Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2015	75 sites across the Caribbean	This study uses the ReefBudget method (with some additional transect and rugosity data measurements)	Same as Perry et al. (2012)	• Same as Perry et al. (2012)	Perry et al. (2015c)
2015	Great Chagos Bank, Peros Banhos, Salomon	This study presents a modified version of the ReefBudget method for the Indo-Pacific region. Sites were also classified based on wave exposure for modelling purposes	Living coral cover, CCA and non-encrusting coralline algal cover, turf and fleshy macroalgal cover, *Halimeda* cover, sand, rubble and reef framework cover, rugosity, coral composition, shape and size, growth rates and skeletal density, parrotfish species, size and abundance, parrotfish bite rates, scars and mass eroded, urchin abundance, size and species, micro and macrobioerosion rates, sediment production rates by macroborers (27 variables)	Key differences with the previously published ReefBudget method include • The use of published rates of clinoid sponge bioerosion rather than in-water surveys • Inclusion of sediment production rates from macroborers • Coral colony size, growth, density and geometric shape are used to calculate coral carbonate production. In addition, • There is also no assessment of encrusting carbonate production rates (excluding CCA) • Areas where published data are used include coral growth rates and skeletal densities, macro- and microbioerosion rates and some data related to parrotfish erosion activity • No assessment of physical or chemical erosion rates	Perry et al. (2015b)
2016	Curacao and Bonaire, Caribbean	Study focusing on the coral community and applies growth rates from the ReefBudget method	Live coral cover, coral composition and size distributions, dead coral cover (four variables)	• Focuses on coral carbonate production only • Does not apply a rugosity factor so coral production estimates are likely underestimated • Uses previously published coral skeletal growth and density rates • Uses a depth correction factor to include differences in growth rates with depth	De Bakker et al. (2016)

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Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2017	Seychelles Islands	This study was carried out using 5 years of data (1994–2014) along the reef front to track changes in net carbonate production over time	Same a Perry et al. (2015b)	• Same a Perry et al. (2015b)	Januchowski-Hartley et al. (2017)
2017	Zanzibar Island chain, close to Stone Town, Zanzibar	This study uses the original ReefBudget approach to assess net carbonate production with biodiversity indices and coral structural complexity along an offshore gradient	Same as Perry et al. (2012)	• Same as Perry et al. (2012)	Herrán et al. (2017)
2017	Gaafu Dhaalu Atoll, Southern Maldives	This study uses the modified ReefBudget approach for the Indo-Pacific to assess changes in carbonate budgets due to a coral bleaching event	Same a Perry et al. (2015b)	• Same a Perry et al. (2015b)	Perry & Morgan (2017)

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Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2017	Lhaviyani Atoll, Central Maldives	This study uses a census-based approach to demonstrate spatial differences in carbonate production at the inter-reef habitat scale	Same as Perry et al. (2015b), study, with the addition of *Halimeda* plant volume, number of non-*Halimeda* calcifying green algae, number of articulated red coralline algae, number of epifaunal gastropods, sediment compositional analysis (33 variables)	• Same a Perry et al. (2015b)	Perry et al. (2017)
2018	Cheeca Rocks, Florida Keys	This study uses the original ReefBudget approach conducted annually on the reef from 2012 to 2016	Same as Perry et al. (2012)	• Same as 2012 Perry et al. study • However, site-specific coral growth rates and skeletal density for *Orbicella faveolata* were determined using X-radiographs and CT scanning, respectively • It was then assumed that all other coral species at the site had the same growth dynamics as the measured *Orbicella faveolata* relative to the default ReefBudget values	Manzello et al. (2018)
2018	86 sites across the Caribbean and 68 sites in the Indo-Pacific region	A meta-analysis of carbonate budgets studies, most using the census-based ReefBudget method or adaptations of this method	Same as Perry et al. (2012)	• Same as Perry et al. (2012)	Perry et al. (2018)

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Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2018	Red Sea, Saudi Arabia	This study adapted the original ReefBudget approach and also deployed carbonate blocks to better estimate rates of net reef accretion and erosion	Living and dead coral cover, CCA cover, turf and macroalgal cover, reef framework cover, rugosity, coral composition and growth rates, CCA growth rates, parrotfish species, size and abundance, urchin abundance, size and species, net accretion/erosion rates (blocks), temperature, salinity, pH, nitrite/ate, ammonia, phosphate, TA (24 variables)	• No assessment of direct carbonate sediment production (or chemical dissolution) • Uses literature-based values to calculate grazing fish and urchin bioerosion rates • No estimates of physical erosion on *in situ* carbonate framework	Roik et al. (2018)
2018	Palau & Yap, Western Pacific Ocean	This study combines *in situ* cover of carbonate producing organisms with published production/ removal rates to produce a spatial visualisation of net carbonate production over the reef	Living and dead coral cover, CCA cover, macroalgal and sponge cover, coral composition, growth rates and skeletal density, rugosity, fish species, abundance and size, urchin species, abundance and size (15 variables)	• Uses published coral linear growth rates • Uses published data on CCA carbonate production rates • Estimates on parrotfish and urchin erosion rates based on published data • Macroboring is not measured but related to the surface area available • Uses published bioerosion rate for sponges • No assessment of direct sediment producers • No assessment of physical or chemical erosion	van Woesik & Cacciapaglia (2018)

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Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2019	Cocos Keeling	A geo-spatial assessment of carbonate budget using *in situ* census-based data together with remote sensing to provide a carbonate budget that covers a considerable spatial area (225 km^2)	Living and dead coral cover, CCA cover, turf cover, encrusters cover, seagrass cover, sand, rubble and reef framework cover, rugosity, coral composition, growth rates and skeletal density, sediment composition, sediment export rates, macroborer erosion rate, parrotfish species, size and abundance, urchin abundance and size (21 variables)	• Used published literature for sediment composition, production and export rates • Uses published data for parrotfish bioerosion rates • Some of the coral growth rates are also calculated using published rates • No assessment of chemical erosion or microbioerosion	Hamylton & Mallela (2019)
2019	Great Chagos Bank, Peros Banhos, Salomon in the Chagos Archipelago	This study used the modified ReefBudget approach for the Indo-Pacific to assess the impacts of a warming event on gross carbonate production rates	Living coral cover, CCA and non-encrusting coralline algal cover, turf and fleshy macroalgal cover, *Halimeda* cover, sand, rubble and reef framework cover, rugosity, coral composition, shape and size, growth rates and skeletal density (15 variables)	This study was based the modified ReefBudget approach (Perry 2015b) with the following differences: • Only included an assessment of carbonate production from corals and key algal species • No assessment of erosion (biological, physical or mechanical) was included • Coral growth rates were assumed to be consistent across biogeographic regions and throughout the bleaching event	Lange & Perry (2019)

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Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2019	Mahutigala reef, Gaafu Dhaalu Atoll, Maldives	This study uses the modified ReefBudget approach for the Indo-Pacific to assess the impact of a warm SST anomaly event on net carbonate production for a reef platform	Live and dead coral cover, CCA and algae cover, rubble and reef framework cover, rugosity, coral composition, shape, growth rates and skeletal density, CCA growth rates, parrotfish bioerosion rates, urchin genera, abundance and erosion rates, micro- and macrobioerosion rates (18 variables)	• Same assumptions as the previously published ReefBudget methods (Perry et al. 2012, 2015b) • Study also assumes that parrotfish bioerosion rates are the same as that recorded for the fore reef (as opposed to the reef flat) in 2016 • Zones of high productivity post-bleaching are now *Heliopora* dominated for which there are no calcification rates available • No correction for inter-blade spaces in benthic cover estimates of *Heliopora*, i.e. likely overestimates carbonate production	Ryan et al. (2019)
2019	Bonaire fringing reef, Caribbean	This study uses the original ReefBudget approach to estimate both net carbonate production and associated reef growth	Same as Perry et al. (2012) study, with the addition of maximum reef height and sponge-specific erosion rates (27 variables)	Same as Perry et al. (2012) with some modifications that include • Takes into account the impact of depth on coral growth rates • The contribution of sponges to gross bioerosion was determined using species-specific erosion rates per unit of infested substrate as defined by De Bakker et al. (2018) • There was some modification to estimates of bioerosion from parrotfish	De Bakker et al. (2019)

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Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2020	Offshore coral reefs, Singapore	This study uses the modified ReefBudget approach for the Indo-Pacific to assess net carbonate production for a highly urbanized reef system	Living coral cover, CCA and non-encrusting coralline algal cover, turf and fleshy macroalgal cover, *Halimeda* cover, sand, rubble and reef framework cover, rugosity, coral composition, shape and size, growth rates and skeletal density, CCA calcification rates, parrotfish species, size and abundance, urchin abundance, size and species, *internal bioerosion rates (macro- and microborers), epilithic algal matrix, microbes and microalgae* (27 variables)	This study was based off of the modified ReefBudget approach (Perry et al. 2015) with some further modifications that include: • Uses published fish and urchin ingestion rates as opposed to measuring activity *in situ* • Uses published ReefBudget coral growth rates for Indo-Pacific corals combined with local growth rates where available • Includes additional methods and variables (in italics) including CCA growth rates and internal bioerosion estimates to provide improved site and time specific data on these variables	Januchowski-Hartley et al. (2020)
2020	Heron Reef, Australia	This study uses the ReefBudget approach to provide a carbonate and sediment budget for five distinct reef zones	Living coral cover, CCA cover, turf and macroalgal cover, *Halimeda* cover and biomass, sand, rubble and reef framework cover, rugosity, coral composition and calcification rates, CCA calcification rates and *Halimeda* sediment production rates, parrotfish species, size and abundance, parrotfish bite rates and mass eroded, external and internal macrobioerosion rates, clinoid sponge cover, microbioerosion rates, carbonate sediment production and dissolution, temperature and light (PAR) (27 variables)	A comprehensive carbonate budget study with the following assumptions/exclusions: • Uses previously published rates of CCA calcification rates (although from the same study site) • CCA are the only encrusters considered • Only direct sediment producer quantified was *Halimeda* • Parrotfish bioerosion rates based on previous models that estimate carbonate removal based on size and life phase • Rates of carbonate removal by worms and bivalves, and internal bioerosion sourced from the literatures • No estimates of physical erosion • No inclusion of rates of sediment import or export	Brown et al. (2020)

responses will lead to increased wave transmission across reefs and decreased shoreline protection, which will be further exacerbated by sea level rise (Harris et al. 2018). Collapse of reef function can therefore result in increased coastal erosion and inundation (Beetham & Kench 2018). Future landform erosion could lead to loss in terrestrial biodiversity, human displacement and in extreme cases loss of life (Ferrario et al. 2014). Incorporating dynamic modelling approaches with data on reef ecological function and carbonate sediment production, and transport at whole-reef scales would provide key insight into the future maintenance of the entire system under future sea level rise and climate change scenarios.

To respond to the dual challenges of enhancing carbonate budget assessments and advancing them to create predictive capacity in the face of global environmental change, our goal was to create a qualitative geo-ecological carbonate reef system model that links geomorphic, ecological and physical processes. First, we reviewed the history and present applications of **census-based** carbonate budgets and highlight their strengths and weaknesses. Second, we employed a novel model elicitation method that aggregated expert knowledge from key disciplines (ecology, sedimentology, biogeochemistry, coastal geomorphology) to develop a new geo-ecological reef system model. This new model was comprised of six sub-system modules (*in situ* carbonate production, acute disturbance events on coral reef communities, coral reef response to sea level rise impacts, bioerosion, net carbonate sediment production and carbonate sediment transport and depositional sinks) that build on existing carbonate budgets and capture connections to sediment dynamics. For each module, we evaluated all known variables through an extensive literature review and selected dominant variables for inclusion in future carbonate budgets and models. In addition, we provided a semi-quantitative assessment of our collective confidence in the model, which highlights knowledge gaps for future research. We anticipate that our qualitative model will provide a blueprint for future reef system studies that aim to quantify net carbonate production and the sediment production processes that influence landform stability, improving the current capacity to predict responses of reefs and reef-fronted shorelines to future climate change.

Census-based carbonate budgets

The first census-based carbonate budget method was published in 1972 and aimed to understand the theoretical relationships between potential carbonate production, gross production and net production (Chave et al. 1972). Following this landmark study, Stearn et al. (1977) were the first to apply this budget method, which they did on Bellairs Reef, Barbados. This work was shortly followed by Land (1979), who conducted a comprehensive study of reef sediment profiles in Jamaica using seismic scanners and sediment cores to assess reef-wide changes in carbonate production and reef framework development. Over the next 20 years, only seven carbonate budget studies of varying focus (e.g. coral carbonate production, bioerosion, sediment dynamics) and complexity (4–11 variables; Table 1) were published. Since 2000, application of the technique has increased, with 29 published census-based studies (Table 1). These studies have focused on community carbonate production rates, with some studies also incorporating site-specific components of benthic cover (e.g. algal, rubble, sediment cover), bioerosion (e.g. fish and sea urchin grazing; Morgan 2014), environmental variables (e.g. light, suspended sediments, nutrients; Mallela 2007) and mechanical erosion (Harney & Fletcher 2003; Table 1). These later, and largely ecological-focused, studies included a greater number of variables than early geological studies (average 20 variables; maximum 33; Table 1) and, as such, provide a more detailed overview of reef ecological state and accretionary potential.

Since the initial publication of the carbonate budget method, however, a number of challenges have arisen. These challenges relate to three main areas: inclusion of ecological complexity; data collection and application; and inclusion of environmental drivers. In addition to these existing challenges, a number of future challenges for census-based carbonate budget studies also exist. These challenges are critical to consider if predictive tools for reef budgetary state and landform stability are to be realized. Future challenges include the integration of carbonate sediment production, loss and transport, and a comprehensive assessment of landform change (Table 2). Furthermore, carbonate budget studies may benefit from improved integration of the three main data collection approaches (census-based, hydro-chemical, coring) to identify mechanisms responsible for changes in budgets that operate over different timescales as well as enabling direct comparisons between methods. Here, we discuss each of these challenges in turn.

Current challenges for census-based carbonate budget studies

Inclusion of ecological complexity

Ecological assessments in census-based carbonate budgets can be biased towards data that is easier to collect, reducing accurate representations of ecological complexity. In other words, the more accessible the data, the more likely it is to be included in an assessment. For example, the most commonly reported variables in carbonate budgets relate to benthic cover (living coral cover – 100%, dead coral cover – 68%, sand/sediment cover – 73% of studies; Table 1). Methods used to estimate benthic cover are relatively easy to carry out (e.g. line intercept transect) because they do not require expensive equipment and can be conducted in a relatively short timeframe (days; English et al. 1997). As such, a large amount of data on benthic cover can be collected quickly.

In contrast, those variables less commonly reported are ones for which the data take longer to collect, such as erosion from borers (39% of studies). Boring organisms are typically small to microscopic, often patchily distributed (e.g. bivalves) and are cryptic in nature (e.g. sponges, polychaetes; Diaz & Rützler 2001, Pari et al. 2002, Hutchings 2011, Schönberg et al. 2017). As a result, their abundance and erosion rates cannot necessarily be determined visually along a transect but instead require, for example, high levels of expertize and expensive analytical equipment (e.g. scanning electron microscopy) to both locate and identify organisms and assess rates of carbonate removal (Enochs et al. 2016, Färber et al. 2016). Other problems arise because internal rates of bioerosion are likely to be non-linear (e.g. Roff et al. 2020), requiring the deployment of experimental substrates over long-time periods (years), onto which these organisms recruit (Pari et al. 1998, Pari et al 2002, Tribollet 2008a,b, Enochs et al 2016, Silbiger et al. 2017). Additionally, their interactions with each other and the environment can be complex (e.g. featuring successional and disruptional feedbacks, Schönberg et al. 2017, Roff et al. 2015b), yet census-based carbonate budget calculations often rely on an 'average' value of bioerosion from snap-shot *in situ* experiments. Long-term studies, expensive equipment and high level of expertize require additional investment of resources, which are limited for many research projects. The consequences of generating assessments that are biased towards easily accessible data (e.g. data from rapid visual assessments) is that key components of the carbonate budget are likely to be under or mis-represented and the estimated net carbonate production may be incomplete or inaccurate.

Data collection and application

Existing studies have typically used different methods to generate data. For instance, estimates of *in situ* calcification rates commonly require the use of two or more different methods to estimate skeletal density and linear growth (review by Fitzer et al. 2019; also see Table 3) due to variable coral morphology (e.g. branching, plating and massive). For example, corals with massive morphologies, and some branching morphologies (e.g. *Isopora* spp.), are long-lived and produce regular annual density bands that enable growth rate measurements along a relatively well-defined growth axis v(Lough & Barnes 1992, Cantin & Lough 2014, Razak et al, 2020). Massive corals, however, grow slowly (~1 cm·yr^{-1}), and calcification rate measurements require the use of x-radiography to identify

Table 2 Summary of current (1–3) and future challenges (4–5) of census-based carbonate budget studies. For each challenge, we summarize why it exists, potential associated impacts and how it can be addressed

Current challenge	Why it exits	Impact/s	Addressing the limitation
1. Inclusion of ecological complexity	• Logistical difficulties associated with certain variables or processes that results in a bias towards data that are easier to collect • Lack of resources to support those more expensive or time-consuming methodologies • A diversity of organisms to include • Perception that some variables are not important due to a lack of knowledge and/or understanding	• Key variables (or processes) of the carbonate budget are under-represented and the estimated net carbonate production may, therefore, be inaccurate	• *Improve current understanding on which variables are key for carbonate budgets and should be included*
2. Data collection (methods and variables) and application	• Lack of resources (e.g. time and money) • Diversity of methods available • Differences in reef types and settings leading to different variables and related methodologies	• Inability to compare data across sites accurately	• *Improve current understanding on which variables are key for carbonate budgets and should be included* • Develop standardized methods that better quantify key variables, e.g. physical erosion • Conduct studies that quantitatively compare different methods to assess inter-useability
3. Inclusion of environmental drivers	• Carbonate budgets are skewed towards biological carbonate production and loss • Logistical difficulties related to methodological requirements (e.g. sediment transport) • Lack of knowledge and understanding of non-biological processes that influence carbonate budgets (e.g. dissolution)	• Incomplete assessment of net carbonate production on a reef. • Furthermore, the lack of environmental data with carbonate budget data reduces ability to predict future changes in net carbonate production	• *Improve current understanding on which variables are key for carbonate budgets and should be included* • Highlight the value of environmental (cause) data with biological data (effect) for future carbonate models

(*Continued*)

Table 2 (*Continued*) Summary of current (1–3) and future challenges (4–5) of census-based carbonate budget studies. For each challenge, we summarize why it exists, potential associated impacts and how it can be addressed

Current challenge	Why it exits	Impact/s	Addressing the limitation
4. Integration of carbonate sediment production, loss and transport	• Methodological difficulties associated with quantifying sediment production • The assumption that the dissolution of existing carbonate sediments is not important (lack knowledge and understanding) • The assumption that carbonate sediments do not contribute to the development of the reef structure	• Rates of carbonate sediment production on coral reefs are poorly quantified, plus a common assumption is that sediments are lost from the carbonate system • Poor understanding of how disturbance-related shifts in reef communities alter rates and types of reef sediment production • Difficult to assess the impacts of future climate change (e.g. OA) on existing detrital sediment reservoirs (e.g. islands)	• *Identify which variables are key to quantifying net carbonate sediment production* • More quantitative studies (including carbonate budget studies) on direct sediment production • More studies that aim to provide better methods (using new technologies) to accurately quantify rates of carbonate sediment production for a range of calcifying taxa
5. Assessments of landform stability	• Limited carbonate sediment production studies due to methodological issues/ difficulties • Logistical and methodological difficulties due to our limited understanding of timescales of biological sediment production and physical sediment transport • Carbonate budgets were never designed to explicitly address these connections	• Difficult to predict how changes in sediment production will influence the stability of associated landforms	• *Identify variables (and processes) key to understanding how changes in reef carbonate sediment production influence landform stability* • Multi-disciplinary (and novel) studies that assess biophysical processes and interactions across a range of timescales • More carbonate budget studies that assess the whole-system (reefs to landforms)

Note: Text in italics indicate areas that are addressed within the geo-ecological carbonate reef system model.

annual growth bands together with quantification of skeletal density using methods such as X-ray computed tomography (Table 3). In contrast, corals with a branching morphology grow relatively fast (3–15 cm·yr^{-1}; Crabbe & Smith 2005, Browne 2012, Morgan & Kench 2012, Pratchett et al. 2015) and are typically the dominant reef building taxa on structurally complex coral reefs (Perry et al. 2018a). Yet, many branching and plating corals lack density banding and are instead characterized by complex growth morphologies, making estimates of calcification more challenging and time-consuming to measure. For branching and plate corals, these methods include visual estimates of changing branch or plate length (e.g. direct linear measurements); buoyant weighing to quantify changes in skeletal mass; skeletal staining to quantify changes in colony growth; and photogrammetry to capture changes in the size of individual colonies in an area of reef (Table 3). To date, few studies normalize growth rates to colony surface area to enable comparisons between the calcification rates of corals that vary in size or morphology, and no study has quantitatively compared these three methods to determine their inter-useability.

One of the main limitations that arises when different methods (and variables) are used is an inability to compare data across sites accurately. Site comparisons are useful for a number of reasons. For example, they provide comparisons between reef types and regions, which is important for assessing broad-scale ecological and reef budgetary states. In addition, site comparisons can be used to identify those reefs that are either more sensitive and/or resilient to future climate changes, which is critical for conservation management actions. Accurate site comparison relies on studies that use the same measured variables and data collection methods, or methods for converting between different collection methods to provide meaningful comparisons.

The ReefBudget census-based approach published in 2012 has made significant steps towards enabling ecological comparisons across a range of spatial scales (Perry et al. 2012). This approach builds on the traditional census-based carbonate budget (e.g. Chave et al. 1972; Table 1, Land 1979, Hubbard et al. 1990) and provides a standardized and rapid method to calculate reef carbonate production and bioerosion via the collection of abundance data on calcifying and eroding organisms. Prior to 2012, carbonate budgets were estimated using a variety of variables (i.e. organisms and their activity, processes; Table 1) and methods (Table 3). In contrast, the ReefBudget approach combines the collection of site-specific data on over 20 selected variables that can be measured within a few days (e.g. coral cover and composition) with previously published data on variables that require longer timeframes to measure (e.g. coral and CCA growth rates and urchin, fish, macroborers and microbioerosion rates). If employed over several years along permanent transects, the ReefBudget approach can be used to track changes in net carbonate production over time, identify changes in reef state (decline, stable, incline) from natural cycles in reef health (e.g. Manzello et al. 2018) and assess impacts of major disturbance events (e.g. Lange & Perry 2019). Furthermore, the approach allows for comparisons among reef habitats (e.g. Perry et al. 2017, Brown et al. 2020) and across biogeographic regions (Perry et al. 2018b), and has since been used in more than 50% of all census-based carbonate budget studies (Table 1). Despite the benefits of this comparison method, a number of challenges remain.

Inclusion of environmental drivers

Census-based assessments capture direct *in situ* metrics of carbonate production and removal, and as such provide limited or no insight into how these processes are influenced by, or respond to, environmental drivers (e.g. light, temperature, water flow). Our comparison of census-based budgets found that, although all reef and benthic cover variables were well described, very few studies (16%) had quantified local environmental variables (e.g. temperature, light, turbidity) when conducting carbonate budgets (Table 1). Thus, because census-based carbonate budgets capture *in situ* metrics of carbonate potential/removal, they typically lack environmental observations, reducing the ability to assess how production/removal processes are influenced by, or respond to,

Table 3 A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework production	Coral	Calcification rate	Corals are typically the main carbonate producer particularly on tropical coral reefs. Due to variable coral morphology both among and within coral species, there are a number of different techniques that address one or more aspects of coral growth. For branching corals, linear extension refers to an increase in length (cm) along the branches growth axis whereas for encrusting, plating or foliose corals an increase in surface area (cm^2) is more common. For those massive corals other techniques that look at changes in total volume (cm^3) are preferred. These variables can then be used to determine the calcification rate (e.g. linear extension * skeletal density). Coral calcification rate can also be measured using the buoyant weight technique and changes in weight can then be normalized to colony surface area (i.e. grams or kg of $CaCO_3$ per unit of surface area per unit in time). The total alkalinity (TA) depletion method is used to measure coral calcification because TA changes in response to the precipitation and dissolution of $CaCO_3$	Linear extension	1. Direct linear measurement *in situ* using callipers along the branch axis. Small cable ties can be put in place on the branch as a point of reference for repeated measurements	Measures the increase in length of the branch over a known time period, but is time intensive and limited to branching corals	Crabbe & Smith (2005), Morgan & Kench (2012)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework production (cont.)	Coral (cont.)	Calcification rate (cont.)	See previous page	Linear extension (cont.)	2. Alizarin red to stain corals *in situ* to create a 'time stamp' on the coral skeleton for future measurements. Corals are placed in an enclosed volume (e.g. a plastic bag) into which the dye is injected. The bag is left over the coral colony for ~4 hours before it is removed. Samples from the coral colony or the whole colony is later retrieved. In the laboratory, the coral tissue is removed to expose the under lying skeleton. Newly laid skeleton (post-dying) is white and old skeleton is pink	Provides an estimate of the weight of new carbonate produced over a known time but is time intensive and destructive to coral community. It can, however, be used on all coral morphologies that can be enclosed in an isolated environment (e.g. plastic bag) for staining	Crossland (1981), Browne (2012), Morgan & Kench (2012)
					3. X-radiography of corals to assess annual density banding in massive corals	Typically only useful for massive corals with distinctive growth bands; destructive and expensive as corals have to be removed	Lough & Barnes (1992); Cantin & Lough (2014)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework production (cont.),	Coral (cont.)	Calcification rate (cont.)	See previous page	Linear extension (cont.)	4. Photogrammetry *in situ* to track change in linear extension and volume over time	A non-destructive technique that estimates increases in coral volume of the whole coral colony over a known timeframe but requires expertize in post-processing of photos. Further changes in volume can only identified from photos when a threshold of change has been reached (e.g. a few mm)	Ferrari et al. (2017), Lange & Perry (2020)
				Surface area	1. Bird's-eye photographs of corals collected and analysed for surface area using computer software (e.g. CpCE)	Comparatively easy and quick but accuracy of the surface areas is highly dependent on coral morphology with better estimates for 'flat' corals	Courtney et al. (2007), Holmes et al. (2008); Browne et al. (2015)
				Surface area	1. Paraffin wax and foil wrapping to determine surface area. Individual colonies are either foil wrapped or coated in paraffin wax. The foil can then be unwrapped to determine the surface area. The paraffin wax technique relies on changes in weight (associated with surface area) using a calibration curve (created using objects of known surface area)	Destructive and can be labour-intensive, but can be applied to all coral morphologies	Marsh 1970; Stimson & Kinzie (1991)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework production (cont.)	Coral (cont.)	Calcification rate (cont.)	See previous page	Surface area (cont.)	2. X-ray computer tomography (CT) and 3D scans of branching coral colonies collected and analysed for surface area	This destructive technique is considered to be the most accurate for surface area estimates but can be labour-intensive and requires expensive equipment	Laforsh et al. (2008), Naumann et al. (2009), Foster et al. (2014), Ross et al. (2015)
				Skeletal density	1. X-ray computer tomography (CT) scans of massive coral cores have been used to calculate annual growth rates, skeletal density and coral calcification rates	Destructive and expensive but provides data on a number of key coral parameters	Cantin et al (2010), DeCarlo et al. (2017)
					2. Water displacement technique where a known weight of coral (sealed in wax) displaces a measured volume of water	Comparatively easy and cheap, but has potential for errors if not replicated appropriately	Bucher et al. (1998); Morgan & Kench (2012)
					3. Gamma densitometry: The use of gamma rays provides an important non-destructive method for determining the density along predetermined tracks	Destructive as it requires samples to be cut to a consistent thickness. However, provides excellent high-resolution, coral skeleton density data	Chalker & Barnes (1990), Lough & Barnes (1992)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework production (cont.)	Coral (cont.)	Calcification rate (cont.),	See previous page	Volume change	1. Photogrammetry (as above)	As above	Ferrari et al. (2015); Lange & Perry (2020)
				Total alkalinity depletion	1. Coral colonies are maintained in water chambers with water samples taken for Total Alkalinity (TA) analysis to quantify coral calcification rates	Labour-intensive method that requires expensive equipment and laboratory analysis	Smith & Kinsey (1978), Schneider & Erez (2006), Sawall et al. (2015)
				Buoyant weight	1. Coral colonies are weighed while submerged in water to obtain skeletal weight. Repeat measurements of skeletal weight over time is used to quantify calcification rate	Direct, accurate, and non-destructive. Beneficial for whole coral colonies, especially those with complex morphologies. This method overcomes the issues of intra-colony density variation and skeletal infilling over time for common genera (e.g. *Acropora*) and is non-destructive allowing the same colony to be measured repeatedly over time. Inexpensive but can be labour-intensive	Bak (1973), Jokiel et al. (1978), Roik et al. (2015) for literature review table of calcification rates measured using buoyant weight

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework production (cont.)	Coral (cont.)	Abundance	The percentage coral cover (per coral species and/or morphology) is used to calculate the weight of carbonate produced (together with the calcification rate) per area per year	Benthic cover	1. Transects conducted using either line intercept transect or photographs or video of the benthos	Transects are cheap and relatively quick to conduct but relie on appropriate experimental design to accurately capture a true representation of benthic cover	English et al. (1997), Jonker et al. (2008)
					2. Photogrammetry can be used to create detailed three-dimensional habitat maps of the reef	Non-destructive technique but requires expertize in post-processing of photos, and may require expensive equipment (e.g. RoV) to provide a whole reef habitat map	Burns et al. (2015), Price et al. (2019)
		Population	The average size of the coral colony (per species and/or morphology) is required to determine the surface area over which new carbonate will be laid (as the coral grows), i.e. calcification rate is a function of the standing coral population size distribution	Coral size distribution	1. Transects conducted to count number of coral colonies in size classes	Transects are cheap and relatively quick to conduct but relie on appropriate experimental design to accurately capture a true representation of population size structure	English et al. (1997), Jonker et al. (2008)
					2. Photogrammetry can be used to create detailed three-dimensional habitat maps from which coral sizes can be estimated for part or the whole reef coral population	As above	Ferrari et al. (2015), Palma et al. (2019)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework production (cont.)	Encrusters	Abundance	Encrusters include organisms such as CCA, serpulid worms, bryozoans etc. They provide additional carbonate to the reef and play important roles in reef cementation and larval recruitment. To determine their contribution to the carbonate budget, percentage cover of encrusters is required	Benthic cover	1. Deployment of tiles or pipes (ceramic, PVC) for a few months to a few years. On removal, the tiles (or pipes) are photographed and analysed using imaging software to determine the percentage cover for the different encrusting taxa over a known area	Tiles are a quick and easy method to assess cover for key encrusters. Key considerations in tile deployment are the length of time (with longer timeframes >1 year considered to be more accurate) and orientation of tiles to assess potential differences between cryptic versus exposed encrusting communities. Different artificial substrates preferentially attract different encrusting organisms (e.g. PVC promotes CCA). Controls with natural substrates should be run to account for these differences	Mallela (2007), Browne et al. (2013); Morgan & Kench (2014); Kennedy et al. (2017); Mallela et al. (2017)
		Calcification rates	Rates of calcification are typically calculated for the total encrusting population due to the difficulties around separating rates per organism	Calcification rates	1. Deployment of tiles or pipes (ceramic, PVC) for a few months to a few years. On removal, the tiles (or pipes) are placed in acid bath (5% HCl) or vinegar (acetic acid) to dissolve the calcium carbonate. Calcification rates are determined using the weight of carbonate normalized to the known area (cm^2) and unit of time (year)	The calculated calcification rate per tile represents the total encrusting community as it is difficult to separate out different rates for different organisms. Some studies have specified a rate per organism (e.g. CCA, serpulids, bryozoans, etc.)	Mallela (2007), Browne et al. (2013), Kuffner et al. (2013), Mallela (2013), Morgan & Kench (2014), Kennedy et al. (2017)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework production (cont.)	Encrusters (cont.)	Calcification rate (cont.)	See previous page	Calcification rates (cont.)	2. The use of *in situ* respirometry chambers or *ex situ* flume chambers to measure calcification rates of CCA. Water samples from the chambers are taken over short periods of time and then regressed against environmental variables (to integrate 24-hour periods) to assess changes in oxygen, pH and total alkalinity (or isotope incorporation), which are then used to track changes in CCA calcification rates	This method provides a detailed assessment of CCA calcification rates over time and with changing environmental conditions, and is one of the few accurate measurements for understanding adult calcification rates *in situ*. It is, however, a labour-intensive method that requires expensive equipment and laboratory analyses. If insufficient time periods are integrated, or too few individuals, it can also yield substantial variation in data	Chisholm et al. (1990), Chisholm & Gattuso (1991), Tambutte et al. (1995), Chisholm (2000), Martin et al. (2013), Comeau et al. (2015), Cohen et al. (2017), Batista et al. (2020)
Carbonate framework removal and sediment production	Parrotfish bioeroders	Abundance	The number of parrotfish is critical in calculating the total weight of carbonate removed from the reef framework	Number of fish	The number of parrotfish are counted along replicate belt transects (30 m by 5 m)	Relatively easy, quick and cheap to conduct, but is reliant on diver experience and expertize	Frydl & Stearn (1978), Scoffin et al. (1980), Perry et al. (2012)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework removal and sediment production (cont.)	Parrotfish bioeroders (cont.)	Population	The size of the fish is directly related to the erosional rate	Size class	During the belt transects, parrotfish length is estimated into different size classes	Relatively easy, quick and cheap to conduct, but is reliant on diver experience and expertize. The use of a calibrated stereo-video system (DOV) could improve data collection and provide a means of data quality check, but has yet to be employed in published carbonate budget studies	
		Activity	The level of parrotfish bioerosion is also dependent on the feeding behaviour of the fish and size of the bite it takes during feeding	Bite rates	Direct observations of parrotfish feeding *in situ*. The observer records the number bites per min and substrate on which the parrotfish was feeding (e.g. live coral, dead coral, rubble)	Relatively easy, quick and cheap to conduct, but is reliant on diver experience and expertize	Bellwood & Choat (1990), Bellwood (1996), Bruggemann et al. (1994, 1996), Morgan & Kench (2016a); Yarlett at al. (2018)
				Bite volume	During direct observations of parrotfish feeding, the size of the scar on the substrate from the parrotfish is measured *in situ* using callipers and photographed	Relatively easy, quick and cheap to conduct, but volumes calculated are typically an overestimation of the actual volume as the maximum width and length are used to calculate it	

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework removal and sediment production (cont.)	Urchin bioeroders	Abundance	The number of urchins (*Diadema* and *Echinothrix* spp.) is critical in calculating the total weight of carbonate removed from the reef framework	Number of urchins	The number of urchins is counted along a belt transect (e.g. 2 m by 10 m)	Relatively easy, quick and cheap to conduct, but urchins are cryptic animals so care needs to be taken to search under ledges and in crevices. It would be beneficial to conduct transects at night as urchins are typically more active during this time	Scoffin et al. (1980), Bak (1994), Perry et al. (2012)
		Population	The erosional rate of urchins is largely a function of size and species with larger individuals causing more erosion	Urchin test size	During belt transects, urchins (per species) are tallied into set urchin size categories		
		Activity	The feeding activity of urchins is directly linked to erosional rates	Erosional rate	Estimates of bioerosional rates can be conducted by analysing gut content or faecal pellets	This method will provide a more accurate estimate of urchin erosion rates as opposed to estimating rates from the urchin test size, but requires additional laboratory analysis. Estimates need to account for carbonate clastic ratios in faecal sediment.	Glynn et al. (1979); Conand et al. (1997); Morgan (2014); Mallela & Perry (2007)
	Other macroborers	Sponge	Sponge cover (similar to density and abundance) is necessary to calculate total carbonate removed	Sponge cover	Estimates are typically made from substrate availability estimates (e.g. dead coral) and take into account the reef complexity (see rugosity below) and a visual estimate of sponge cover from benthic transects	It is very difficult to measure sponge cover accurately as sponges will invade coral skeletons internally. Hence, estimates could potentially be vastly underestimating the amount of sponge in the system	Rutzler (1975); Glynn (1997); Lopes-Victoria & Zea (2005), Schonberg (2015)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework removal and sediment production (cont.)	Other macroborers (cont.)	Sponge (cont.)	Sponge erosion rates are known to be influenced by the substrate (e.g. dead versus live coral) and coral density, and will vary with nutrient concentration and aragonite saturation	Sponge erosion rate	Through the collection of rubble samples or the deployment of carbonate blocks, the rate of carbonate loss can be calculated. Rubble samples are typically cut into cross sections and volume of bioeroded material is estimated from the void volumes per bioeroding taxa and calculated to a rate by determining the timeframe of substrate available for bioerosion. The blocks can also be CT scanned before and after deployment to provide the same variables	Unless rubble samples are C_{14} dated, estimates of timeframes of substrate availability could be inaccurate and would have a considerable influence on the final calculated erosion rates. The use of blocks does overcome this limitation, but the length of time blocks needs to be deployed for to allow the establishment of a 'typical' bioerosional community (e.g. >3 years) may far exceed timeframe available for the study	Stearn & Scoffin (1977), Kiene & Hutchings (1994), Risk et al. (1995), Morgan (2014)
		Polychaetes	Bioeroding worms are considered to occur exclusively in dead coral and can be an important bioeroder for reefs exposed to high amounts of nutrients	Polychaete density	Deployment of carbonate blocks (e.g. *Porites*) for a few months to years. On collection and treatment of the blocks, the number of individuals are estimated per block volume	This method likely provides an accurate assessment of polychaete density but will depend on timeframes for deployment with long timeframes more likely to give a better estimation of polychaete densities on the reef	Sammarco & Risk (1990), Hutchings et al. (2008)
				Polychaete erosion rate	As per sponge erosion rate	As per sponge erosion rate	

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework removal and sediment production (cont.)	Other macroborers	Bivalves	Bivalves can also be a key boring organism across a range of reef depths although can occur in patchy distributions	Bivalve density	As per polychaete density	As per polychaete density	Sammarco & Risk (1990), Hutchings et al. (2008)
(cont.)				Bivalve erosion rate	As per sponge erosion rate	As per sponge erosion rate	
	Microborers	Microborers	The importance of microborers for carbonate budgets is poorly understood and little data exists on their bioerosion rates	Microborer density and bioerosion rates	Deployment of carbonate blocks (e.g. *Porites*) for a few months to years. Subsamples of the blocks can then be scanned using either a light or scanning electron microscope (SEM)	Estimates of rates of microbioerosion likely to be relatively accurate (if blocks left out for a few years) but requires extensive time and expertize for the data collection	Chazottes et al. (1995), Chazottes et al. (2002), Tribollet et al. (2002)
	Physical erosion (currently poorly captured in census-based carbonate budgets)	Cyclonic events		Coral breakage threshold	Theoretical modelling based on approximating coral shape as standard geometries (e.g. cylinder) combined with hydrodynamic modelling (computational fluid dynamics, phase-averaged wave models); mechanical/structural integrity testing (compressive/tensile strength tests)	Limited to no direct observations of measured hydrodynamic force leading to coral breakage/fracture (e.g. flume/wave tank experiment)	Rodgers et al. (2003), Madin (2005), Storlazzi et al. (2005), Baldock et al. (2014b)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework removal and sediment production (cont.)	Physical erosion (cont.)	Cyclonic events (cont.)		Volume of breakage	Combined analysis of above (breakage threshold) with *in situ* data on coral cover/ morphology; ‘trait-based’ approaches		Massel & Done (1993), Storlazzi et al. (2005), Madin & Connolly (2006), Baldock et al. (2014a), Madin et al. (2014)
Direct sediment production	Direct sediment producers	Abundance	Direct sediment producers are those organisms that contribute directly to reef sediments upon death (e.g. molluscs, foraminifera, calcareous algae, echinoids, crustaceans, serpulid casings, sponge spicules). Their abundance in reef sediments is critical to determine their relative importance to the carbonate sediment budget		Reef sediment samples are collected and sieved into sieve fractions (commonly 4, 3, 2, 1, 0, –1 phi). For each size fraction 100–300 grains are identified to taxa level under either a compound microscope or a petrographic microscope following the embedding of sediments into epoxy and thin sectioning	The collection of sediments is quick and cheap, and a lot of data can be collected in a short timeframe. The laboratory analysis requires sedimentology expertize and can take several weeks to months to complete the data collection (depending on the number of grains per sieve fraction)	Harney et al. (2000), Browne et al. (2013), Morgan (2014), Morgan & Kench (2016b), Perry et al. (2019)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Direct sediment production (cont.)	Direct sediment producers (cont.)	Sediment volume	Calcification rates from direct sediment producers need to be normalized to a known volume of sediment, which is turn is converted to a weight (kg) per area (m^2) by taking into account the average sediment depth (m)		The collection of sediments (by hand) from the reef benthos using a container of known volume pressed into the reef benthos	This is a very imprecize method that relies on diver sediment collection techniques and experience. As such, there is a large potential for error in sediment volume estimates	Harney et al. (2000), Browne et al. (2013), Perry et al. (2017)
		Turnover rates	Turnover rates provide an estimate of carbonate release rates into the system when the organism dies. For example, a turnover rate of 2 per year implies that within a year there will typically be 2 populations of living assemblages contributing to reef sediments		To estimate turnover rates, data on annual sediment production rates as well as the weight of the standing living assemblage collected over several months (to determine when organisms die) is required. This method is most commonly used for foraminifera and molluscs	This method requires collection of sediments over several months and the subsequent analysis of both the living and dead assemblages. This is extremely labour-intensive and requires a high level of expertize. There has been no advancement in methods since the 1990s and limited data on this variable is available	Hallock (1981), Hallock et al. (1995)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Direct sediment production (cont.)	Direct sediment producers (cont.)	Turnover rates	See previous page		For calcareous algae (e.g. *Halimeda*), turnover rates are from the number of new segments produced over time using the Alizarin staining method (see corals)	The staining period is short (approx two weeks) due to fast growth but should be replicated throughout the year. Field surveys of algal biomass can be very time-consuming if in high abundance. New algal growth segments are often lightly calcified sediments, i.e. may not be representative of heavily calcified basal segments/whole plant. Once growth and calcification rates are known, you must then convert to a rate and must know number of crops per year, for which there are often very little data available. New growth can be grazed by fish, which can lead to an underestimation of calcification/turnover rates	Multer (1988), Freile & Hills (1997), Vroom et al. (2003), Perry et al. (2016, 2019)
Carbonate sediment loss	Chemical erosion	Sediment dissolution	Dissolution is a loss term as the sediments dissolve into the overlying water	Alkalinity fluxes	Benthic chambers are placed *in situ* on the sediment surface and the change in alkalinity concentration over time is measured	Need to make sure alkalinity flux is only derived from dissolution of carbonate sediments, and not anaerobic processes like sulphate reduction	Cyronak et al. (2013), Eyre et al. (2018)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate sediment loss (cont.)	Chemical erosion (cont.)	Sediment dissolution (cont.)	See previous page	Alkalinity fluxes (cont.)	Sediment is placed in *ex situ* flumes and the change in alkalinity concentration over time is measured	*Ex situ* so need to make sure conditions reflect *in situ* conditions	Lantz et al. (2020)
				Pore water carbonate chemistry	Pore water wells	Sampling distinct depths is difficult in permeable sands	Drupp et al. (2016)
Reef factors	Habitat complexity	Rugosity (or roughness)	Rugosity is a measure of reef habitat complexity. This variable is used to calculate the actual surface area available for carbonate production by multiplying the planar surface area by a measure of rugosity. Rugosity is defined as a measure of deformation or roughness of the reef surface (Dustan et al. 2013; Denis et al. 2017).		The traditional method of measuring rugosity is to lay a fine chain over the reef benthos ensuring that it closely follows the substrate. The length of the chain is divided by the straight line between the same two points. Values of 1 represent a flat surface whereas values >2 indicate a rugose surface	This method is easy, cheap and quick to carry out, and can be used to collect lots of data points. However, it is difficult to replicate over time given the diver bias associated with laying the chain and it only provides a measure of two-dimensional changes in reef complexity	Risk (1972), Dahl (1973), Friedman et al. (2012), Perry (2012), Dee et al. (in review)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Reef factors (cont.)	Habitat complexity (cont.)	Rugosity (cont.)	See previous page		Using photogrammetry *in situ* to capture three-dimensional habitat maps and changes in reef complexity	The collection of photographs by the diver along set transects is relatively straight forward. However, the post-processing of the data requires specific software, computing power and expertize. This is potentially the best method for capturing reef complexity	Leon et al. (2015), Storlazzi et al. (2016), Bryson et al. (2017), Anelli et al. (2019), Bayley (2019)
					Remote sensing (either from satellites or airborne LiDAR) to collect high-resolution digital elevation models	This technique provides the highest spatial resolution over the largest reef areas. It involves dividing the surface area of the reef (incorporating the fine scale complexity of features such as corals) by the planar surface area, accounting for the slope of the reef surface. However, the technique is expensive and its ability to identify small scales changes in rugosity is heavily dependent on the data collection parameters (e.g. pixel size)	Hamylton (2014), Du Preez (2015), Hamylton et al. (2017), Purkis (2018), Hamylton & Mallela (2019), Dee et al. (2020)

environmental change. Future carbonate budget studies should aim to capture physical drivers (e.g. hydrodynamics, nutrients, temperature and seawater carbonate chemistry) and develop empirical relationships for rate of change between two co-dependent variables (e.g. nutrient concentration and macroboring). Doing so could, for example, enable budgets to be applied to reefs where logistical difficulties prevent the collection of (multiple) data on variables that require more resources (e.g. time and money). For example, Langdon et al. (2000) examined empirical relationships by defining linear coral growth curves for several coral genera that related to aragonite saturation state. These types of studies, particularly those that target highly variable aspects of the carbonate budget (e.g. coral growth rates; Anderson et al. 2017, Lewis et al. 2017), would reduce the use of non-site-specific data and, therefore, increase the accuracy of the carbonate budget. A more complete understanding of the physical and chemical drivers that are typically quantified in geomorphological and biogeochemical studies will also enable the expansion of carbonate budgets beyond censuses and towards reef-scale processes, such as reef framework accretion or shoreline dynamics.

An important example of an environmental driver and associated variables rarely reported is flow velocity and rates of physical or mechanical erosion (1 of the 38 published census-based studies; Harney & Fletcher 2003). Physical erosion relates to the loss of carbonate material due to the force of water over the reef surface (Hubbard et al. 1990). This form of erosion is most obvious during storm and cyclonic events when current flow velocities and wave forces increase, resulting in coral breakage and increased coral rubble production (Massel & Done 1993, Storlazzi et al. 2005). Flow velocity and rates of physical erosion can therefore have significant effects on carbonate budgets as well as the transport of rubble (and sand) from reefs to shorelines (Massel & Done 1993, Madin et al. 2014). Yet, the responses to these acute events (e.g. cyclones) and their impact on carbonate budgets are often difficult to capture due to the need to collect pre- and post-event measurements. To date, estimates of reef accretion from census-based carbonate budget have focused on reef accretion ‘potential’ (RAP; Perry et al. 2018b), which assumes that the impacts of physical erosion are consistent between locations and through time due to a lack of existing data. Yet, the relative importance of environmental drivers, such as flow velocity, will vary among reef types and settings, with associated rates of physical erosion being more critical for shallow reefs and those found in cyclone hotspots (Fabricius et al. 2008, Puotinen et al. 2016). Therefore, consideration of environmental drivers and how they influence reef system processes is key for determining how the system (and budget) will respond to acute events (e.g. bleaching, cyclones) and future climate change.

Future challenges for census-based carbonate budget studies

The application of census-based carbonate budgets as a predictive tool for reef budgetary state and landform stability will require integrating data on sediment dynamics (production, loss and transport) and landform stability. These inclusions will require recognising differences in temporal and spatial scales between ecological processes (days to decades, millimetre to metres), sediment transport processes (seconds to decades, millimetre to kilometres) and reef accretionary processes (decades to centuries, metres to kilometres). In terms of temporal scales, census-based carbonate budgets record ecological processes that occur over annual timescales, yet it is not clear how such processes of coral growth and bioerosion scale up to longer-term (decadal and longer) processes of reef construction, sediment infilling and cementation of reef frameworks (Roff 2020). In terms of spatial scales, understanding how carbonate budgets translate from reef habitats (e.g. reef crest) to whole reef-scale processes is also challenging and requires insight into net carbonate production and sediment flux at larger spatial scales than previously considered in carbonate budget approaches (e.g. Morgan & Kench 2016b).

Integration of carbonate sediment production, loss and transport

Traditionally, carbonate budget studies have inadequately quantified critical processes relating to reef sediments (i.e. the carbonate sediment budget). Although carbonate sediments have no influence on a reef's budgetary state, they influence long-term rates of reef accretion through framework infilling ($\mathrm{mm \cdot yr^{-1}}$; Ginsburg 1983, Hubbard et al. 1990, Milliman 1993), as well as providing the carbonate material for shoreline maintenance (Morgan & Kench 2014, Perry et al. 2015a, Cuttler et al. 2019). Of the 38 published census-based carbonate budget studies, only eight provide data on carbonate sediment production rates (e.g. Harney & Fletcher 2003, Browne et al. 2013, Morgan & Kench 2014, Brown et al. 2020), only four provide estimates on sediment transport within and off-reef (e.g. Land 1979, Hubbard et al. 1990), and only one includes sediment dissolution rates (Brown et al. 2020; Table 1). Lack of inclusion of data on carbonate sediment production in most carbonate budgets is likely due to at least one of two main reasons. First, these data could be lacking due to the technical and logistical difficulties in accurately quantifying sediment production and subsequent transport and deposition (Sadd 1984, Harney & Fletcher 2003, Morgan & Kench 2014, Cuttler et al. 2019, Castro-Sanguino et al. 2020). Secondly, and potentially more importantly, the amount of carbonate sediment produced relative to *in situ* carbonate production (e.g. corals) is in most (but not all) cases comparatively small (e.g. Browne et al. 2013). In contrast, the lack of data on carbonate sediment dissolution is most likely because it was not considered important in early carbonate budgets (Eyre et al. 2014). If, however, we are to expand the scope of carbonate budgets beyond the reef framework and consider the larger spatial connection between reefs and associated landforms, the inclusion of the carbonate sediment dynamics will be a necessary step. For example, carbonate budgets could be linked to sediment dynamics through the quantification of 'net sediment available', which would be derived from classical census-based budget calculations. This 'net sediment' is then available for transport through the system and/or deposition within various sediment sinks (lagoons, beaches, etc.).

For those studies that have incorporated carbonate sediments into their budgetary calculations (often termed the carbonate sediment budget), a number of sediment-related variables have been measured to assess the abundance of direct sediment producers per volume of sediment (e.g. sediment composition, particle size, sediment depth). These variables are relatively straightforward to measure because they rely on the collection of surface sediment over a known area and sediment depth (Harney & Fletcher 2003, Browne et al. 2013). The practical difficulties here relate to estimating rates of sediment production (activity of the organisms), which requires determining turnover rates in populations of direct sediment producers (e.g. foraminifera, molluscs, bryozoans, *Halimeda*). Turnover rates, defined as 'fraction of the total amount of a substance ($CaCO_3$) in a component (organism) that is released in a given length of time' (Odum 1959), provide an estimate of carbonate release rates into the system when the organism dies. To measure turnover rates effectively, data on annual sediment production, as well as weight of the standing 'living' assemblage collected over several months, are required (Hallock 1981). Such measurements are logistically difficult to collect because they require extensive (and multiple) field sampling, followed by a considerable amount of microscopic laboratory work by an experienced field taxonomist for a large number of species or molecular analysis. Very few carbonate budget studies have the resources required to support the time and expertize required to complete these analyses accurately.

As a result of these challenges associated with estimating carbonate sediment production, many carbonate budget studies have adopted pre-existing sediment production rates. Studies that calculated turnover rates were largely carried out during the 1970s and 1980s (Hallock 1981, Drew 1983, Kay & Kawamoto 1983, Hallock et al. 1995). These original rates have been extensively used in subsequent carbonate budget studies (e.g. Harney & Fletcher 2003, Browne et al. 2013), despite the likelihood of differences in environmental conditions (e.g. light and nutrients) on reefs, which drive turnover rates. As such, most carbonate budget studies either ignore sediment production or have non-site-specific estimations of sediment production rates. It remains, therefore, very difficult to determine the importance of carbonate sediments to reef framework infilling, density and stability, and evaluate how sediment production will be affected by future climate change, specifically increased sediment dissolution from ocean acidification (Cyronak et al. 2013, Eyre et al. 2014, Cyronak & Eyre 2016). To further determine outcomes of shifts in sediment production for the maintenance and stability of associated landforms, census-based carbonate budget studies need to consider reef-scale carbonate sediment production and transport processes (see Morgan & Kench 2016b).

Assessments of landform stability

To date, no census-based carbonate budget has incorporated links between reef carbonate sediment production and associated landform stability. Yet these links are necessary to capture if we are to quantify how changes in reef budgetary state relate to carbonate sediment supply and coastal sediment budgets. Reef-fronted shorelines (e.g. beaches and islands) are some of the most at risk landforms to climate change due to their low-lying nature and reliance on reef-derived sediment (Storlazzi et al. 2018). However, our ability to quantify, and potentially mitigate, the threats to these shorelines is poor. The hazards to these landforms include both changes in physical drivers (e.g. future sea level rise and changing wave climate) and ecological shifts (e.g. loss in coral cover and reduced carbonate production) in response to warming seas and ocean acidification (Reyns et al. 2013).

Although we can assess the response of physical processes to future change (e.g. model wave or water level variability at the shoreline in response to reduced reef rugosity; Grady et al. 2013; Harris et al. 2018), quantifying links between ecological (sediment generation) and geomorphic processes (sediment transport, shoreline erosion/accretion), and therefore predicting future landform stability, remains a challenge. The link between sediment production and reef-fronted shorelines is further confounded by our limited understanding of the timescales of sediment production, dissolution and transport mechanisms. For example, previous studies have shown that the active sediment reservoir (i.e. lagoon and beach) can be comprised of either contemporary (<100 years old; Yamano et al. 2000, Dawson et al. 2012) or ancient/relic (longer-time scales of sediment supply; Harney et al. 2000, Cuttler et al. 2019) reef-derived material. However, few studies quantify transport mechanisms and rates due to methodological difficulties in tracking sediment particles over large spatial scales (Hubbard et al. 1990, Storlazzi et al. 2004, Becker et al. 2007, Morgan & Kench 2014, Pomeroy et al. 2017, Cuttler et al. 2019), and the effect of dissolution on sediment supply for reef-fronted beaches has yet to be considered. Thus, the timescales of sediment delivery to reef-fronted landforms (beaches, islands) are poorly resolved. Given that the sensitivity of these landforms is strongly linked to ecological shifts in reef organisms that produce carbonate, a multi-disciplinary approach (ecologists, sedimentologists, biogeochemists and coastal geomorphologists) is required to assess and resolve differences in timescales over which these processes operate (e.g. seconds to years to decades).

Integrating census-based, hydro-chemical and geological carbonate budgets

Of the three carbonate budget approaches detailed above, we have focused on the census-based approach because it is the only method that attempts to differentiate among key organisms, drivers and processes (variables) on ecologically relevant (weeks to months) and measurable timescales. These considerations are paramount in the development of a quantitative model that can calculate how changes in variables (over different spatial and temporal scales) lead to changes in outputs, such as net carbonate production and reef accretion. Critically, census-based budgets quantify loss from the system, which is becoming increasingly relevant information to capture as widespread reef degradation begins to switch many reefs into net negative budgetary states (Perry et al. 2013b). Future studies may consider combining, comparing and/or reconciling data among methods to provide further insights into future reef trajectories, although they will have to overcome current limitations as described below.

The main advantage of the hydro-chemical approach is that it provides a higher temporal resolution (real-time) assessment of net reef calcification than the census-based approach and can be used to investigate daily and seasonal differences (Lange et al. 2020). But these instantaneous, snap-shot readings do not provide an accurate representation of longer-term rates (years) of net carbonate production and cannot differentiate between co-varying (dominant) environmental variables or other co-varying processes (Lange et al. 2020), which are better captured using the census-based approach. Recently, Cornwall et al. (2021) conducted a meta-analysis of coral reef taxa calcification and bioerosion rates from 142 studies, ranging from *in situ* and laboratory coral and CCA calcification to full census-based carbonate budgets and hydro-chemical studies, to predict the impacts of climate change on net reef carbonate production rates on 183 reefs worldwide. This study highlighted that the largest issue when attempting to integrate and compare data between census-based and hydro-chemical methods related to rates of carbonate loss (e.g. bioerosion by physical and chemical processes). At present, there are insufficient measurements of the contribution of different bioeroding organisms (that use either physical, chemical or both processes) to total bioerosion. This data paucity makes it difficult to determine the contribution of physical and chemical erosion to total bioerosion rates when using either the hydro-chemical or census-based approach. For example, some components of chemical bioerosion are inherently measured in hydro-chemical budgets, but physical erosion is rarely considered. Given that bioerosion by physical eroders has been found (on some reefs) to be greater than the sum of net carbonate production, estimating long-term net carbonate production via the hydro-chemical method could be problematic in locations where physical erosion is not included.

Geological cores provide net estimates of carbonate accumulation and reef accretion over decades to centuries, but are spatially limited and cannot differentiate rates at fine temporal resolutions (<1–2 years). Few studies have attempted to combine core and census-based data, and of those that have, there has been mixed success. Browne et al. (2013) found that the hindcast rates of reef accretion using contemporary rates of net carbonate production from census-based methods and sediment budget data were remarkably similar to core data collected for two inshore turbid reefs on the GBR. However, Roff (2020) found that ecological processes (as measured using the census-based method) were decoupled from the geological processes (as measured using the geological cores) resulting in different rates of reef accretion. The study provided possible hypotheses that may account for this decoupling including (1) the transportation of carbonate material off-reef, (2) higher rates of bioerosion in core data than observed in present-day carbonate budget assessments and (3) the inclusion of non-carbonate material into the reef framework. Therefore, the extent of decoupling between ecological processes, which heavily focus on carbonate production, and long-term reef accretion will depend on the relative importance of processes that are either poorly understood (e.g. sediment inputs/removal) and/or not typically captured in census-based carbonate budgets. It should be noted, however, that both studies were conducted on turbid reefs where sediments promote rapid reef accretion rates, so it is unclear whether a closer coupling between processes would be observed on clear-water reef systems (e.g. atolls) where external sediment inputs are limited. Regardless, studies that attempt to include both approaches yield important insights into site-specific processes and their relative importance to future reef trajectories.

Summary

Coral reefs are complex systems that exhibit significant spatial and temporal variation. They are influenced by, and in turn influence, a number of geomorphological, ecological and physical processes, which are challenging to both understand and integrate. Advancing beyond census-based carbonate budgets and developing a reliable geo-ecological carbonate reef system model, however, is increasingly necessary as ecological and human communities face the exacerbating threats of climate change. Climate change has the capacity to influence all of the processes within the reef system, leading to considerable implications for populations that rely on these systems.

Here, we develop a geo-ecological carbonate reef system model that goes beyond the scope of the traditional census-based carbonate budget by incorporating sediment production (sediment budget) and sediment transport and sinks (e.g. reef-fronted shorelines; Figure 1). The model also

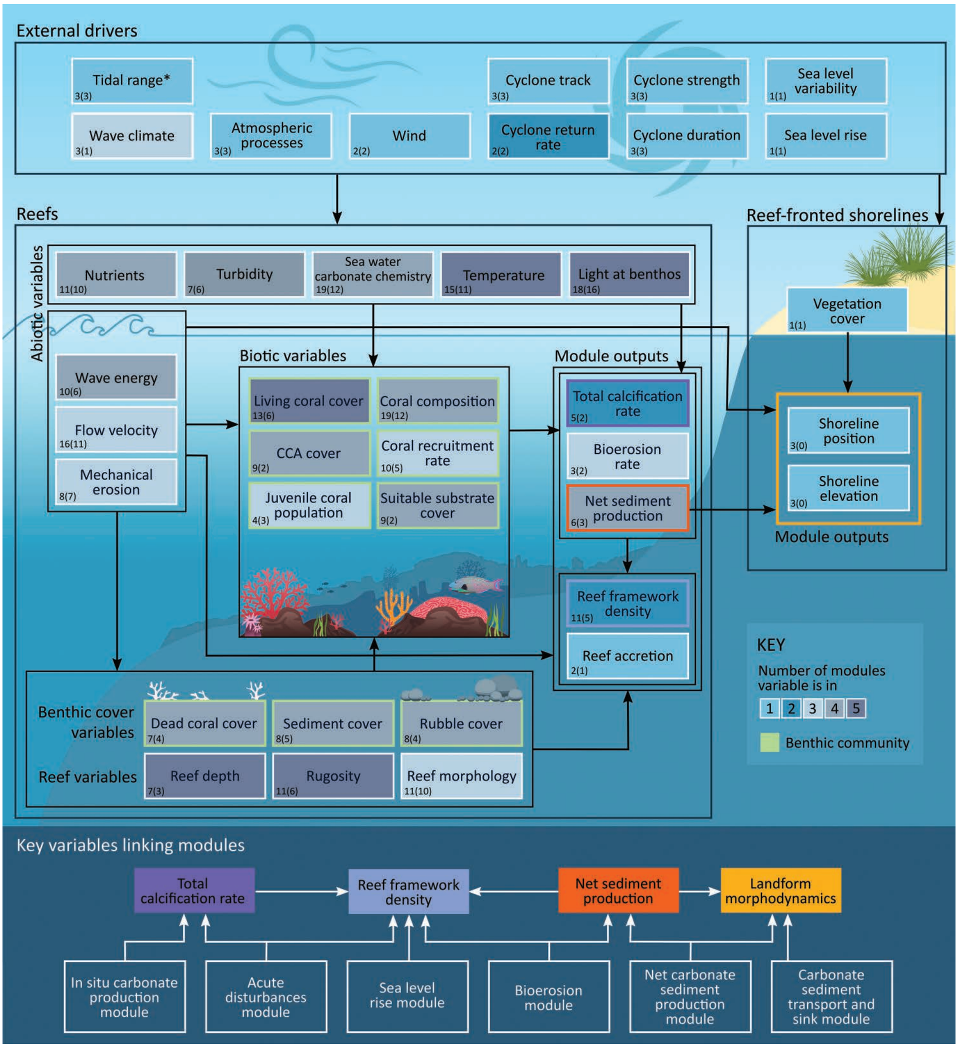

Figure 1 A high-level summary of the geo-ecological carbonate reef system model, which contains 80 variables and 265 relationships. Here, we identify 31 critical variables (with seven output variables) for modelling reef carbonate budgets, sediment transport and landform stability. Variables were considered critical if they were integrated into three or more modules (Reefs box) and/or were root nodes and considered to have a pervasive influence throughout the system (external drivers' box). All external drivers (except 'Tidal range') are influenced by anthropogenic climate change (or are a co-variate), which in turn influence local conditions (e.g. temperature). Additional regional and local anthropogenic impacts (e.g. eutrophication, sediment run-off) are captured in the abiotic variables box (e.g. nutrients and turbidity). Each variable is provided with a number combination in the bottom left-hand corner (measure of centrality). These numbers indicate how connected and influential this variable is among all modules. For example, living coral cover – 13(6) – has a total of 13 arrows connecting it to the system, of which six are influential arrows (leaving the variable). Variables are grouped into categories (e.g. biotic variables), and broad influential relationships between categories are provided by the directional arrows. For specific details, please refer to the module sections. Module outputs are highlighted in the bottom panel (e.g. total calcification rate) together with a 'map' of how the six modules are linked (through their module outputs) within the complete geo-ecological model. Colours used here are also incorporated within module models to illustrate which variables are required within modules to estimate module outputs. For example, all those variables in dark blue (e.g. total calcification rate) in the module models relate to total calcification rates and carbonate production.

responds to the present and future challenges for carbonate budgets (complexity, data collection, environmental drivers, integration of sediments and landform stability) by deconstructing current census-based budgets and examining specifically how the system functions. As such, the first step in producing a geo-ecological carbonate reef system model is to determine (1) which variables are necessary to include; (2) how those variables interact with one another; and (3) what methods or knowledge we have to support the quantification of both variables and the relationships between them. This reconstruction delivers a conceptual, qualitative model that documents the full suite of carbonate reef system variables and their relationships. Below, we outline the method used to develop a conceptual, qualitative geo-ecological carbonate reef system model. This novel framework can provide the context for establishing a new quantitative model that can be used to determine a reliable and comprehensive estimate of net carbonate production for a reef under existing and future conditions.

Our approach – a novel model elicitation method

We developed a novel model elicitation method to develop the first conceptual, qualitative geo-ecological carbonate reef system model. This method was specifically designed for developing a shared, expert-elicited qualitative model (see Table 4 for modelling terminology) of a complex system. Here, we describe the relevant details for this reef model, but for further details, refer to Moon & Browne (2020). The method comprises four phases: (1) module development; (2) elicitation method development; (3) elicitation of individual mental models; and (4) co-creation of the shared qualitative model (Moon & Browne 2020; Figure 2).

Phase 1: Module development

The coral reef and associated landform ‘system’ was disaggregated into smaller sub-system modules that each represented a functioning unit focused on either a key process or an element (Table 4) of the reef carbonate system (Table 5). For example, the first sub-system module (1) ‘*in situ* carbonate production’, focused on corals and CCA carbonate production where the dominant process is calcification in the form of calcium carbonate ($CaCO_3$). Other modules included acute disturbance events on coral reef communities (2), coral reef response to sea level rise impacts (3), bioerosion (4), net carbonate sediment production (5), and carbonate sediment transport and depositional sinks

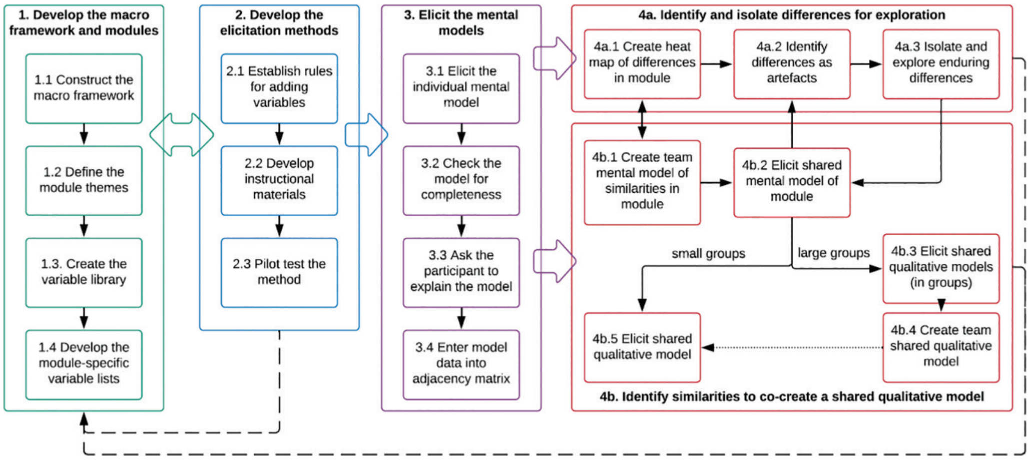

Figure 2 Overview of the mental modelling method for complex systems from Moon & Browne (2020).

Table 4 Definitions for eliciting mental models, and describing variables and relationships within mental models

Term	Definition
Geo-ecological carbonate reef system model	A model that includes all known variables that influence carbonate budgets and tracks reef health with carbonate sediment production and associated landform change. Here, the reef system is broken down into six sub-system modules
Sub-system modules	A sub-system module will focus on a dominant process or element that is integral to the complex system framework. The sub-system module should be a functioning unit of the system framework, i.e. a model in its own right with a defined output
Mental model	A mental model is an individual's internal model of the (sub-) system
Team mental model	A team mental model represents two or more individuals' mental models of a (sub-)system that have been elicited and aggregated
Shared qualitative model	A shared qualitative system model represents two or more individuals' agreed model of a (sub-) system. Development of the shared mental model can be supported by the team mental model
Variable library	The variable library consists of all known variables for all sub-system modules that may be included in the modelling process along with their definitions and associated units
Variable list	Sub-system specific list of variables the modeller uses in the elicitation of their model
Functioning unit	A defined sub-system that can be modelled separately to produce a defined and tangible output
Processes	A series of actions required to achieve an end goal. For example, biological processes include many chemical reactions that result in change and relate to a living organism
System elements	Entities, such as organisms, minerals and chemicals
Rooted nodes	Variables that are the first node in a rooted (directed) graph, which all paths originate from. These variables essentially 'drive' the system as they have a pervasive influence through the whole model
In and out degrees	These refer to the direction of relationships (arrows). In degrees refer to the number of arrows going into the variable in the conceptual model, and out degrees refer to the number of arrows leaving the variable
Variable centrality	The level of variable centrality indicates the number of relationships the variable has. For example, high degree of centrality suggests a number of relationships with other variables

Table 5 A summary of the six sub-system modules outlining the dominant process (P) or element (E.) for modelling together with their dominant driver and module output

Module	Dominant process (P) or system element (E)	Number of variables	Dominant driver	Module output
1. *In situ* carbonate production	Calcification (P)	28	Local environmental drivers (e.g. temperature, light)	Total calcification rate
2. Acute disturbance events on coral reef communities	Coral community (E)	36	Physical erosion (e.g. cyclones) and local environmental drivers (e.g. temperature, DHW)	Total calcification rate
3. Coral reef response to sea level rise	Reef accretion (P)	27	Sea level rise	Reef framework density and reef accretion
4. Bioerosion	Bioerosion (P)	23	Environmental drivers (e.g. nutrients, temperature) and benthic cover	Net sediment production and reef framework density
5. Net carbonate sediment production	Carbonate sediments (E)	28	Environmental drivers (e.g. temperature, nutrients) and physical erosion	Net sediment production
6. Carbonate sediment transport and depositional sinks	Sediment transport (P) and island change (P)	21	Reef hydrodynamics	Shoreline position and elevation

(6; Table 5). These sub-system modules represent targeted knowledge areas for which an individual is more likely to have more comprehensive knowledge and, therefore, a better understanding of how variables are linked within the system.

Phase 2: Elicitation method development

To elicit individual mental models of these six sub-system modules, we developed and tested instructional materials (e.g. instructional video, written instructions, and a variable library with 110 variables) (Phase 2). Model elicitation was conducted remotely and participants self-elicited their mental models, which were digitally recorded in PowerPoint. Models (expressed as digraphs) included three main components: (1) an arrow from one variable to another to indicate the direction of influence, (2) an assessment of participant's perception of the strength of each influence (1= weak to 5 = strong) and (3) an assessment of their level of confidence in their knowledge for each influence (a = low, b= moderate, c = high confidence).

We developed the elicitation method for the qualitative model to serve three main purposes. First, we sought to elicit an individual model from each participant. This output was important in determining both the breadth, but also the diversity and relative confidence of knowledge within a given domain. We elicited the model by asking participants to use the same variables, which enabled quantitative comparison between individual models. Second, we sought to create a team mental model, which involved representing those relationships that were common across sub-system models within modules, but also identifying those relationships that were present in fewer models. Similarities were important to identify because they assisted in determining the overall confidence in underpinning knowledge within the model. Meanwhile, differences were important to identify because they enabled exploration of existing knowledge and associated gaps. Third, we sought to elicit a shared qualitative sub-system model of the module, on the basis of both the individual and team models. The individual and team models supported engagement and discussion on variables and relationships, providing an important 'starting point' for elicitation of the shared model.

Phase 3: Elicitation of individual mental models

For each module, mental models were self-elicited from four to six experts (i.e. a total 28 mental models elicited; Phase 3). We developed the elicitation method to support a modular approach. Modellers were purposely selected according to their area of expertize and assigned a specific module (Table 5). Each modeller was provided with information about the whole geo-ecological carbonate reef system model, including a full list of variables and definitions across all six sub-system modules (Table 6). Modellers were asked, however, to focus on *their* module and its associated output/s.

We developed the elicitation method for the qualitative model with the intention of building towards a quantifiable model. With this goal in mind, we collected data pertaining to each relationship that would provide insight into the likelihood or capacity of quantifying each relationship. We therefore asked each modeller to 'qualify' each of the relationships they recorded. Modellers were asked to classify each relationship on the basis of (1) their perception of the strength of the influence (1 – weak to 5 – strong) and (2) their confidence of the existence of that relationship (a – low to c – high). This step in the elicitation process revealed critical knowledge gaps.

The confidence ratings proved useful in two main ways. First, they provided information as to the extent of existing knowledge of the relationships between variables within carbonate reef systems. Of the 265 relationships identified among module models, 74% were rated with high confidence, 17% were rated at moderate confidence, and 9% were rated with low confidence. Second, they provided opportunities to identify knowledge gaps and determine future research needs. Future research needs were revealed by the relationships rated with low confidence and/or where there was

Table 6 List of variables used in model development together with their units and definition

Type	Units	All variables	Definition
Environmental		Atmospheric processes:	Physical processes in the atmosphere (see below for specific variables*)
	ppm	*Greenhouse gases (atmospheric processes)	Atmospheric concentrations of greenhouse gases (i.e. carbon dioxide, methane, nitrous oxide, ozone, water vapour)
	W/m^{-2}	*Solar radiation (atmospheric processes)	Rate of energy received per unit area
	N/A	*Atmospheric convection (atmospheric processes)	Convection currents in the atmosphere (e.g. driver of ENSO)
	$\mu g \cdot L^{-1}$	Chlorophyll-a	Concentration of chlorophyll-a in the surface waters
	hours	Cyclone duration	The duration of the cyclone over a point
	years	Cyclone return rate	Frequency of cyclone occurrences in an area
	scale	Cyclone strength	Cyclone strength measured from 1 to 5 with 5 being the strongest
	km	Cyclone track	The distance in km from the shoreline and the track of the cyclone
	N/A	Degree heating weeks	Degree heating week (DHW) indicates how much heat stress has accumulated in an area over 12 weeks by adding up any temperature that exceeds the bleaching threshold during that time period
	$m \cdot s^{-1}$	Flow velocity	General term for the speed of water motions throughout the reef system including mean currents, tidal currents and wave orbital velocities
	PAR	Light at benthos	Photosynthetic active radiation (PAR) available at the benthos from 400 to 700 nm
	kg or kg yr^{-1}	Mechanical erosion	Amount of reef material broken down by physical processes (waves, grain–grain interaction during transport)
	$\mu mol \cdot L^{-1}$	Nutrients	Using nitrate as a proxy for nutrient pollution
	$L \cdot m^{-2} \cdot day^{-1}$	Pore water advection	Physically driven flow of seawater through permeable sediments
	pH	Pore water pH	pH of the sediment pore water
	$cm \cdot yr^{-1}$	Sea level rise	The rate of current sea level rise at a location
	m	Sea level variability	Non-tidal fluctuation of local sea level above still water depth occurring on seasonal to interannual timescales (excluding sea level rise)
	^{o}C	Temperature	Represents *in situ* temperature at the benthos
		Seawater carbonate chemistry:	Seawater carbonate chemistry (see below for specific variables*)
	mmol kg^{-1}	*Seawater dissolved inorganic carbon (DIC)	Sum of inorganic carbon species
	N/A	*Seawater pH	pH of the seawater

(*Continued*)

Table 6 (*Continued*) List of variables used in model development together with their units and definition

Type	Units	All variables	Definition
Environmental (cont.)	mmol·kg^{-1}	*Seawater total alkalinity	Total alkalinity of the seawater
	N/A	*Seawater saturation state (W)	Saturation state of the seawater
	mg·cm^{-2}day^{-1}	Sedimentation	The daily rate of sediments settling on the benthos per area
	m	Tidal range	The difference between the average lowest and average highest tidal cycle
	mg·L^{-1}	Turbidity	Concentration of suspended sediments in the water column above the reef benthos
	m, s, deg	Wave climate	Regional-scale (order 10s–100s of kms) average wave characteristics (wave height, wave period and direction)
	kW·m^{-1}	Wave energy	Local-scale (order kms) wave characteristics that result from the interaction of the regional wave climate with local bathymetry and reef morphology. Wave energy is proportional to the product of wave height squared and wave period
	m	Wave setup	Increase in mean sea level (‘still water’) due to wave breaking
	m s^{-1}	Wind	Magnitude and direction of wind
Reef factors	%	CCA cover	The percentage of the reef area covered in CCA
	%	Living coral cover	The percentage of the reef area covered in living coral cover
	%	Dead coral cover	The percentage of the reef area covered in dead coral cover
	%	Macroalgal cover	The percentage of the reef area covered in macroalgae
	%	Rubble cover	The percentage of the reef area covered in rubble
	%	Suitable substrate cover	Indurated limestone (including dead coral, cemented rubble, bioeroded limestone) suitable for coral and algal settlement
	%	Colonisable substrate	Hard surfaces (generally freshly dead coral surfaces, but in cases also living coral, coralline algae) suitable for settlement of internal reef bioeroders
	%	Grazable substrate	Benthic surfaces (generally turf covered framework, but also coralline algae, and in some cases, live coral) suitable for grazing by external bioeroders (bioeroding urchins, fish and molluscs)
	mm yr^{-1}	Reef accretion	Rate of vertical reef growth
	m	Reef depth	The difference between the height of the reef flat and the bottom of the reef slope where corals stop growing
	kg·m^{-3}	Reef framework density	The mass of the reef carbonate framework per unit of volume. This takes into account the weight of carbonate but also the void volume
	N/A	Reef morphology	Geomorphological structural features of an individual reef, characterized by differences in combinations of depth (light), slope and exposure (water flow), dominated by different substrate types and often hosting different benthic communities. Examples include fore reef slope, reef flat, channel width and lagoon
	m^2·m^{-2}	Rugosity	The measure of deformation or roughness of the reef surface
	min·m^{-2}	Herbivory	The rate of fish grazing intensity per area of reef substrate
In situ carbonate production	cm	Coral diametre	The average width of corals on the reef

(*Continued*)

Table 6 (*Continued*) List of variables used in model development together with their units and definition

Type	Units	All variables	Definition
In situ carbonate production (cont.)	cm	Coral height	The average height of corals on the reef
	$cm \cdot yr^{-1}$	Coral extension rate	The average rate of linear extension of corals on the reef
	$g \cdot cm^{-3}$	Coral skeletal density	The average density of the coral skeleton on the reef
	N/A	Coral composition	Term encompassing the different coral morphologies, genus and species on the reef
	N/A	Coral size distribution	Variable that reflects the population size structure of the living coral community
	no. per m^2	Coral juvenile population	The number of juvenile (<5 cm) corals on the reef
	no. per m^2	Coral recruitment rate	Rate of successful coral recruitment to the reef
	kg $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$	Coral calcification rate	A variable that covers all coral calcification on the reef
	N/A	CCA composition	The species CCA composition on the reef
	kg $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$	CCA calcification rate	The average CCA calcification rate
	N/A	OA sensitivity	The sensitivity of corals to changes in the aragonite saturation
	N/A	Temperature sensitivity	The sensitivity of corals to changes in the temperature
	kg $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$	Total calcification rate	A variable that represents the gross carbonate produced on the reef by all calcifying organisms
Bioerosion	N/A	Biotic controls	Includes factors such as recruitment, disease, predation, competition that influence population densities and size-frequency distributions of reef-associated organisms
	cm	Grazer size	Body size (e.g. fish length, urchin test size) of grazing organisms
	no. ind. per m^2	Grazer density	Abundance per unit area of reef of grazing bioeroders (e.g. bioeroding fish, urchins, molluscs)
	no. ind. per m^2	Macroborer density	Abundance of macroboring bioeroders (e.g. molluscs, sponge, crustaceans, worms) per unit volume of reef framework
	no. ind. per m^2	Microborer density	Infestation per unit volume of reef framework of microboring organisms (all fungi, bacteria, algae) – often measured by % surface area and depth of penetration
	kg $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$	Bioabrasion activity	The rate of physical framework removal from all grazing organisms
	kg $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$	Biocorresion activity	The rate of reef framework removal from macro- and microborers
	kg $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$	Bioerosion rate	The total amount of carbonate removed from the reef framework by both bioabrasion and biocorrosion
Sediments	N/A	Sediment characteristics	This term encompasses all sediment descriptives including size, shape, density and porosity
	%	Sediment cover	The percentage of the reef covered in a sediment layer
	m	Sediment depth	The average depth of the sediment layer at a location
	%	Sediment organic content	The percentage of the sediment layer that contains organic material
	years	Turnover rates	The time it takes for a new population of sediment producers to occur in the sediments

(*Continued*)

Table 6 (*Continued*) List of variables used in model development together with their units and definition

Type	Units	All variables	Definition
Sediments (cont.)	mmol·m^{-2}·day^{-1}	Benthic metabolism	Benthic productivity and respiration
	kg CaCO$_3$·yr^{-2}	Sediment dissolution	The rate of sediment dissolution on the reef
	kg CaCO$_3$·yr^{-2}	Sediment loss	The rate of sediment loss on the reef
	kg CaCO$_3$·m^{-2}·yr^{-1}	Direct sediment production	The rate of carbonate sediment production from direct sediment producers such as *Halimeda*, molluscs, foraminifera and bryozoans
	kg CaCO$_3$·m^{-2}·yr^{-1}	Net sediment production	Amount of carbonate sediment produced from direct and indirect sediment producers minus sediment loss from dissolution
	kg CaCO$_3$·m^{-2}·yr^{-1}	Sediment re-incorporation	The rate of sediment infilling of the reef framework
	kg CaCO3·m^{-1}·yr^{-1}	Aeolian transport	The amount of sediment transported by wind
	kg CaCO3·m^{-1}·yr^{-1}	Bed load transport	The amount of sediment transported as bed load
	kg CaCO$_3$·m^{-2}·yr^{-1}	Lagoon infilling	The rate of sediment supply to lagoon areas
	kg CaCO$_3$·m^{-2}·yr^{-1}	Off-reef sediment export	The rate of sediment loss via the transport of sediments off the reef (into deeper water)
	kg CaCO$_3$·yr^{-2}	Suspended load transport	The amount of carbonate sediment transported in suspension
Landforms	%	Beach rock armouring	Percentage of shoreline made up of bedrock
	m	Shoreline position	Horizontal position of the shoreline
	m	Shoreline elevation	Maximum height of the cross-shore beach profile
	%	Vegetation cover	The percentage of the subaerial landform covered in vegetation

Note: Note that there are two variables (atmospheric processes and seawater carbonate chemistry) that include several important processes that have been further defined (*).

a lack of empirical data to support the relationship, representing significant gaps in our knowledge and understanding.

Given our intention of quantifying the model, we sought an additional data set during the individual and group (see Phase 4) elicitation processes. We asked participants to document any literature that supported the relationships in the model/s. This step has allowed us to identify where relevant peer-reviewed literature that provides empirical data that explains or quantifies relationships exists (Table 7).

Phase 4: Co-creation of shared qualitative system model

After the remote self-elicitation process, we invited modellers to attend a two-day workshop. The first day of the workshop involved organising modellers according to their module group. They were asked to elicit a shared model of their module, on the basis of the team model (i.e. aggregated individual models) provided to them. They were also provided with all of the individual models that comprised the team model for sharing and comparison. Each of the phases of elicitation was accompanied by the creation of a knowledge database to support each of the relationships described. This database was deemed critical in moving towards a quantitative geo-ecological carbonate reef system model.

Table 7 Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
In situ carbonate production	Drivers of the key *environmental* parameters	Atmospheric processes such as increases in anthropogenic CO_2 reduce seawater pH (seawater carbonate chemistry) through a process known as ocean acidification. Macroalgae influences the seawater carbonate chemistry by drawing down CO_2 through photosynthesis and may mitigate the negative effects of OA. Macroalgae productivity is influenced by nutrient flux, temperature and light. Coral reef primary producers modify their seawater carbon chemistry during calcification whereby there is a release of H+ during the conversion of bicarbonate to carbonate	1–6	Atmospheric processes (greenhouse gases) and seawater carbonate chemistry: Caldeira & Wickett (2003), Feely et al. (2004), Sabine et al. (2004), Raven et al. (2005). Macroalgae and seawater carbonate chemistry: Delille et al. (2009), Cornwall et al. (2013). Macroalgae and OA: Cornwall et al. (2013), Rivest et al. (2017), Wahl et al. (2018). Macroalgae and temperature, nutrients and light: Carpenter et al. (1991), Renken et al. (2010), Smith et al. (2010), Reef et al. (2012), Ji et al. (2016). Calcification and seawater carbonate chemistry: Cohen (2003), Jokiel (2011), Ries (2011), Anthony et al. (2013)
		Atmospheric processes influence temperature and DHW because solar radiation penetrating the surface of the oceans is responsible for warming of the surface layers. Greenhouse gases warm the atmosphere, which reduces the amount of heat lost to the atmosphere from the ocean surface, allowing the oceans to steadily warm over time. Water flow velocities influence water residence time and therefore temperature and DHW. Temperature influences the solubility of CO_2 in the surface oceans and the carbonic acid constants	7–10	Temperature and carbon dioxide solubility: Dickson & Millero (1987)
		Flow velocities influence sediment cover	11	Storlazzi et al. (2011)
		Reef depth influences the light reaching the benthos. Chlorophyll-a increases with light and nutrients and causes increased turbidity. Turbidity (water cloudiness) attenuates light in the water column and can reduce light reaching the benthos	12–16	See review by Gattuso et al. (2006)
	Benthic cover, species composition and coral recruitment (*benthic community*)	Seawater carbonate chemistry influences CCA cover	17	Hall-Spencer et al. (2008), Fabricius et al. (2011, 2015), Cornwall et al. (2017)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
In situ carbonate production (cont.)	Benthic cover, species composition and coral recruitment (cont.)	Nutrients influences CCA cover	18	Belliveau & Paul (2002), Smith et al. (2010)
		Temperature influences CCA cover	19	*No references for this*
		Light at benthos influences CCA cover due to the production of photosynthetically fixed carbon by the photosynthetic pigments produced by CCA	20	Steneck (1986)
		Flow velocities influence CCA cover	21	*No explicit test of this exists to our knowledge*, but Steneck (1986) discusses some implications
		Suitable substrate cover for colonisation influences CCA cover. Macroalgae (and turf algae) can influence the amount of suitable substrate. High cover of large macroalgae typically has a negative influence, particularly on degraded reefs. For instance, most but not all studies suggest that elevated nutrients drive shifts from high coral cover (low algal cover) to low living coral cover with an accompanying high cover and biomass of fleshy alga influencing the suitable substrate cover. Sediment, rubble and dead coral cover can also influence the amount of suitable substrate cover available	22–24	Suitable substrate and CCA: Steneck (1986). Macroalgae and suitable substrate: Kuffner et al. (2006), Birrell et al. (2008), Hoey et al. (2011), Jorissen et al. (2016). Sediment/rubble/dead coral: Birrell et al. (2005), Cameron et al. (2016). High coral cover to high macroalgae cover: McCook (1999), Hoey et al. (2011), Szmant (2002), Hughes et al. (2007), Jupiter et al. (2008)
		Suitable substrate cover is required for coral recruitment. CCA cover can create more suitable substrate cover for coral recruitment. Some CCA facilitate coral recruitment. Coral recruitment rates can influence the juvenile coral population and therefore influence coral cover. Living coral cover is the adult stock for reproduction, thereby influencing coral recruitment rate, but also coral recruits can arrive from distant (i.e. non-local) adult populations	25–29	Coral cover and recruitment: Bramanti & Edmunds (2016), Hughes et al. (2019). CCA and coral recruitment: Heyward & Negri (1999); Vermeij (2005), Birrell et al. (2008), Tebben et al. (2015), Fabricius et al. (2017)
		Spatial variation in temperature influences the living coral cover. Thermal stress (DHW) resulting in bleaching and/or mortality can also drive changes in living coral cover	30	Moore et al. (2012), Hughes et al. (2018a), Hughes et al. (2019), Gilmour et al. (2019)
		Light at benthos influences coral cover. Different coral taxa have different light preferences	31	Glynn (1976), Harriott & Banks (2002), Francini-filho et al. (2013)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
In situ carbonate production (cont.)	Benthic cover, species composition and coral recruitment (cont.)	Flow velocities can influence coral cover	32	Grigg (1995), see review by Lowe & Falter (2015)
		Coral and CCA responses to the seawater carbonate chemistry can vary between species and therefore the overall response may vary depending on coral and CCA composition	33	Comeau et al. (2013, 2017a, 2018, 2019a), Schoepf et al. (2013), Cornwall et al. (2017), Okazaki et al. (2017)
		Temperature influences coral composition of species spatially and geographically (e.g. with latitude), and temporally (e.g. repeated stressors over time)	34	Veron (1995), Kleypas et al. (1999), Harriott & Banks (2002), Hughes et al. (2018a,b), Zinke et al. (2018)
		Temperature influences CCA composition of species spatially and geographically (e.g. with latitude) and temporally (e.g. repeated stressors over time)	35	*No assessment of this*
		Reef depth (and hence light reaching benthos) causes vertical zonation and influences coral composition and CCA composition	36	Coral: Kahng & Kelley (2007), Tamir et al. (2019). CCA: Steneck (1986)
	Carbonate production (includes acclamatory and adaption responses, and calcification)	Flow velocities influence OA sensitivity, but the response is species-specific	37	Comeau et al. (2014c, 2019b), Cornwall et al. (2014)
		Coral and CCA composition influences OA sensitivity (different species show different levels of sensitivity)	38	Comeau et al. (2014d, 2017a, 2018, 2019a), Okazaki et al. (2017), Schoepf et al. (2017), Cornwall et al. (2018), DeCarlo et al. (2018), Kornder et al. (2018)
		Light at benthos influences ocean acidification sensitivity	39	Comeau et al. (2013, 2014b), Dufault et al. (2013), Suggett et al. (2013), Enochs et al. (2014)
		Coral and CCA composition will influence temperature sensitivity because different species have varying sensitivity to temperature	40	Coral: Loya et al. (2001), Grottoli et al. (2014). CCA: see review by Cornwall et al. (2019)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
In situ carbonate production (cont.)	*Carbonate production* (cont.)	Light and flow velocities influence temperature sensitivity (and coral bleaching)	41,42	Light and temperature sensitivity: see review by Fitt et al. (2001), Smith & Birkeland (2007), Brown & Dunne (2008). Water flow and temperature sensitivity: Nakamura & Van Woesik (2001), Nakamura & Yamasaki (2005)
		Changes in coral skeletal density and extension rate (and thus calcification rate) in response to OA will depend on species-specific OA sensitivity	43	Comeau et al. (2014a, 2019a), Okazaki et al. (2017), Cornwall et al. (2018), DeCarlo et al. (2018), Kornder et al. (2018)
		Temperature influences coral calcification rate (skeletal density and extension rate) due to the rate kinetics of aragonite precipitation and temperature driven increases in metabolism. However, the seasonal response of calcification to temperature varies among species and locations	44	Jokiel & Coles (1977), Lough & Barnes (2000), Marshall & Clode (2004), Kuffner et al. (2013), Roik et al. (2015), Ross et al. (2015), Courtney et al. (2017). Variable response of coral calcification rate to temperature: Ross et al. (2018, 2019)
		Nutrients influences coral calcification rate. Very high concentrations can reduce rates of calcification while modest increases can enhance calcification rates	45	Ferrier-Pagès et al. (2000), Koop et al. (2001), Tanaka et al. (2007)
		Changes in external seawater carbonate chemistry can influence the calcification process, given that the calcifying fluid is generally thought to be sourced from seawater. For this reason, seawater carbonate chemistry influences skeletal density and extension rate and thus coral calcification rate. The influence of seawater chemistry on density and extension differs	46, 47	Cohen & Holcomb (2009), Venn et al. (2013), Comeau et al. (2014c, 2017a,b, 2018, 2019a), Schoepf et al. (2017), Cornwall et al. (2018), Kornder et al. (2018), Mollica et al. (2018)
		Temperature sensitivity influences coral calcification rate. Corals are strongly adapted to their local temperatures and different species/genera also show different thermal sensitivities	48	Coles et al. (1976), Jokiel & Coles (1977), Marshall & Clode (2004), Ross et al. (2015), Samiei et al. (2016)
		Water velocities influence coral calcification rate. Water flow influences the boundary layer thickness, and thus, the diffusion of gases, exchange of ions, uptake of nutrients, and transport of metabolites required for physiological processes	49	Patterson et al. (1991), Atkinson & Bilger (1992), Comeau et al. (2014c, 2019b)
		Higher light levels can increase skeletal growth through the increased production of photosynthetically fixed carbon by the symbiont and the production of lipid biomass from translocated photosynthates. Calcification rates are higher in the light than the dark and the relationship between light and calcification rate typically follows a hyperbolic function	50	Chalker & Taylor (1975), Chalker (1981), Gattuso et al. (1999), Marubini et al. (2001), Allemand et al. (2011)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
In situ carbonate production (cont.)	*Carbonate* production (cont.)	Reef-scale calcification rates would be expected to be positively correlated with higher coral and CCA cover. However, this is not necessarily always the case	51, 59	Coral: DeCarlo et al. (2017), Page et al. (2017), McMahon et al. (2019). CCA: *No specific studies*
		Coral calcification rate is a product of skeletal density and linear extension rate	52	Carricart-Ganivet et al. (2000), Lough & Barnes (2000)
		CCA calcification rate is influenced by light at benthos due to the production of photosynthetically fixed carbon by the photosynthetic pigments produced by coralline algae	53	Ichiki et al. (2001), Lewis et al. (2017)
		CCA calcification rate is influenced by seawater carbonate chemistry	54	Kuffner et al. (2008), Cornwall et al. (2018), Johnson & Carpenter (2018), Comeau et al. (2019a)
		Temperature sensitivity and temperature influences CCA calcification rates	55, 56	Cornwall et al. (2019) (meta-analysis)
		Nutrients influence CCA calcification rates. Nitrogen enrichment (nitrate + nitrite and ammonium) can increase calcification	57	Ichiki et al. (2000), Johnson & Carpenter (2018), Schubert et al. (2019)
		Changes in CCA calcification rates in response to OA will depend on species-specific OA sensitivity	58	Cornwall et al. (2017, 2018), Comeau et al. (2019a)
		CCA and coral calcification rates combined are the total calcification rate	60, 61	Rasser & Riegl (2002), Perry & Larcombe (2003), Tierney & Johnson (2012)
Event (acute)-driven disturbances	Acute climate-driven disturbances on coral reef ecosystems (*physical erosion*)	Cyclone damage depends on the reef's geomorphology and its position with respect to the cyclone track, the cyclone duration and strength	1, 6	Puotinen (2007), Fabricius et al. (2008), Poutinen et al. (2016)
		Cyclones influence reef wave climate and wave energy, which causes direct physical damage to corals via mechanical erosion and mediates community-level calcium carbonate production	2, 3	Dollar (1982), Done (1993), Dollar & Tribble (1993), Storlazzi et al. (2004), Hamylton et al. (2013)
		On the long term, the magnitude of cyclone reef damage will depend on the return time of severe cyclones, which is predicted to increase with warming oceans	4	Webster et al. (2005), Emmanuel et al. (2008), Keim et al. (2007), Elsner et al. (2008), Mumby et al. (2011), Wolf et al. (2016)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Event (acute)-driven disturbances (cont.)	Acute climate-driven disturbances on coral reef ecosystems (*cont.*)	Coral bleaching is strongly correlated to heat stress (DHW) and impacts carbonate budget trajectories. Yet, bleaching events can be mitigated by cyclones that may slow down the build-up of thermal stress associated with temperature. Cyclones events have longer-term effects on temperature via wind-induced upwelling and vertical mixing of cooler subsurface water	5	Eakin (2001), Carrigan & Puotinen (2014), June Chang et al. (2016), Januchowski-Hartley et al. (2017), Perry & Morgan (2017), Courtney et al. (2018), Manzello et al. (2018), Hamylton & Mallela (2019), Lange & Perry (2019), Ryan et al. (2019)
	Changes in the abiotic reef *environment* due to acute disturbances	Indirect impacts of cyclones include changes to water quality (WQ) through reduced light availability, increased turbidity, nutrients and chlorophyll-a concentrations. This occurs when sediment is resuspended due to wave action and heavy rainfall (which further exacerbates river flood impacts). These changes in WQ can in turn cause coral bleaching and/or exacerbate bleaching from heat stress. Changes in WQ and high temperature also affect specific coral-growth parameters	7–13, 30–32	Harmelin-Vivien (1994), Larcombe et al. (1995), Jokiel (2006), Anthony & Connolly (2007), Vaselli et al. (2008), Larsen & Webb (2009), Wooldridge (2009), Carricart-Ganivet et al. (2012), Fabricius et al. (2013) Yang & Goodkin (2014), Roik et al. (2016), Edmunds et al. (2019), Evans et al. (2020)
		Changes in light availability will impact colony growth parameters (size, skeletal density and extension rates), which differ among species. This ultimately alters estimates of coral and reef-level calcification rates	20–23, 59, 60	Huston (1985), Meesters et al. (2001), Enochs et al. (2014), Pratchett et al. (2015), Madin et al. (2016)
		Changes in water quality alter the dynamics between corals and algae including macroalgae and CCA, the latter of which is a key component of total reef calcification	25–29, 33, 34, 38, 58, 61	Leukart (1994), Fabricius & De'ath (2001), Diaz-Pulido & McCook (2003), Littler et al. (2006), Castro-Sanguino et al. (2017), Bessell-Browne et al. (2017), Johns et al. (2018), Ceccarelli et al. (2020)
	Spatial and temporal dynamics of *benthic community* composition and *carbonate production*	At the community level, cyclones and bleaching directly reduce the amount of living coral cover and influence the structuring of coral communities given species-specific susceptibilities to each stressor. Hence, the magnitude of the impact of cyclones and bleaching on reef carbonate production will vary spatially depending on the environmental background (water quality conditions), which influences how coral communities are structured (i.e. relative abundance of coral types)	14, 15, 18, 19	Done (1992), Massel & Done (1993), Cheal et al. (2002), Storlazzi et al. (2004), Madin et al. (2006, 2014a), Osborne et al. (2011), Grottoli et al. (2014), Hughes et al. (2018b)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Event (acute) driven disturbances (cont.)	Spatial and temporal dynamics of benthic community composition and carbonate production (cont.)	Indirect impacts to the coral community occur via altering ecological interactions of corals with other benthic components such as macroalgae, which rely on free substrate available for colonisation of space. Free space available for colonisation increases after disturbances following coral mortality	36–39, 40–46	Highsmith et al. (1980), Connell et al. (1997), Lirman & Fong (1997), Mallela & Crabbe (2009), Foster et al. (2013), Doropoulos et al. (2014), Graham et al. (2014), Beeden et al. (2015), Elmer (2016), Yadav et al. (2016), Davidson et al. (2019), Hughes et al. (2000, 2019a)
		Coral community composition will determine reef recovery and coral recruitment patterns (sexually or by fragmentation) after disturbance events with cascading effects on the structuring of coral demographics and overall coral size distribution, which ultimately affect coral calcification rates. The balance between carbonate production and loss via growth and mortality processes of calcifier organisms determines the overall volume of reef framework per unit area (density)	24, 52–54, 57, 62, 63	
		Physical coral breakage will affect quantity (and type) of reef sediments and the amount of rubble on reefs, which may affect coral recruitment success and colonisation of other benthic organisms	17, 35, 38, 39, 40, 46	Perry (2001), Fox et al. (2003), Fox & Caldwell (2006), Cameron et al. (2016)
		Cyclones reduce colony size (i.e. diametre and height) impacting reef-scale rugosity via changes in coral size distribution, coral community composition and eventual degradation of dead colonies	16, 47, 48, 55, 56	Crabbe (2009), Graham & Nash (2013), Bozec et al. (2015), Darling et al. (2017)
		Reef-level rugosity may affect the amount of fish grazing necessary to control macroalgal abundance. Macroalgae is also controlled by environmental drivers (e.g. light, nutrients), which interact with grazing. Therefore, water quality degradation due to cyclones and bleaching can also impair grazing upon algae	49–51	Mantyka & Bellwood (2007), Nemeth & Appeldoom (2009), Bennett et al. (2010), Alvarez-Filip et al. (2011), Bozec et al. (2013), Castro-Sanguino et al. (2016)
Coral reef response to sea level rise	Sea level rise drives changes in *environmental* conditions and coral reef processes	Sea level rise changes the initial depth of the reef. The change in reef depth influences the propagation of wave energy into the reef system (see reef hydrodynamics) and the light at benthos, which in turn impact on living coral cover	1, 2, 4, 8	Hearn et al. (1999), Cooper et al. (2007), Baldock et al. (2014a), Beetham & Kench (2018a), Harris et al. (2018)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Coral reef responses to sea level rise (cont.)	Sea level rise drives changes in environmental conditions and coral reef processes (cont.)	A change in wave energy directly impacts the mechanical erosion processes on the reef. A change in mechanical erosion will result in differences in dead coral cover and then rubble cover. Different mechanical erosion processes will result in a change to the composition of corals and the CCA cover	3, 5, 7	Storlazzi et al. (2005), Madin & Connolly (2006), Baldock et al. (2014b), Madin et al. (2014)
	Environmental controls on coral reef carbonate production	Turbidity influences water column light attenuation and light at benthos (as a function of water depth). Light availability is an important control on coral cover and community composition	9, 10	Cooper et al. (2007), Tamir et al. (2019)
		Elevated water temperature can cause coral mortality and lead to a change in coral composition, and living and dead coral cover. Ambient temperate can also influence the coral composition and CCA cover. Seasonal changes in temperature also influence the calcification rates of coral and CCA	6, 11–15	Comeau et al. (2013, 2017a, 2018, 2019a), Schoepf et al. (2013), Cornwall et al. (2017), Okazaki et al. (2017)
		Ocean carbonate chemistry can influence the cover of CCA and the suitable substrate cover for coral recruits and the coral recruitment rate. The ability of corals and CCA to calcify are strongly influenced by the carbonate chemistry, so too is the composition of corals likely to be present	16–22	Fabricius et al. (2011), Doropoulos et al. (2012a), Cornwall et al. (2019), Comeau et al. (2019)
	Benthic community dynamics and controls on coral recruitment and calcification rates.	Sediment cover will be an important factor in determining CCA cover and the suitable substrate cover for coral recruitment	24, 25	Fabricius & De'ath (2001), Babcock & Smith (2002)
		Variability in living coral cover is the driver that determines the response of a coral reef to sea level rise. A change to living coral cover will result in differences in other benthic variables such as dead coral cover, suitable substrate cover for coral recruits and coral recruitment rate, and the benthic rugosity of the reef. The cover of living corals will be a key driver of the coral calcification rate	26–30	Perry et al. (2012), Gouezo et al. (2019), Hughes et al. (2019)
		CCA cover can create more suitable substrate cover for coral recruitment. Some CCA facilitate coral recruitment. CCA cover directly influences CCA calcification rate	24, 31, 32, 41	Bak & Engel (1979), Heyward & Negri (1999), Vermeij (2005), Doropoulos et al. (2012a), Ritson-Williams et al. (2014), Tebben et al. (2015), Elmer (2016), Doropoulos et al. (2020)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Coral reef response to sea level rise (cont.)	*Benthic community* dynamics and controls on coral recruitment and calcification rates (cont.)	Coral composition is influenced by a number of oceanographic and environmental variables (see links above) and also the juvenile coral population present on the reef (see coral recruitment links below). Live coral cover and the overall calcification rate of the reef is controlled by the composition of corals on the reef	23, 52	Doropoulos et al. (2012a), Perry et al. (2012)
		Rugosity of the coral reef is governed by the different types of benthic cover, primarily live coral cover, dead coral cover and rubble cover. It is an important variable in the propagation of wave energy through the reef system, coral recruitment rate and total calcification rate	28, 33, 35, 36, 38, 39	Smith (1992), Rogers et al. (2001), Wilson et al. (2007), Alvarez-Filip et al. (2009), Perry et al. (2012), Harris et al. (2018)
		Coral recruitment is an important driver for the juvenile coral population and the eventual composition of corals. Suitable substrate cover, CCA cover (see above) and live coral cover as well as seawater carbonate chemistry directly influence the potential recruitment of corals. There is a feedback loop between suitable substrate cover and living coral cover, where suitable substrate cover influences the juvenile coral population and eventual living coral cover	17, 18, 22, 27, 30, 31, 34, 37, 40–43	Doropoulos et al. (2012a,b, 2015), Bramanti & Edmunds (2016), Gouezo et al. (2019), Hughes et al. (2019)
	Balance of coral calcification, removal and sediment incorporation that leads to accretion (*reef geomorphology*)	The total reef accretion is a balance between carbonate production and removal processes. Accretion is also a function of the reef framework density, which describes the structure of carbonate material produced through CCA and coral calcification. Bioerosion rates influence reef framework density and also drives important processes of carbonate framework removal and production of sediment (see bioerosion module). Sediment is also incorporated back into the coral reef influencing the reef framework density	46–52	Perry et al. (2012, 2013b), Morgan & Kench (2016b)
		The combination of coral and CCA calcification rates are the main contributors to the total calcification rate of the coral reef	44, 45	Perry et al. (2012)
		Coral reef accretion leads to change in coral reef morphology and a shallowing of the reef reducing coral reef depth. This forms a feedback loop between the change reef depth due to rising sea levels and the resultant coral reef accretion at a later time point	53, 54	Davies (1983), Neumann & Macintrye (1985), Woodroffe & Webster (2014), Harris et al. (2015b)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Bioerosion	*Benthic community* and reef framework (reef framework properties influence erosion)	Reef morphology influences the diversity and distribution of key bioerosional taxa with presence/absence of major bioeroding groups like grazing urchins and parrotfish (grazers), sponges (macroborers) and even light-limited microborers closely linked to reef zonation. It also influences benthic cover. Framework types are also influenced by sub-environment with different benthic communities found in different zones. Feeding activity of grazers are influenced by zonation (parrotfish move to certain zones to graze), and population density size of individuals (e.g. urchins) can be depth dependent. Activity of light limited microborers is also linked to depth/zonation. Reef morphology here is a proxy for light, depth and flow	1–3	Parrotfish and reef morphology: Bruggeman et al. (1996). Urchins and reef morphology: Ruengsawang & Yeemin (2000), Griffin et al. (2003). Marcoborers and reef morphology: Scott (1985), Perry (1998), Chiappone et al. (2007). Feeding rates and reef morphology: Hoey & Bellwood (2008)
		Availability of suitable substrate for either colonisation by internal bioeroders (colonisable substrate, often dead coral cover, although many internal bioeroders can infest living corals) or grazing by external eroders (grazable substrate, namely turfs and CCA) will influence bioerosion through dictating bioeroder biomass	4, 5	Glynn (1988); Eakin (1996)
		Properties of the reef framework determine bioerosion rates, with surface area (Rugosity), volume and ratio of dead to living coral (living coral cover) and substrate density (reef framework density) all influencing bioeroder infestation and boring rates. A feedback loop here as high density of grazers can influence benthic community composition	6–8	Highsmith (1981), Hutchings (1983), Bellwood & Choat (1990), Roff et al. (2020)
		Physical density of the substrate (reef framework density) both affects infestation by internal borers and can stimulate bioerosion rates (particularly in macroborers), or retards it (parrotfish). Low substrate density may aid quicker and deeper penetration, but there is also evidence that dense reef framework enhances endolithic boring rates. Coral composition influences reef framework density. Redistribution of bioeroded calcium carbonate into reef cavities, and eventual recrystallisation and cementation in the cavity also strengthens the reef framework	8–11	Hutchings (1983); Macroborers: Neumann (1966), Highsmith (1981), Highsmith et al. (1983), Rose & Risk (1985), Schonberg (2002), Tribollet & Golubic (2005); Parrotfish: Neumann (1966), Rutzler (1975), Ward & Risk (1977), Ginsburg (1983), Hallock (1988), Ong & Holland (2010), Tribollet et al. (2002)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Bioerosion (cont.)	*Benthic community* and reef framework (cont.)	Coral composition not only influences rugosity and other framework properties, but macroborers show strong preferential tendencies towards certain species, perhaps due to skeletal density or nutrition	10, 12	Stearn & Scoffin (1977), Highsmith et al. (1983), Scoffin & Bradshaw (2000), MacDonald & Perry (2003), Chiappone et al. (2007)
	Abiotic *environmental* drivers (both bioeroder densities and activity rates influenced by environmental factors)	Sedimentation negatively affects available substrate for colonisation and grazing, and inhibits macrobioerosion through smothering, especially for sponges. However, it may boost bivalve and polychaete erosion through heterotrophic nutrition. There is some evidence that microborers can thrive under high sedimentation rates	13, 14	Wilkinson (1983), Perry (1996), Holmes (1997), MacDonald & Perry (2003), López-Victoria & Zea (2005), Mallela & Perry (2007)
		Light at benthos is thought to be the number one determinant of microborer density. There is some limited evidence it may also drive rates, although very high irradiance can inhibit boring. This is because microborers are mainly photoautotrophs. Light may also boost macroborer rates, particularly in zooxanthellate sponges through stimulating growth and faster boring rates, but also in sponges more generally	15–17	Rützler (1975), Wilkinson (1983), Hoskin et al. (1986), Vogel et al. (2000), Fine & Loya (2002), Weisz et al. (2010)
		Temperature effects on bioerosion are variable, with some evidence it influences parrotfish grazing rates and sponge boring, and slows microborer activity. High temperatures can also inhibit and damage bioeroders (e.g. in sponges). The best evidence for temperature increasing bioerosion is indirectly, though, increased substrate availability. Seasonal changes and upwelling can also boost bioerosion	16–18	Glynn (1988), Eakin (1996), Reaka-Kudla et al. (1996) Fonseca et al. (2006), Ong & Holland (2010), Achletis et al. (2017), Alvarado et al. (2017), Wizemann et al. (2018)
		Nutrient availability is the most important abiotic control of macrobioerosion, controlling density and to a lesser extent rate. This is because most endolithic macroborers are heterotrophic suspension or filter feeders. There are some evidence nutrients can positively influence microborer densities, although this is not supported by everyone	16, 17, 19	Hallock (1988); Macroborers: Risk & MacGeachy (1978), Highsmith (1981), Rose & Risk (1985), Meesters et al. (1991), Goreau (1992), Edinger & Risk (1994), Holmes (1997), Holmes et al. (2000), Zubia & Peyrot (2001), Callahan (2005), Ward-Paige et al. (2005), Carreiro-Silva et al. (2009). Microborers: Chazottes et al. (1995), Peyrot-Clausade et al. (1995), Kiene (1997), Vogel et al. (2000), Carreiro-Silva et al. (2009)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Bioerosion (cont.)	Abiotic *environmental* drivers (cont.)	Flow velocity boosts macroborer (particularly sponge) erosion, both through higher abundances on more exposed fore reefs but also through rates being boosted under high flow conditions, although this effect is variable. Flow is also important in determining how much sediment is re-incorporated back into the framework and how much is removed	16, 17, 20	Naumann (1966), Rützler (1975), Wilkinson (1983), Lopez-Victoria & Zea (2005), Chiappone et al. (2007); Leys et al. (2011)
		Seawater carbonate chemistry influences bioerosion activity. Microborers and sponges increase their growth and activity under ocean acidification. It is believed low pH conditions might promote bioerosion indirectly by weakening framework, or making the cost of acidic excretions less metabolically costly in chemical borers, and also is thought to directly ease the process of chemical bioerosion via reduced alkalinity and pH. It is also assumed to indirectly accelerate bioerosion by stimulating energy capture in phototrophic bioeroders. However, many eroding organisms (e.g. echinoids, molluscs) have calcium carbonate shells and therefore might be expected to be negatively affected. A feedback loop exists as chemical boring influences aragonite locally. Aragonite may also influence framework density through coral skeletal density, and how much sediment gets incorporated into the framework	16, 17, 21–23	Glynn (1997), Tribollet et al. (2009), Wisshak et al. (2012), Enochs et al. (2016), Schonberg et al. (2017)
	Bioerosion (Bioeroder densities and rates affected by biological factors like population characteristics)	Biotic factors (recruitment, disease, competition, predation) directly affect population densities of bioeroding taxa, particularly mobile grazers like urchins and parrotfish, who may also show seasonal shifts in abundance and activity. For example, recruitment is an important driver of polychaete abundance. Population densities influence mean size, and size can be influenced by biological factors like recruitment. A bioerosion loop also exists between macro and microborers and grazer densities. This loop magnifies and distorts bioeroder roles as bioerosion-mediated local changes in environmental conditions, substrate or predation and recruitment control, which then influence densities and rates	24–26	Hutchings (2001), Schoenberg et al. (2017)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Bioerosion (cont.)	Bioerosion (Bioeroder densities and rates affected; cont.)	Bioerosion rates by grazers are heavily size dependent (Grazer size), as larger individuals can have a disproportionate effect, e.g. fish smaller than 25 cm have little effect, while a 7 cm diametre *Diadema savignyi* consumes >500 times more carbonate than their 1.2 cm counterparts. Urchin test size is often used as a proxy for bioeroder pressure, while eroding fish bite volume is linked to fish body length. Feedback loop here as grazer density can influence grazer size (e.g. in urchin outbreaks), which reduces the bioerosive power of grazers	26, 27	Bak (1990), Griffin et al. (2003)
		Grazer density is the primary driver of mechanical bioabraision, the mechanical removal of carbonate substrate most usually as an unintentional consequence of herbivory. External eroders (principally reef fish and echinoids) are often apportioned a substantial budgetary contribution. The presence of particular species – such as the excavating fish Bolbometapon – can also be influential. To characterize the contribution of external eroders, they can be further subdivided into scrapers and excavators, the latter of which take substantially more material. Some urchins also excavate cavities. Macroborers contribute to bioabrasion too – most use combination of mechanical and chemical erosion, e.g. the mollusc Lithophaga uses combination of chemical softening (excreting acid from glands along the edge of the mantle) and a mechanical 'grinding' involving mechanical scraping of shell	28	Hein & Risk (1975), Bak et al. (1984), Hutchings (1986), Kiene (1988), Bellwood & Choat (1990), Kiene & Hutchings (1994), Pari et al. (2002), Tribollet et al. (2002), Bonaldo et al. (2014)
		Macroborer density has a significant influence on bioerosion, with macroborers adopting biocorrosion, abrasion or both. Sponges are often the most important organisms on the reef capable of erosion rates that exceed mean reef carbonate production rates. But macroborers also include bivalves (Pholadidae (angelwings), Gastrochaenidae (clams) and Mylitidae (mussels)), crustaceans (e.g. hermit crabs), barnacles (e.g. Lithotrya), shrimp (excavate large chambers) and worms including – Phoronids, Polychaetes, Sipunculans. Polychaetes are probably the best studied with polychaete families containing boring species: Eunicidae, Lumbrineridae, Dorvilleidae, Spionidae, Cirratulidae and Sabellidae, all of which employ combinations of mechanical and chemical bioerosion to various extents	29	Smith & Kinsey (1976), MacGeachy (1977), Stearn & Scoffin (1977), Wilkinson (1983), Hutchings (1986), Lazar & Loya (1991), Risk et al. (1995), Nava & Carballo (2008)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Bioerosion (cont.)	*Bioerosion* (Bioeroder densities and rates affected; cont.)	Microborer density influences bioerosion through biocorrosion – erosion by chemical dissolution to penetrate while exploiting fissures and colonising cavities in porous substrates. Defined by the creation of borings <100 μm in diametre, they are small, commonly autotrophic euendolithic microorganisms or microendoliths. Microboring communities colonise reef substrate more rapidly than any other bioeroding group (arriving on freshly exposed substrate within four to nine days of exposure), and may weaken substrate to speed up action of larger borers	30	Golubic et al. (1975), Tudhope & Risk (1985), Chazottes et al. (1995), Vogel et al. (2000), Tribollet (2008), Tribollet et al. (2011)
	Bioerosion output (carbonate removal, net sediment production and framework density)	Bioerosion has three main outputs. First, the total bioerosion rate that relates to the total amount of carbonate removed from the reef framework. Some of this framework removal produces sediments from bioabrasion processes, which feeds into the sediment budget production (net sediment production), and where it connects to the sediment production module. Net sediment production is, therefore, the second output of the module. Some of the carbonate removed is through chemical dissolution, so no sediments are produced. The removal of carbonate from the framework reduces reef framework density (third module output). However, some sediments that are produced from bioerosion may get re-incorporated back into the reef filling in the void volumes (reef framework density)	11, 31–34	Hubbard (1990), Perry & Hepburn (2008), Glynn & Manzello (2015)
Net sediment production	*Environmental* controls on reef calcifiers and sediment producers	Seawater turbidity (i.e. cloudiness) directly influences water column light attenuation and light at benthos (as a function of water depth). Light availability is an important control on coral community distribution and composition	1–3	Cooper et al. (2007), Storlazzi et al. (2015), Morgan et al. (2016)
		Elevated sea surface temperature can cause coral mortality and major increases in dead coral cover and rubble on bleaching-impacted reefs. Climate-disturbance (e.g. temperature extremes) events alter sediment production regimes by changing the relative abundance of calcifiers on reefs. Seasonal changes in temperature also influence the growth, calcification and turnover rates of calcifying algal species and foraminifera (i.e. direct sediment producers)	4, 5, 10, 15	Harney et al. (1999), Perry & Morgan (2017), Hughes et al. (2018a), Prathep et al. (2018); Perry et al. (2019, 2020), Castro-Sanguino et al. (2020), Taylor et al. (2020)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Net sediment production (cont.)	Environmental controls on reef calcifiers and sediment producers cont.)	Nutrient loading may increase internal bioerosion activity in live coral heads and detrital coral rubble. Sponge intensity exhibits increases in cover and bioerosion rate across gradients of water quality. Excess nutrients can increase productivity in calcifying green algae (e.g. *Halimeda* spp., *Amphiroa* spp.)	9, 11	Acker & Risk (1985), Holmes et al. (2000), Holmes (2000), Rice et al. (2020)
	Benthic community composition	Reef rugosity and benthic composition determine the total amount of available carbonate for internal boring organisms and grazing bioeroders (e.g. parrotfish and urchins). Higher bioeroder activity will produce greater quantities of detrital sediment	6, 7, 8, 13, 27	Alvarez-Filip et al. (2009), Perry & Morgan (2017)
		Sediment cover on reefs determines available habitat for specific direct sediment producers (e.g. calcifying algae, infaunal bivalves/molluscan species, foraminifera)	14	Schlacher et al. (1998), Van Tussenbroek & Van Dijk (2007), Parker & Gischler (2011)
	Physical erosion/ framework breakdown/grain diminution	Wave breaking and surging currents increase frictional drag on coral and promote physical damage, breakage and dislodgement of corals. The amount of physical stress on corals is related to the local wave climate. Physical breakage results in very coarse sediment clasts (i.e. whole and/or partial colonies) and rubble/gravels (i.e. detrital branches)	27–30	Rasser & Riegl (2002), Madin (2005), Madin et al. (2006, 2014), Baldock et al. (2014b)
		Storm activity (e.g. cyclones/hurricanes) can cause major mechanical destruction of coral reefs by storm waves. Wave energy decreases with reef depth and distance from reef edge (i.e. zones of the highest primary productivity). Damage can occur over large spatial scales (100 km) and coral clasts may form extensive boulder ramparts on the reef flat and/or storm ridges at the coast	27–31	Maragos et al. (1973), Baines & McLean (1976), Ogg & Koslow (1978), Highsmith et al. (1980), Edmunds & Witman (1991), Scoffin (1993), Harmelin-Vivien (1994), Richmond and Morton (2007), Álvarez-Filip et al. (2009)
	Bioeroder (*biological*) *sediment production* (grazing organisms)	Urchins produce sediment as the by-product of grazing algae growing on dead reef substrates. Sand-sized sediment particles are produced as reef carbonate is excavated, ingested and excreted. Higher urchin densities and grazing rates will increase sediment production	12	Hunter (1977), Ogden (1977), Reaka (1985), Ostrander et al. (2000), Peyrot-Clausade et al. (2000), Morgan (2014)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Net sediment production (cont.)	Bioeroder sediment production (cont.)	Parrotfish graze directly on filamentous algae and endolithic microbes in reef substrate and dead corals. Carbonate material is excavated during feeding, ground by the pharyngeal mill into sand-sized particles. Parrotfish are major producers of new sediment. Parrotfish abundance, size, species and functional group (i.e. scrapers versus excavators) influence the rate of sand production	12	Ogden (1977), Bellwood (1995, 1996), Bruggemann et al. (1996), Perry et al. (2015), Morgan & Kench (2016a)
		Bioeroding sponges (e.g. Cliona sp.) use chemical mechanisms to etch silt-to-sand sized carbonate chips (15–80 μm) from reefs. Chips have a characteristic shape and are easily transported by currents	12	Futterer (1974), Rützler & Macintyre (1978), Acker & Risk (1985), Nava & Carballo (2008), Carballo et al. (2017)
		Other boring organisms (e.g. *Lithophaga*, polychaetes, sipunculids) use chemical mechanisms (i.e. acid) to weaken the carbonate before mechanically removing it. This typically produces silt-sized particles that are transported off-reef	12	Scoffin (1992), Chazottes et al. (1995), Rice et al. (2020)
	Direct (biological) sediment production (e.g. foraminifera, *Halimeda*)	Large benthic foraminifera directly add to sediment reservoirs upon death. Foraminifera are often important in beach and island sediments because of the preferential transport capacity by reef currents and relative durability that promotes preservation. Growth and calcification vary between taxa and are influenced by changes in light and nutrient conditions	16–18, 26	Muller (1974), Hallock (1981), Harney et al. (1999), Fujita et al. (2009), Dawson & Smithers (2014)
		Halimeda are direct sediment producers and are often abundant within sediments. *Halimeda* sediments are typically bimodal: (1) whole or broken plates that are shed through growth or upon death and (2) fine sand- and silt-sized aragonite needles following breakdown	16–18, 26	Folk & Robles (1964), Drew (1983), Hoskin et al. (1986), Multer (1988), Perry et al. (2016, 2017, 2019), Castro-Sanguino et al. (2020)
		Halimeda have rapid growth and turnover rates (produce a new segment every two to four days). Turnover rates can vary seasonally on high-latitude reefs. Understanding rates of turnover/crops per year is crucial for estimating rates of direct sediment production	10, 15–18, 26	Freile (2004), Perry et al. (2016, 2019)
	Carbonate sediment dissolution (chemical)	Carbonate dissolution results in a loss of material when sediment pore waters become under-saturated with respect to the dissolving mineral phase. Undersaturation occurs through sediment metabolic processes and/or seawater composition. Organic matter decomposes in sediments releasing dissolved inorganic carbon (DIC) into the pore water. Reef sediments have a strong diel cycle of productivity and respiration (i.e. organic matter decomposition) that controls dissolution and precipitation	20–25	Cyronak et al. (2013), Eyre et al. (2014, 2018), Courtney et al. (2016), Cyronak & Eyre (2016)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Carbonate transport and sinks	*Reef hydrodynamics*	Incident wave climate is primarily driven by regional wind patterns. As regional storms generate waves, these waves propagate until they interact with a local reef	1–11	Young (1999), Young et al. (2011), Hemer et al. (2013), Hoeke et al. (2013), Reguero et al. (2015)
		Reef depth is controlled by water level above the underlying reef geomorphology and can vary on daily (e.g. tidal) timescales as well as seasonal to interannual timescales		Lugo-Fernández et al. (1998b), Potemra & Lukas (1999), Monismith (2007), Taebi et al. (2011), Lowe & Falter (2015), Buckley et al. (2018)
		When swell arrives, the local reef depth, reef morphology, and rugosity directly control wave dissipation		Hardy & Young (1996), Lugo-Fernández et al. (1998a), Massel & Gourlay (2000), Lowe et al. (2005), Becker et al. (2014), Buckley et al. (2014), Rogers et al. (2016)
		Wave dissipation at the reef crest drives wave setup, which in turn determines circulation patterns around the reef system (dependent upon reef-lagoon-channel morphology). When no waves are present, circulation is driven by tidal processes		Hearn (1999), Gourlay & Colleter (2005), Monismith (2007), Hench et al. (2008), Lowe et al. (2009b, 2010, 2015), Buckley et al. (2015, 2016), Quataert et al. (2015)
	Sediment supply and transport	Reefal sediment supply is directly linked to the reef ecosystem and abundance of reef-dwelling organisms (net sediment production)	12–14	Chevillon (1996), Harney et al. (2000), Yamano et al. (2000), Perry et al. (2011, 2015), Dawson et al. (2012), Morgan & Kench (2016a,b)
		The sediment composition ultimately determines the size, shape and density of the sediment reservoir and how it interacts with overlying flows		Sorby (1879), Folk & Robles (1964), Smithers (1994), Kench & McLean (1996), Ford & Kench (2012), Cuttler et al. (2017)
		Sub-aqueous sediment is entrained and transported via mean currents and wave orbital motions; subaerial (beach face) sediment is entrained transported by wind		Shields (1936), Soulsby & Whitehouse (1997), van Rijn (2007a,b), Storlazzi et al. (2011), Grady et al. (2013), Pomeroy et al. (2015, 2016, 2018), Cuttler et al. (2018)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Carbonate transport and sinks (cont.)	Island geomorphology and other *depositional sinks*	Alongshore gradients in sediment transport determine areas of deposition and erosion, which directly influence island shape and area	15–22	Kench & Brander (2006), Kench et al. (2006), Mandlier & Kench (2012), Grady et al. (2013), Beetham & Kench (2014), Duvat et al. (2017a), Cuttler et al. (2018), Costa et al. (2019), Ortiz & Ashton (2019), Shope et al. (2019)
		Sediment can be transported to inshore environments (dunes) via aeolian transport or storm over-wash		Stoddart (1964), Kench et al. (2008), Jackson & Nordstrom (2011), Ford & Kench (2014), Mann & Westphal (2016)
		Vegetation cover can stabilize backshore deposits to facilitate dune establishment/growth and long-term sediment storage		Short & Hesp (1982), Flood & Heatwole (1986), Wasson & Nanninga (1986), Buckley (1987), Hesp (2002), Bauer et al. (2009), Charbonneau et al. (2017)
		Sediment can also be deposited in off-reef areas (e.g. fore reef talus deposits) or contribute to lagoon infilling		Hubbard et al. (1990), Kench (1998b), Kench & Mclean (2004), Perry et al. (2013a), Harris et al. (2014), Morgan & Kench (2016a)

Note: Italicized variables (process column) relate to groupings in figures.

The development of the shared qualitative system model was conducted on the second day of the workshop, which focused on combining all shared sub-system models into one shared qualitative system model (i.e. the geo-ecological carbonate reef system model). We randomly organized modellers into three multi-disciplinary groups, each containing a representative from each sub-system module group. We began the modelling process by identifying those high-level variables that were common to two or more sub-system models. These variables were typically influencing environmental variables (e.g. atmospheric processes, wave climate) that acted as 'root nodes' (i.e. the first node in a rooted (directed) graph from which all paths originate). Below, we outline the development of each individual sub-system model and how these fit together to form the qualitative geo-ecological system model.

Developing the qualitative sub-system models of the geo-ecological carbonate reef system

The collective knowledge and understanding that support carbonate budgets provides the building blocks from which we developed the geo-ecological carbonate reef system model (Figure 1). We begin by first outlining the opportunities, limitations and challenges associated with transitioning from carbonate budgets to (predictive) models. Opportunities provide the foundations upon which to develop the qualitative model, whereas limitations and challenges reveal both the knowledge gaps that we should seek to fill, and the immense difficulty in collecting and analysing spatially and temporally relevant data from carbonate reef systems. Second, we provide a model summary and a detailed description of how each sub-system model was developed. The summary details the model's main outputs and influences, providing context for how each sub-system model relates to the geo-ecological carbonate reef system model. These summaries discuss how the model was developed in the context of previously identified opportunities, limitations and challenges of census-based carbonate budgets. Numbers in parentheses (#) relate to the numbered relationships in the sub-system model figures (Figures 3–8), which are further explained with additional references in Table 7. We explore our ability to quantify the relationships of the sub-system models in the 'Towards a quantitative geo-ecological carbonate reef system model' section.

In situ *carbonate production sub-system*

Transitioning from budgets to models

Primary carbonate production from coral and CCA calcification is the core component of conventional carbonate budgets. Estimates of *in situ* primary carbonate production can be obtained by coral (primary carbonate source) and CCA cover, multiplied by the calcification rate. Existing census-based carbonate budget studies typically include coral cover with calcification rates of one or a few coral species within or close to the site (Perry et al. 2012) predominantly due to the challenge of quantifying calcification rates for all coral species on a reef. Most studies include CCA cover (32 of 38 census-based studies; Table 1) and sometimes include CCA calcification rates (7 of 38 studies; Table 1). Other variables that are frequently included are coral composition, macroalgae cover, rugosity, reef topography and reef depth (Table 1). Rugosity and reef topography are critical because they are used to account for reef surface complexity and accurately quantify carbonate production over the three-dimensional (not planar) surface area. Most studies record coral composition (36 of 38; Table 1), rugosity (30 of 38 studies; Table 1) or reef topography, and all include reef depth. A total of 19 studies record the presence of macroalgae and a further six record 'algal' cover, although the type of algae (calcareous or fleshy) is not always specified (Table 1).

Measurements of primary carbonate production are generally short term (<1 year), and therefore, the majority of net carbonate production estimates that use census-based carbonate budgets are essentially snap-shots in time, which aim to assess what is present on the reef at one specific time, and usually in one geographic location. For this reason, there is a growing need to incorporate the ecological (e.g. macroalgae cover, recruitment rates of calcifying taxa, species composition) and physical (e.g. temperature, light, nutrients, seawater carbonate chemistry, water depth, water flow) variables that influence calcification rates, and are thus important for quantifying and understanding variation in *in situ* primary carbonate production over spatial and temporal scales.

Model summary

This model summarizes the drivers of coral and CCA calcification rates (Figure 3). Coral and CCA control primary carbonate production in coral reefs (Hubbard et al. 1990) and create the three-dimensional reef framework through the bio-calcification of their $CaCO_3$ skeletons, providing the foundation of the geo-ecological carbonate reef system model (# 60–61, Figure 3). Together,

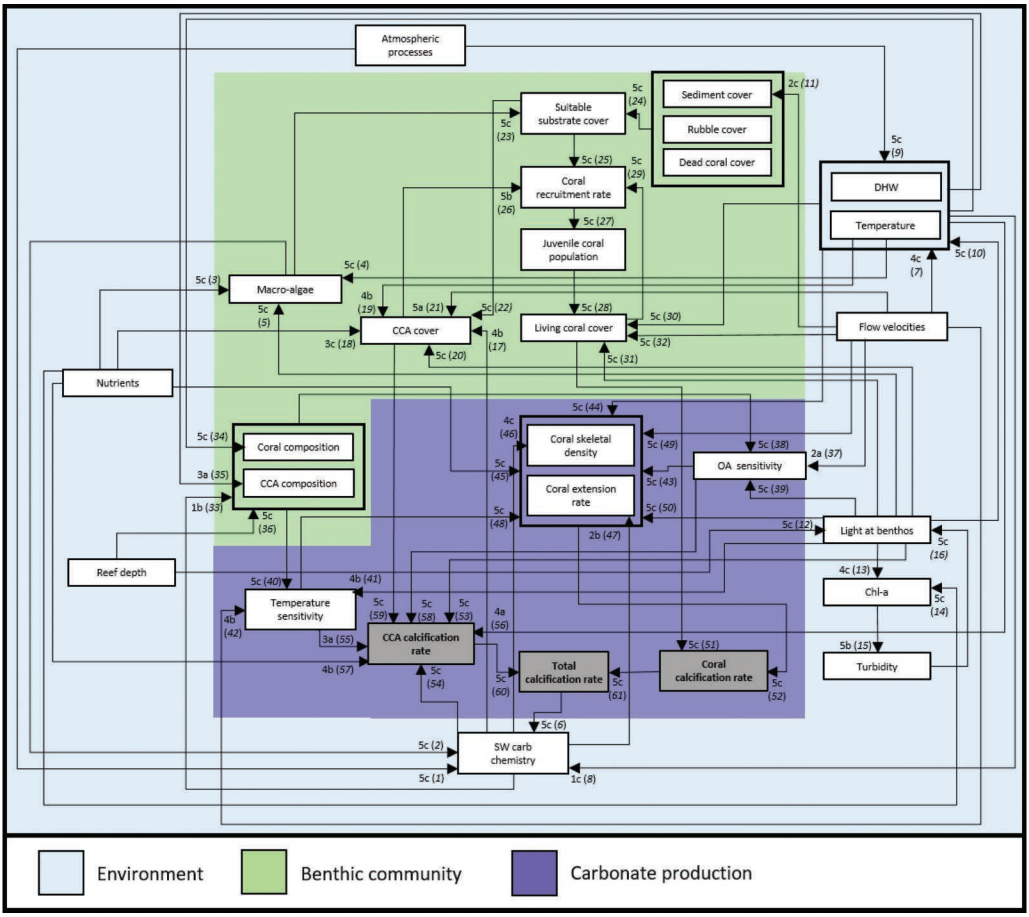

Figure 3 Conceptual model of *in situ* carbonate production. This model contains 28 variables and 61 relationships. Variables are grouped in three broad categories; environment (light blue), benthic community (green) and carbonate production (dark blue). Module output (grey-shaded variables) is from both coral and CCA calcification rate, which together provide total *in situ* carbonate production or total calcification rate. Each relationship is provided with a strength (1 to 5; 5 being the strongest) and confidence score (a–c; c being most confident). Numbers in brackets next to the strength/confidence score relate back to Table 7, which provides details on the relationships with relevant references.

coral and CCA calcification rate dictate the total calcification rate, which is designated as the main output of the model (Figure 3). Corals are the primary framework builders, calcifying rapidly in three dimensions, while CCA bind the reef framework, providing substrate for coral settlement and stabilisation. Thus, the geo-ecological carbonate reef system model requires a module that accounts for the dominant variables responsible for primary carbonate production in coral reef systems (Figure 3; Table 7). Five dominant physical variables explain the overall function of the model, represented by the total number of 'out degrees' (in parentheses; Figure 3): light (9), temperature and degree heating weeks (DHW) (8), water flow velocities (7), seawater carbonate chemistry (5), nutrients (5) and reef depth (2). The dominant ecological variables that are critical for model function include macroalgae cover (2), coral and CCA species composition (2), sensitivity to temperature (2) and ocean acidification (2), and coral recruitment rates (1). The incorporation of these physical variables, in particular flow velocity, directly seeks to resolve a significant limitation of current census-based budgets. These relationships are discussed below.

Photosynthesis and light

Critical to the calcification process is the production of photosynthetically fixed carbon by the microalgal symbionts (*Symbiodiniaceae*) that live within the coral tissue, and the photosynthetic pigments produced by CCA. While not specifically stated or included as a variable in our subsystem module, any variable that affects photosynthetic activity can influence calcification rates (Chalker 1981; Tambutté et al. 2011). This phenomenon, known as 'light-enhanced calcification', is due to the strong influence of light on both rates of photosynthesis and calcification (Chalker 1981) (# 5, 20, 31) with light at the benthos being a function of water depth, turbidity and chlorophyll-a (# 12–16, Figure 3). The influence of light on photosynthesis and calcification rates can be modelled based on the light reaching the benthos (i.e. in the form of photosynthetically active radiation) given that increases in light increase metabolic rates and stimulate calcification until a threshold has been reached, after which photosynthesis and calcification rates 'plateau' (Jokiel & Coles 1977, Chalker 1981, Marshall & Clode 2004, Rodolfo-Metalpa et al. 2008, Ulstrup et al. 2011, Al-Sofyani & Floos 2013, Samiei et al. 2016). Different coral species, however, and even sometimes individuals (e.g. different sized colonies) of the same species, can have different intrinsic rates of calcification that vary between different locations (Pratchett et al. 2015, Ross et al. 2015, Jury et al. 2019). Differences in coral calcification rates ultimately influence community primary carbonate production (# 51, 52). Yet, quantifying this effect is complicated because it requires highly detailed knowledge of the abundance of species within reef communities and the species- and location-specific responses of calcification rates to environmental and ecological parameters (see Kleypas 1997).

Temperature and bleaching

Corals are very sensitive to changes in temperature and are known to be highly adapted to their local seasonal temperature regimes (review by Sweet & Brown 2016). Rising ocean temperatures and the repeated occurrence of abrupt marine heatwaves are driving declines in coral reefs worldwide (Hughes et al. 2018b, Eakin et al. 2019). When sea surface temperatures exceed the local summer maximum monthly mean by just 1°C for three to four weeks, coral bleaching and mortality can occur due to the loss of the Symbiodiniaceae, resulting in declines in calcification and a reduction in live coral cover, respectively (Glynn 1996, Howells et al. 2012, Hughes et al. 2018a). For CCA, the bleaching threshold is based on a few existing studies, yet appears to vary substantially between species, and the negative effects of increasing temperature on calcification rates only seem to appear once temperature exceeds the ambient conditions by 5°C (see meta-analysis by Cornwall et al. 2019). Given that coral and CCA are often already living close to the upper thermal limits in the tropics (Coles & Jokiel 1977, Howells et al. 2012, 2013, Cornwall et al. 2019), further increases to ocean temperatures are expected to cause ongoing losses to coral reef health, species diversity and resilience (Hughes et al. 2017).

Temperature also plays a strong role in *directly* controlling both species distributions worldwide (# 34, 35) and individual rates of coral calcification (# 19, 30, 44, 56; Figure 3). This role is due to the positive effect of temperature on coral metabolism and biomineralisation (Coles & Jokiel 1977, Burton & Walter 1987). Clear trends in coral calcification rates have been observed on seasonal timescales (e.g. Kuffner et al. 2013, Courtney et al. 2017) and along latitudinal gradients in temperature (Grigg 1981, Lough & Barnes 2000). Separating the effects of light and temperature on calcification rates at these spatio-temporal scales can be challenging though, due to the co-variation of temperature and light (Kleypas 1997, Falter et al. 2012, D'Olivo et al. 2019, Ross et al. 2019). With respect to temperature, our model assumes that temperature effects can be modelled based on the local seasonal temperature range, given that increases in temperature drive metabolic rates and stimulate calcification until an 'optimum' has been reached, after which calcification rates decline (Jokiel & Coles 1977, Chalker 1981, Marshall & Clode 2004, Rodolfo-Metalpa et al. 2008, Al-Sofyani & Floos 2013, Samiei et al. 2016). We note, however, that the latitudinal trends and bell curve-shaped responses to temperature are species- and location-specific and not generally applicable to all coral genera, particularly those growing in sub-tropical and temperate environments (Ross et al. 2019). Temperature also plays an important role in controlling rates of CCA calcification (Ichiki et al. 2001, Lewis et al. 2017). Compared to corals, however, the temperature sensitivity of different CCA species is less well understood (# 34, 35, Figure 3; Cornwall et al. 2019).

Nutrients, macroalgae and suitable substrate cover

Nutrients can directly influence coral and CCA calcification rates at the individual level (# 18, 45, 57, Figure 3). Results for corals, however, are highly variable such that very high concentrations can reduce rates of calcification (Ferrier-Pagès et al. 2000) and modest increases in nutrients such as phosphorous can, in some cases, enhance calcification rates (Koop et al. 2001, Tanaka et al. 2007). Similarly, the effects of nutrients on CCA calcification rates are highly variable (# 57). For example, a positive influence of elevated nutrients on CCA calcification rates has been found to offset the negative effects of ocean acidification (Johnson & Carpenter 2018), while others found a negative impact of elevated nutrients on CCA calcification rates (Schubert et al. 2019) and cover (Belliveau & Paul 2002). Thus, although there are established relationships between nutrients and coral and CCA calcification rates, our knowledge of the specific effects of nutrients remains inadequate.

Much work has been done to understand the effects of macroalgae and available suitable substrate on coral recruitment and coral cover, providing a strong framework for modelling these interactions. Several factors, including the flux of nutrients in addition to light and essential elements (e.g. iron), can influence the growth of different algal species (Carpenter et al. 1991, Larned & Atkinson 1997, Renken et al. 2010) (# 3), many of which can compete with CCA and coral for suitable substrate (Szmant 2002, Jupiter et al. 2008, D'Angelo & Wiedenmann 2014). In addition, sediment cover and changes in the physical reef structure (e.g. available suitable substrate) can influence CCA colonisation, coral recruitment rates and coral cover (# 23–26) (Steneck 1986, Birrell et al. 2005, Cameron et al. 2016).

Flow velocities

The influence of water flow velocities is not typically included when modelling carbonate primary production. Water flow velocities, however, have an important influence on suitable substrate cover and calcification rates, because reef-scale hydrodynamics dictate the spatial distribution of algae and suitable substrate for CCA colonisation and thus coral recruitment, including sediment cover, rubble cover and dead coral cover (see net sediment production and sediment transport, # 11). Less is known about the impact of water flow dynamics on the growth of calcified algae, although recent work has investigated the interactive effects of environmental drivers such as temperature, light, nutrients and herbivory on *Halimeda* sp. (e.g. Castro-Sanguino et al. 2017). Higher water flow velocities influence calcification rates by reducing the size of the diffusive boundary layer surrounding coral and CCA, thereby increasing rates of nutrient uptake and exchange of metabolites (Atkinson & Bilger 1992). For this reason, water flow rates have been found to influence ocean acidification sensitivity in certain species of coral and CCA (Comeau et al. 2014c, 2019b); however, these relationships require more research for a range of coral and CCA species encompassing reef-scale diversity (# 37, Figure 3).

Seawater carbonate chemistry

Perhaps, the most complicated variable to relate in the model was the influence of seawater carbonate chemistry on reef-scale calcification rates (# 17, 33, 46, 47, 54, Figure 3). Our current understanding of the effect of ocean acidification on calcification rates is largely based on short-term aquaria experiments that simulate forecasted end-of-century $p\mathrm{CO}_2$. These studies indicate that ocean acidification will result in decreased rates of calcification for many marine calcifiers, including corals and CCA (Kroeker et al. 2013, Comeau et al. 2014d, 2018, 2019a, Kornder et al. 2018). While much work has been done to understand these relationships, the effects of seawater carbonate chemistry are not typically incorporated into census-based carbonate budgets. Characterising these relationships is challenging, in part, due to highly variable species- and location-specific responses to ocean acidification (Gibson et al. 2012). Insights into these responses can be gained from investigating the physiological mechanisms of calcification. For calcification to occur, coral and CCA must take up calcium and dissolved inorganic carbon to precipitate their CaCO_3 skeletons internally in a semi-isolated, seawater supplied calcifying fluid located between the living polyp and the skeleton (Cohen & McConnaughey 2003, Gagnon et al. 2012). While coral have some degree of control over their internal carbonate chemistry, the process of calcification is still sensitive to changes in the seawater carbonate chemistry because it alters the internal chemistry of many species (Comeau et al. 2014a, 2017a, 2018, 2019b, Schoepf et al. 2017, Kornder et al. 2018). Thus, there are species-specific responses, with some taxa showing high sensitivity and others showing resistance and resilience to experimentally induced acidification (Schoepf et al. 2013, Comeau et al. 2014d, Cornwall et al. 2018, DeCarlo et al. 2018). The effect of seawater carbonate chemistry on calcification rates can also be buffered or exacerbated by other environmental variables, such as light and nutrients, but these interactive effects are less well documented. Given that the responses to these interactive or additive effects are species-specific, they are challenging to model on the community-wide reef-scale.

Seawater carbonate chemistry is also influenced by the bio-calcification process (Bates & Amat 2010, Anthony et al. 2011). This relationship arises because photosynthesis and respiration results in the metabolic release and/or drawdown of CO_2. In addition, during the calcification process, bicarbonate is converted to carbonate, producing H^+, which are then eliminated from the site of calcification (Allemand et al. 2004). This relationship is included in the model for completeness with the assumption that the relationship operates on short (diurnal) and intermediate (seasonal) timescales more so than interannual or decadal (# 1, 2, 6). Furthermore, we recognize that the diurnal and seasonal variability of seawater pH in coral reefs due to these ecological processes can be highly variable. These fluctuations are generally minor on well-flushed reefs (i.e. 0.1–0.2 pH units), compared to other environments, such as kelp forests and macrotidal pools (Rivest et al. 2017, Cornwall et al. 2018), but can be up to 1.4 pH units on shallower back reefs (e.g. Ohde & van Woesik 1999, Shaw et al. 2012, DeCarlo et al. 2017).

Acute disturbance events sub-system

Transitioning from budgets to models

To understand the processes that drive carbonate production in the face of disturbance events (e.g. bleaching, cyclones), carbonate budgets need to incorporate the effect of changing environmental conditions on ecosystem processes (e.g. growth rates measured during heat stress versus 'normal' conditions) and capture the status of the reef system pre- and post-disturbance events. These conditions are often logistically difficult to measure, resulting in limited evidence on the impact of bleaching events, and even less of cyclone impacts, on reef budgetary state.

To date, only five census-based carbonate budget studies have included carbonate production data pre- and post-bleaching, all of which have been published since 2017 (Januchowski-Hartley et al. 2017, Perry & Morgan 2017, Hamylton & Mallela 2019, Lange & Perry 2019, Ryan et al. 2019). When bleaching has been included, the reliability of the data is related to the time lag between pre- and post-disturbance assessments. Furthermore, these assessments mostly rely on census-based approaches that represent annual production rates for specific reef habitats and, therefore, do not account for event-specific and spatial variability in carbonate production (Perry & Morgan 2017, Lange & Perry 2019, Ryan et al. 2019). Consequently, census-based approaches can result in an overestimation of gross carbonate production compared to approaches that use locally derived calcification rates measured during bleaching years (Manzello et al. 2018).

There is also a distinct lack of pre- and post-cyclone event measurements. These limitations arise from the unpredictable nature of cyclones (Puotinen et al. 2016), making it logistically challenging to mobilize on short notice (e.g. days before a cyclone) to collect pre-cyclone data. Similarly, as cyclones are often destructive, post-cyclone data cannot always be collected immediately post-event (e.g. within a few weeks). Timely pre- and post-cyclone surveys are necessary to understand factors such as initial reef state (e.g. high versus low cover per coral taxa) and local disturbance history, which have the potential to influence the assessment of acute impacts and reef recovery trajectories.

Census-based carbonate budgets are based on the fundamental assumption of spatial additivity (i.e. amount of $CaCO_3$ produced by a single organism per unit area of reef surface covered) and do not consider how interactions between benthic organisms may also modulate carbonate production. This limitation can be exacerbated by acute disturbance events, which differentially influence reef organisms. For example, it has been estimated that the calcifying algae *Halimeda* produces three times as much carbonate when it occupies habitat alongside structurally complex corals such as *Acropora*, which provide refugia from grazing organisms (Castro-Sanguino et al. 2016). Coral bleaching and cyclone events more severely affect branching *Acropora*, which likely has indirect impacts on *Halimeda* carbonate sediment production (Castro-Sanguino et al. 2016, 2020). Consequently, the impacts of acute disturbance events on the reef system are not fully captured using census-based carbonate budgets.

Model summary

This model summarizes the complex interactions between the reef system and acute disturbance events (Figure 4). Alterations in the frequency and timing of acute, climate-driven disturbances, such as tropical cyclones and marine heatwaves, can trigger extensive coral mortality with potentially important impacts on reef carbonate production (Kennedy et al. 2013). We include the effects of wave energy and temperature (as variables for cyclones and heatwaves, respectively) on *in situ* carbonate production in the model in an attempt to encourage future researchers to collect these data, therefore addressing a current limitation of carbonate budgets.

The main outputs of the model are total calcification rate and reef framework density. As a result, the model differentiates the pathways by which disturbance events will influence carbonate production (and reef accretion) via changes in benthic community composition and their ecological

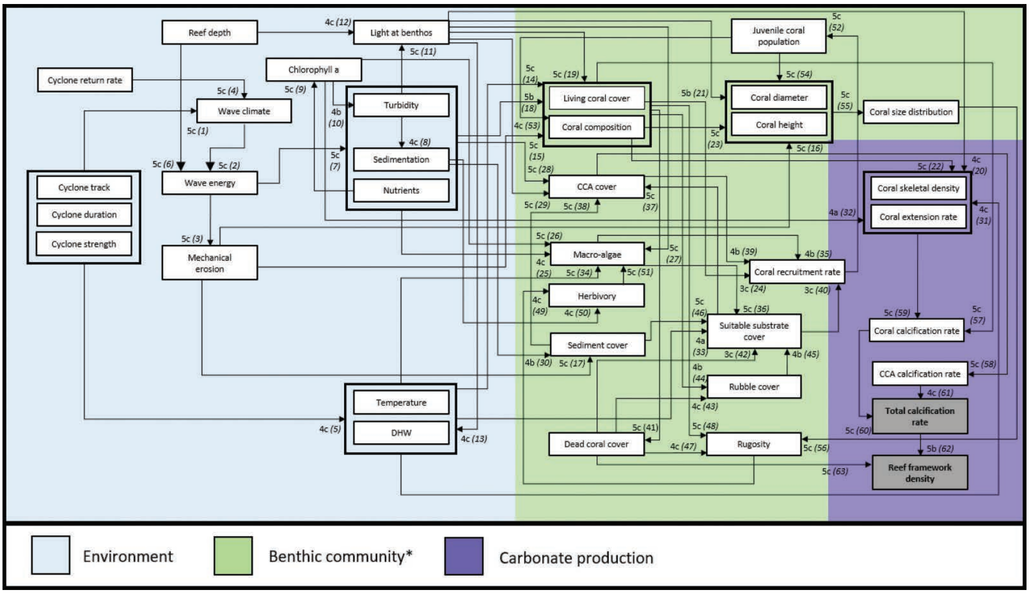

Figure 4 Conceptual model of event-driven (acute) impacts on coral reef communities. This model contains 36 variables and 63 relationships. Variables are grouped into three categories; environment (light blue), benthic community (green) and carbonate production (dark blue). Note that the * next to benthic community is to accommodate the variable herbivory, which is not part of the benthic community. Module outputs (grey shaded variables) include total calcification rate, which feeds into changes in the reef framework density. This module captures the impact of acute events, such as bleaching and cyclones events, and importantly incorporates how changes in benthic community will respond to these large disturbance events. Each relationship is provided with a strength (1–5; 5 being the strongest) and confidence score (a–c; c being most confident). Numbers in brackets next to the strength/confidence score relate back to Table 7, which provides details on the relationships with relevant references.

interactions (Figure 4; Table 7). We note that the variability of the responses from the benthic communities requires generalisations based on one to a few species, potentially limiting the reliability of any subsequent effort at quantification. The model seeks to capture variability of impacts at different spatial and temporal scales by focusing on the influence of wave energy (out degrees = 2; Figure 4) and mechanical erosion (3), temperature (4) and coral composition (6) on total calcification rate and reef framework density.

Wave energy and mechanical erosion

The variation in cyclone damage on a particular reef depends on the reef's position with respect to the cyclone track, the cyclone duration and strength (# 1, Figure 4; Puotinen et al. 2016, 2020). Wave energy variation around a reef provides a direct assessment of exposure to physical stress generated by cyclones (# 2, 3; Massel & Done 1993, Puotinen et al. 2016, Callaghan et al. 2020). The frequency and return period of severe cyclone events (# 4) can also have important implications on long-term ecosystem responses (Mumby et al. 2011, Wolff et al. 2016). Cyclone return rate is particularly important for modelling net carbonate production given the potential effects of global warming on increasing cyclone intensity and frequency (Emanuel 2005, Webster et al. 2005).

The consideration of the direct and indirect mechanisms by which climate-driven disturbances may impact coral communities was critical in building the model. For instance, cyclone waves cause direct physical damage to corals by breaking and dislodging colonies, affecting coral cover and size distribution through colony mortality and reductions in coral diametre and height (# 15–16,

Figure 4). Indirectly, cyclone waves may cause coral mortality via sediment resuspension, leading to coral burial (# 18) and increased turbidity (Edmunds & Witman 1991, Harmelin-Vivien 1994, Larcombe et al. 1995), which can impair coral reproduction and recruitment (Ricardo et al. 2015, Ricardo et al. 2016), and calcification and growth in some species (# 21–24; e.g. Kendall et al. 1985, Freitas et al. 2019). In addition, storm damage generates a considerable amount of loose coral rubble and framework debris that can delay coral recovery by reducing coral recruitment (# 38–40; Fox et al. 2003).

Temperature

For coral bleaching, we considered accumulated heat stress (as degree heating weeks (DHW); Eakin et al. 2010) as a proxy for bleaching severity (e.g. Hughes et al. 2018a). To capture habitat-specific responses to impacts of heat stress (# 12–14, Figure 4; Lenihan et al. 2008, Green et al. 2019) rather than assuming bleaching will occur equally in all habitats from reef crest to deep reef slope, we included variables such as reef depth and rugosity. Bleaching events have increased in severity and frequency due to global warming (Hughes et al. 2017, 2018a). Yet, although thermal stress may be responsible for most large-scale bleaching events, other environmental factors such as high UV radiation (Gleason & Wellington 1993) or reduced salinity associated with cyclones (Goreau 1964, Van Woesik et al. 1995) can also trigger bleaching. These additional processes were captured by incorporating relationships with water quality in the model (e.g. # 7–11).

During warming events, water column mixing induced by cyclones, known as 'cyclone cooling' is believed to reduce the heat stress associated with coral bleaching (Carrigan & Puotinen 2014). This process is captured in the model with a relationship between cyclone characteristics and DHW/temperature (# 5). Direct impacts of chronic ocean warming (i.e. increase in seawater temperatures) include effects on species growth and calcification (# 31; Cooper et al. 2008), whereas acute heat stress can trigger coral bleaching and lead to direct coral mortality as well as impaired coral reproduction and growth (Baird & Marshall 2002, Cantin & Lough 2014, Levitan et al. 2014). Indirect impacts include reduced coral larval supply following mass bleaching (Hughes et al. 2019), which has the potential to reduce coral recovery. Furthermore, coral mortality increases substrate availability for macroalgal overgrowth, potentially preventing coral recruitment (Doropoulos et al. 2014, Bozec et al. 2015). The acute disturbance model captures these complex interactions by incorporating feedback loops within components of the benthic community to consider alternative pathways by which coral communities respond to disturbances (# 30–48).

Coral composition

Coral community composition was a central variable in developing the acute disturbances model (Figure 4). Coral species differ in their vulnerability to cyclone-generated waves (Massel & Done 1993, Storlazzi et al. 2005, Madin & Connolly 2006, Madin et al. 2014) and heat stress intensity (Marshall & Baird 2000, Loya et al. 2001, Hughes et al. 2018b). Therefore, shifts in coral community composition due to recurrent disturbance regimes will influence reef-scale carbonate production dynamics (Courtney et al. 2020). Variability in community responses to disturbances is represented in the model with the consideration of species vulnerabilities and life-history traits (Darling et al. 2013, Madin et al. 2016) to inform variations in reef carbonate production (e.g. coral extension rate, coral skeletal density) (e.g. # 59–63).

Coral reef response to sea level rise sub-system

Transitioning from budgets to models

Although sea level dictates a range of environmental conditions that influence reef system development (e.g. accommodation space, light), the effects of sea level rise on carbonate budgets remain inadequately understood. The challenges to our understanding of coral reef response to sea level rise can be considered in the same way as spatio-temporal constraints between ‘geological’ and ‘ecological’ perspectives of coral reef change (Woodroffe 2008, Hubbard 2015). Geological approaches benefit from time-averaging processes that operate within a year to provide the average response of a coral reef system to a slow changing boundary condition (such as sea level rise). This approach is robust on temporal scales of millennia but struggles to provide insights into critical ecosystem processes that operate over shorter timescales and influence coral reef accretion (Hubbard 2015). Geological approaches are further limited by the features that can be derived from the stratigraphic record and the sampling regime (which typically consists of a spatially limited distribution of coral reef cores). Conversely, ecological approaches provide data on mechanisms that may drive net carbonate production and are thus more suited to examining the spatial heterogeneity in coral reef response to higher sea levels. Limitations of ecological studies (and carbonate budgets), however, relate to difficulties in translating these short-term ecological processes into long-term geological processes, such as coral reef accretion, that are accurate on scales of decades to centuries (Roff 2020). These limitations are due, in part, to the lack of *in situ* observations of coral reef accretion to recent and/or rapid sea level rise beyond that of the individual response of corals and other calcifiers.

Important recent attempts to cross the temporal gaps in geological and ecological understanding borrow approaches from both perspectives. High-resolution stratigraphic records of coral reef accretion combined with a reconstruction of oceanographic and some ecological processes are now possible (Roff et al. 2015b, Webster et al. 2018). When combined with a transect approach to coring coral reefs, a three-dimensional understanding of coral reef development is also possible (e.g. Cabioch et al. 1999, Dechnik et al. 2016, Webb et al. 2016). Numerical models that incorporate multiple variables from geological and ecological fields are used to hindcast and forecast coral reef accretion under rising sea levels and are starting to provide the links between census-based observations and geological perspectives on reef accretion (Salles et al. 2018, Pall et al. 2020). However, there are a number of interactions on coral reefs that are still poorly understood over the scales relevant to future sea level rise (decades to centuries). Examples include the influence of new substrate (following sea level rise) on coral recruitment and carbonate production (Doropoulos et al. 2012a); the processes that break down coral reefs into rubble and carbonate sediment; and the subsequent re-incorporation of coral reef-derived sediment and rubble into reef framework (Kennedy & Woodroffe 2002).

An ongoing challenge in translating ecological processes to geological timeframes relates to the conversion of *in situ* net carbonate production to reef accretion. To date, most studies that convert carbonate budgets ($kg{\cdot}m^{-2}{\cdot}yr^{-1}$) to reef accretion rates ($mm{\cdot}yr^{-1}$) follow the approach of Smith & Kinsey (1976). While this approach can provide useful insights into the *maximum* potential accretion (e.g. Perry et al 2018a), several assumptions in linking carbonate production to reef accretion remain, including (1) porosity of reef frameworks, which is based upon species-specific estimates from the geological literature (e.g. Davies & Kinsey 1977); (2) accretion derived from annual production estimates, which is assumed to be constant over decadal-centennial timeframes (e.g. De Bakker et al. 2019); (3) sediment incorporation, which is assumed to be constant through time and is uncoupled from framework production (Roff 2020); (4) carbonate production, which is assumed to remain *in situ* with no accounting for off slope transport from periodic storm disturbance (Schlager et al. 1994, Hughes 1999); (5) various conditions and processes, which are assumed constant but will likely change over time (e.g. increased reef flat wave energy under higher sea levels; Hearn 1999, Harris et al. 2018); (6) complex dynamics, such as feedback between reef structure and environmental processes and non-linear system responses, which are ignored (Woodroffe 2008); and (7) increased bioerosion on ecological timeframes, which may weaken reef frameworks resulting in loss of physical structures and reduced reef accretion potential (Glynn & Manzello 2015). These challenges are not easily resolved, but will be critical to understand in more detail if we are to increase our confidence in linking (and modelling) census-based carbonate budget results to the realities of coral reef change.

Model summary

Under rising sea levels, a coral reef system will accrete to mean sea level if the rate of sea level rise does not surpass the maximum rate of coral reef accretion and environmental conditions support carbonate production (Woodroffe & Webster 2014). Therefore, the main goal was to develop pathways that lead to the net vertical accretion of coral reefs in response to higher sea levels. However, the net accretion of a reef is a complex interplay of processes that produce, erode, dissolve, transport and incorporate carbonate material in coral reef systems (Perry et al. 2018b). We attempt to capture this complexity in the model by combining the geological knowledge of coral reef response to climate and sea level change over millennia with the ecological knowledge of coral recruitment, growth, carbonate production and response to environmental conditions over scales of seasons to years (Figure 5; Table 7). Although census-based carbonate budgets have been used to predict how reefs could respond (in terms of reef accretionary potential) to sea level rise, limited attention has been paid to how processes that drive reef ecology and carbonate dynamics might also change. The

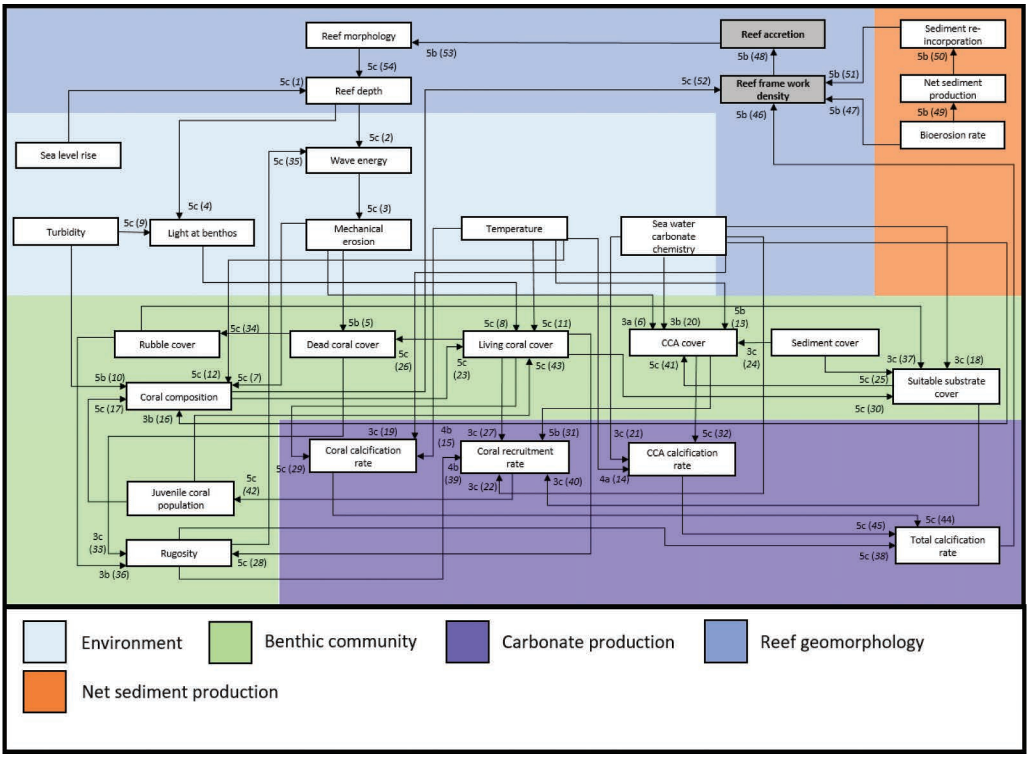

Figure 5 Conceptual model of sea level rise impacts on net reef accretion. This model contains 27 variables and 54 relationships. Variables are grouped in five categories; environment (light blue), benthic community (green), carbonate production (dark blue), net sediment production (dark orange) and reef geomorphology (medium blue). The module combines the geological knowledge of coral reef response to climate and sea level change over millennia with the ecological knowledge of coral recruitment, growth, carbonate production and response to environmental conditions over scales of seasons to years. Module outputs (grey-shaded variables) relate to changes in the reef framework density, which feed into longer-term reef accretion rates together with sediment re-incorporation. The bioerosion rate and net sediment production variables are module outputs from other modules, so includes all variables and relationships captured in these two modules. Each relationship is provided with a strength (1–5; 5 being the strongest) and confidence score (a–c; c being most confident). Numbers in brackets next to the strength/confidence score relate back to Table 7, which provides details on the relationships with relevant references.

coral reef response model seeks to overcome this limitation by articulating the relationships that require future consideration.

The main outputs of the model are reef framework density and reef accretion. As such, the model focuses on how changes in reef ecological process such as coral recruitment (out degrees = 1; Figure 5) and carbonate production (1) and environmental variables such as wave energy (1), light (1) and ocean chemistry (6) could change due rising sea levels and greater accommodation space, and how this could influence reef accretion.

Coral recruitment

A dominant component that differentiates this model to other previous models of reef response to sea level rise is that we specifically include coral recruitment as a central process in a coral reef's response to sea level changes (# 22, 27, 31, 40; Figure 5; e.g. Doropoulos et al. 2015, Bramanti & Edmunds 2016, Gouezo et al. 2019, Hughes et al. 2019). This process is often overlooked due (in part) to the longer temporal scales of most sea level change research when compared to coral recruitment studies. This component, we believe, is essential to consider because it allows an investigation into the processes that lead to rapid or subdued increases of carbonate production rates under rising sea levels.

Intertidal reef flats contain comparatively few, if any, live corals, but under rising sea level, intertidal reef flats will become fully submerged. If the environmental conditions and substrate are favourable, coral reef flats will recruit new corals and allow for the growth of live coral (# 17, 18, 22, 27, 30, 31, 34, 37, 40–43; Figure 5). A key unknown on coral reef response to higher sea levels is the length of time it takes for a reef flat to recruit new corals and begin vertical coral growth (Buddemeier & Hopley 1988, Buddemeier & Smith 1988). This model provides the relationships to investigate these responses by tracking the recruitment of new corals (# 22, 27, 31, 39) on to suitable substrate (# 31, 40, 41). The amount of suitable substrate cover (e.g. m^2) is influenced by rubble (# 37) and sediment cover (# 25) as well as seawater carbonate chemistry (# 18) and living coral cover (# 30). We consider suitable substrate cover to be a key variable that links sea level rise with coral recruitment: as the water depth over the reef increases, it not only increases the accommodation space, but also creates new areas for coral recruitment (i.e. by increase depth over reef flats). Coral recruitment rate is linked to eventual carbonate production because the survival and growth of juvenile corals (# 42) drives the subsequent adult coral composition (# 17), cover (# 43), and rates of coral (# 29) and total (# 44) calcification, together with CCA calcification and rugosity (# 38, 45; Figure 5). The breakdown of corals into rubble and sediment (# 5, 26, 34) via mechanical and bioerosion and subsequent incorporation (# 50, 51; Figure 5) and/or loss of this carbonate material is also an important but poorly understood factor.

Environmental variables

We also include hydrodynamic processes (such as changes in wave energy, # 1–3) and environmental conditions (such as ocean chemistry and turbidity, # 9, 18–22; Figure 5) that could influence carbonate production and the breakdown of live coral. The higher sea levels lead to changes in other environmental conditions that influence coral reef ecosystem functioning, such as light at benthos (Cooper et al. 2007) and wave energy propagating into the reef system (# 1–4; Figure 5; Hearn 1999, Baldock et al. 2014a, Beetham & Kench 2018, Harris et al. 2018). Changes in wave energy and subsequent mechanical erosion will impact the benthic cover (e.g. CCA, coral and carbonate rubble, # 3, 5, 6), and alter coral composition and rugosity (# 7, 23, 28, 33, 36), which are the primary drivers of coral reef carbonate production (# 38, 44,45; Figure 5; Storlazzi et al. 2005, Madin & Connolly 2006, Perry et al. 2012, Perry et al. 2013b, Madin et al. 2014). We also include processes such as net sediment production (# 50) and bioerosion (# 49) that are described fully in the other modules.

Reef framework density and coral reef accretion are the products of processes that produce (coral and CCA calcification) and remove carbonate (mechanical and bioerosion) (# 46–48, 51, 52;

Perry et al. 2013b, Perry et al. 2018b). The rate of reef accretion feeds back into the initial drivers of change in the coral reef system by influencing the difference between mean sea level and depth over the coral reef benthos (# 53, 54). If the rate of coral reef accretion keeps pace with the rate of sea level rise, the change in water depth on the reef flat will be minimal (i.e. similar water depth to present) and therefore conditions on the reef will not change substantially (Beetham et al. 2017, Harris et al. 2018, Perry et al. 2018b). If, however, the rate of sea level rise outstrips coral reef accretion many of the processes will change, leading to different trajectories in coral reef response to rising sea levels (Harris et al. 2018).

Bioerosion sub-system

Transitioning from budgets to models

Bioerosion is a dominant control of net reef accretion, but can be challenging to quantify and is therefore often poorly captured in carbonate budgets (Hutchings 1986, Spencer 1992, Glynn 1997). As widespread loss of corals frees up colonisation space and conditions such as increased nutrient pollution shift the balance in favour of filter feeding organisms, it is predicted that the role of bioeroders on coral reefs will become increasingly important in the future (Perry & Harborne 2016). As such, more reliable measures of bioerosion are paramount to any carbonate budget assessment. The main challenges to modelling bioerosion include (1) the taxonomic diversity and density of bioeroding organisms, which range from microorganisms to large vertebrate grazers (Hutchings 1986), (2) the divergent range of bioeroding mechanisms employed by these organisms, (3) lack of knowledge regarding species-specific responses to external biophysical and water quality variables; and (4) a high amount of variation in bioeroder abundances over time and space. These challenges are discussed below.

Census-based budgets rely on bioeroder density and calcifier abundance data, but rapid field surveys cannot accurately capture density estimates of buried framework eroders (e.g. sponges), motile/transitory grazers (e.g. parrotfish), nocturnal scrapers (e.g. urchins) or microborers invisible to the human eye (e.g. algae). Thus, bioeroders – diverse and largely cryptic – are significantly more difficult to survey than the predominately sessile and conspicuous benthic calcifier community. In the absence of direct measures, proxies are used, which come with underlying assumptions (e.g. that visible infestation of sponges at the surface relates to sub-surface density, or parrotfish numbers on a timed swim relate to activity at that site; Perry et al. 2012, Schönberg 2015). Consequently, many carbonate budgets are published with inadequate knowledge of site-specific bioeroding agents – which agents are present, active and their abundances. These knowledge gaps will have greater consequences in systems where bioeroding organisms are removing a significant portion of carbonate from the system.

Bioeroding mechanisms are as divergent and diverse as the bioeroders themselves – ranging from internal chemical etching by microbes to targeted mechanical excavation by parrotfish. This diversity multiplies the problem of poorly quantified bioeroder abundances when census-based budgets combine existing (i.e. published) activity rates with bioderoder density data to estimate reef-scale bioerosion. Knowledge gaps around activity rates of many species means that estimates are often derived from a few well-cited studies that might not represent the full range of rates across different sites within a species (Ogden 1977, Scoffin et al. 1980, Perry et al. 2012, Lange et al. 2020).

External physical (e.g. temperature, nutrients, sedimentation, wave energy) and biological (e.g. recruitment, competition, predation, disease) variables further propagate complexity by modulating bioeroder diversity, density and activity. For some species, external influences are well parameterized (e.g. multiple lines of evidence for positive association between nutrients and macroborer erosion; Hallock 1988), but for other species, they are not (reviews of knowledge gaps in Hutchings 2011, Perry & Harborne 2016, Schönberg et al. 2017, Lange et al. 2020). Furthermore, because most studies have focused on a single taxon and its relationship to external variable/s, we have insufficient knowledge about the interactive effects of multiple external variables on the bioeroding community's ability to remove carbonate (Hutchings et al. 2005). In addition to external physical and biological variables, bioerosion is also regulated by characteristics of the substrate itself, with factors like framework density, depth and length of exposure (following coral death) affecting bioeroder density and activity (Highsmith 1981, Kiene 1988). To date, substrate characteristics have been insufficiently accounted for in carbonate budgets.

Finally, scaling bioerosion from snap-shot estimates to broader space and time is hugely problematic: bioerosion on a newly exposed reef surface does not occur uniformly either in time (it is strongly successional and also influences itself in feedback loops) or space (bioeroders are often patchily distributed across reefs, so bioerosion pressure is highly variable spatially; Roff et al. 2015b). Bioerosion also fluctuates on orders of magnitude with explosions and crashes in bioeroder population densities (e.g. urchins; Uthicke et al. 2009), which in turn may be influenced by external drivers such as declining water quality, increasing temperatures or removal of predators, as well as showing longer-term trends (e.g. driven by reducing water quality, introduction of diseases).

Model summary

Here, we take an expansive view of bioerosion (due to particularly complex nature) that aimed to capture broad relationships within and between major bioeroding guilds and external (biological, abiotic and habitat) variables. The main model output is gross calcium carbonate removal (termed here total bioerosion rate; # 31, Figure 6), which represents the total material excavated from the framework by bioeroders (# 33; Table 7). How this excavated material is then redistributed (either dissolution, off-reef transport or re-incorporation into the framework) is not something most published budgets attempt to capture. Here, we seek to resolve this limitation by including the relationship between the production of bioeroded sediment and its re-incorporation into the framework (# 11, 20 and 22, 32, 34). Additionally, some sediment will be temporarily stored either on the surface of the reef or inside bioeroder guts ('storage'), and the remainder will be dissolved, ingested or transported to reef depositional sinks or out of the system (see the 'Carbonate Sediment Transport and Depositional Sinks sub-system' section).

Bioerosion is dictated primarily by the *presence* and *activity* of bioeroders; therefore, the model was organized around these two fundamental biological factors: (1) the diversity and density of bioeroding organisms (e.g. Figure 6 Box 1; out degrees = 4) and (2) their activity rate (Figure 6 Box 2; out degrees =2). Variation in bioeroder density will drive differential bioerosion pressure; thus, the knowledge of the composition and absolute abundance of bioeroders present on reefs is critical to any mechanistic understanding of bioerosion. Likewise, reliable knowledge of activity rates is critical for deriving bioerosion estimates from species abundances (Figure 6 Box 2).

Bioeroder density

To keep the model broad and applicable to different biogeographic regions, bioeroders are classified simply into functional guilds (Figure 6, Box 1). Although several classifications exist (e.g. Golubic et al. 1975, Ginsburg 1983, Hutchings 1986), the most widely applied categorisation groups bioeroders into *grazers* – mainly fish and echinoids that remove surficial material by scraping and excavating often as a consequence of herbivory (# 28, Table 7 for more details); *macroborers* – endolithic sponges, bivalves and worms that either occupy holes or are buried within framework (# 29); and *microborers* – euendolithic microorganisms living in shallow framework creating borings <100 μm in diametre (# 30) (Perry 1999). These groupings allow us to portray different types of bioerosion, such as external versus internal framework removal (Figure 6, Box 1) and mechanical (bioabrasion) versus chemical (biocorrosion) activity (Figure 6, Box 2) and, therefore, group different taxa into trophic groups that are more likely to be influenced by environmental changes in similar ways (Hutchings 1986, Glynn 1997). Microborers, including algae, fungi, cyanobacteria and foraminifera, are both the most ubiquitous and poorest studied of the guilds (Tribollet 2008a). Although the

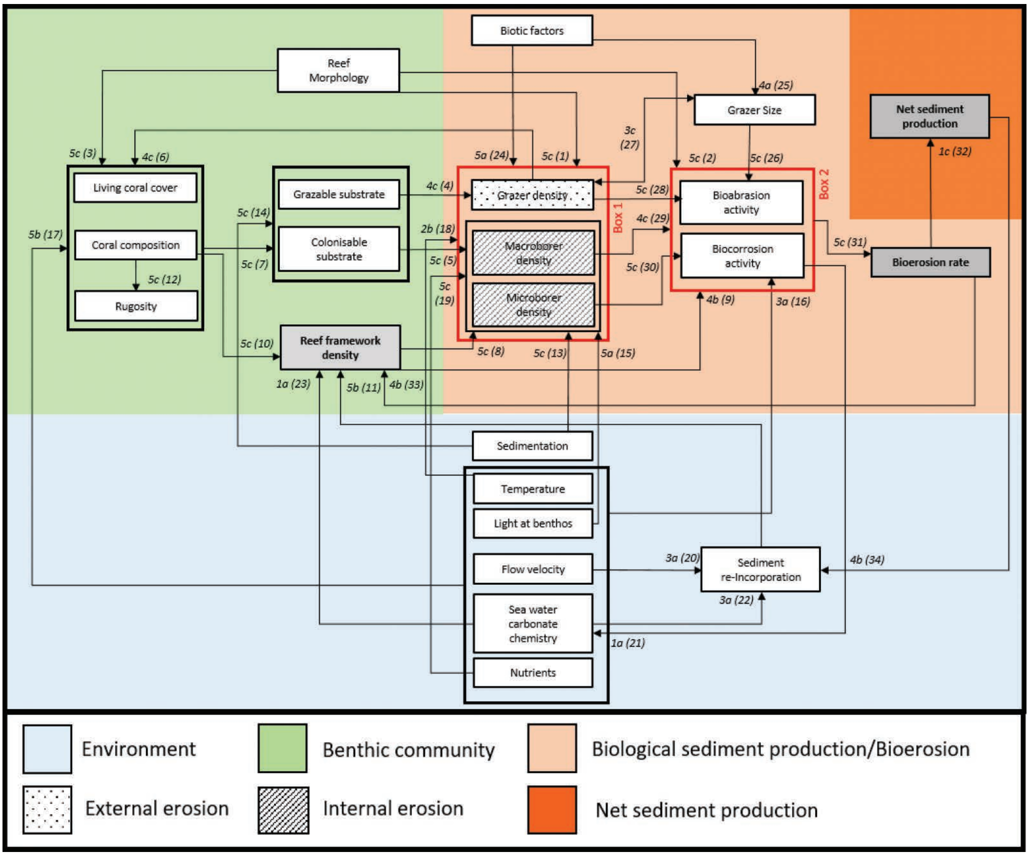

Figure 6 Conceptual model of bioerosion on the reef. This model contains 23 variables and 34 relationships. Variables are grouped into four categories: environment (light blue) and benthic community (and reef properties; green) and bioerosion (light orange). The link to the net sediment production module is also provided (orange box). Module outputs (grey-shaded variables) include the total carbonate removed from the reef (bioerosion rate), some of which (from bioabrasion) feeds into the net sediment production, together with those other biological, physical and chemical processes captured in the net sediment production module. The reef framework density is also a module output as it is influenced by both the removal of carbonate and sediment infilling from bioeroded sediments that are re-incorporated into the reef. The two red boxes relate to bioeroder density (Box 1) and activity (Box 2). In Box 1, we also differentiate between those bioeroders that are external (dotted) and internal (stripped). Each relationship is provided with a strength (1–5; 5 being the strongest) and confidence score (a–c; c being most confident). Numbers in brackets next to the strength/confidence score relate back to Table 7, which provides details on the relationships with relevant references.

roles of grazers and macroborers are better characterized (Bak 1994, Londono-Cruz et al. 2003, Alwany et al. 2009), there is a lack of consensus on their comparative contribution, perhaps due to geographic variation in activity and abundance, and experimental design and focus.

Bioeroders demonstrate clear community zonation, directly linked to depth and light (# 1), habitat availability (# 3, e.g. grazable and colonisable substrate: Table 6 for definitions), substrate type and rugosity (# 7), and reef framework density (# 8; Figure 6). Depth ranges (as well as other environmental variables that influence habitat and substrates) are captured in the model under reef morphology, since bioeroders are often related to certain reef zones. Habitat availability for either grazing or colonisation (by endoliths) – which may increase with higher rugosity (# 7 and 12) – is of particular relevance since large shifts in benthic cover in recent decades (# 4, 5) may have caused the escalation in bioeroder abundance (Schönberg et al. 2017). For example, urchin erosion increased 5-fold on Panamanian reefs after bleaching-induced coral losses in 1983 following an El Niño event (Eakin 1996, Glynn 1997). The type of substrate available will also influence the composition and density of bioeroders (# 7). For example, urchins typically graze CCA (Breitburg 1984), most parrotfish selectively graze algal turfs (Bruggemann et al. 1994), and many microborers infest living coral (Zubia & Peyrot-Clausade 2001). Coral community composition becomes important where we see different types of microbioeroding communities inhabit living and dead skeletons, while some macroborers show preference for certain species of coral skeleton (Peyrot-Clausade et al. 1992, Reaka-Kudla et al. 1996). Reef framework density (# 10, 11, 23) can also influence bioeroder density because denser substrates typically attract greater internal infestation, particular for bioeroding sponges (# 8; Schönberg 2002). The fact that bioeroder activity by its very nature influences the habitat locally (e.g. increasing framework porosity, affecting microhabitat complexity, e.g. Roff et al. 2020) further highlights the difficulty in capturing the complex nature of bioerosion in a model.

We include biotic controls on bioeroder population density (e.g. recruitment, disease, competition and predation) that are highly influential but also are too numerous, variable and species-specific to detail (biotic factors; # 24; Figure 6). The 'Bioerosion Loop', for example between grazers, macro- and microborers, represents feedback cycles where bioerosion activity by one guild creates changes in population or substrate that can alter local environmental conditions, further promoting or limiting bioerosion by other guilds (Schönberg et al. 2017).

The influence of abiotic factors, such as light, nutrients, sedimentation and temperature, on the abundance of bioeroding taxa is largely related to mobility, with sessile bioeroders more responsive to variability in environmental conditions. Most endoliths (e.g. macro- and microborers) are either photoautotrophic or heterotrophic filter feeders, and are therefore light or nutrient limited (Hallock 1988, Tribollet et al. 2002). The abundance of microborers is highest where light is abundant, and a reduction in available light will both decrease microborer density and alter the community composition given that certain species are more successful at using the limited light (# 15, Figure 6; Chazottes et al. 1995). Nutrient availability is one of the most influential and well-studied determinants of macroborer abundance, although the influence of nutrients can be both positive and negative (# 19; Chazottes et al. 2002, Wisshak et al. 2012, DeCarlo et al. 2015). The impact of sedimentation on bioerosion is complex, where increased sedimentation can either increase or decrease the abundance of bioeroders (# 13). Ocean warming can also influence the density of microborers (Reyes-Nivia et al. 2013), while temperature-induced bleaching, and subsequent coral mortality, increases the availability of dead coral substrate for subsequent colonisation by bioeroders. (# 18). The species-specific responses to environmental influences challenge any effort to predict how total bioerosion rates will vary with future environmental change.

Bioeroder activity

Bioeroder activity can be classified into either mechanical bioabrasion or chemical biocorrosion (although many macroborers employ a combination of both; Hutchings 1986). Bioabrasion is the mechanical removal of framework and includes both scraping and excavation by grazers, and internal bioerosion from some macroborers. Bioabrasion rates are more strongly influenced by biotic factors, such as the individual size of the eroding species (particularly for external eroders; # 26 and 27; Figure 6), where certain species or larger-sized individuals have a disproportionate impact (e.g. parrotfish < 25 cm have minimal bioerosive effect, while a 7 cm diametre urchin consumes >500 times more carbonate than their 1.2 cm counterparts (Bak 1990)). Biocorrosion is a biologically mediated process involving chemical dissolution of substrate, usually by internal eroders, particularly microborers (Tribollet 2008b). The process affects the local seawater chemistry within the framework and can quickly deplete carbonate content of seawater (# 21). Like any chemical reaction, biocorrosion rates are more likely to be directly influenced by abiotic factors that improve conditions for the reaction (# 16).

Information on how activity rates are influenced by external variables is generally lacking, or context-dependent and specific to individual taxa and locations (Perry & Harborne 2016). In the absence of data on how rates are influenced by external abiotic processes, an understanding of the bioerosion mechanism and organisms can help predict how activity may be modulated by external factors. For example, microborers are largely autotrophic, meaning activity is light-limited, while heterotrophic macroborer activity would be nutrient limited (Zubia & Peyrot-Clausade 2001, Carreiro-Silva et al. 2005). Evidence suggests that ocean acidification has a positive effect on micro-bioerosion (Reyes-Nivia et al. 2013) with growth and bioerosion increasing (by 48%) under doubled $p\mathrm{CO}_2$ (Tribollet et al. 2009).

As such, our model suggests that temperature, light, flow velocity, seawater carbonate chemistry and nutrients (# 16) influence biocorrosion rates, but at present, more evidence and quantitative data would be required to disentangle these relationships for specific taxa. We also identify reef framework density as having an influence on both bioabrasion and biocorrosion (# 9; Figure 6), the availability of other potential resources within the substrate (e.g. shelter, water and nutrients) that could encourage organisms to bore more rapidly into substrates (# 2), and the influence of substrate properties (e.g. live or dead coral, coral species and morphology) on boring rates (# 7; Goreau & Hartman 1963, Hubbard 1986, Scoffin & Bradshaw 2000).

Net carbonate sediment production sub-system

Transitioning from budgets to models

Sediment production is not considered a central component of a conventional carbonate budget, and therefore, the mechanisms that generate sediments on reefs are rarely included. This omission is made despite their close association with many of the processes that drive reef bioconstruction and erosion. Pioneering studies in the 1970s were principally interested in the geological implications of carbonate budgets for reef development, and therefore often incorporated aspects of sediment dynamics (e.g. off-reef transport, framework infill), but notably excluded sediment dissolution (e.g. Chave et al. 1972, Stearn et al. 1977, Scoffin et al. 1980, Harney & Fletcher 2003). In contrast, more recent carbonate budget studies do not consider sediment produced by living reef communities or have regarded it as a loss to the reef system, particularly as the focus of many carbonate budgets has shifted towards assessing reef biological functioning and health (Januchowski-Hartley et al. 2017, Lange & Perry 2019). Detrital carbonate sediments, however, are widely distributed and have long residence times on reefs (Hubbard et al. 1990, Smithers 1994, Dawson & Smithers 2014, Morgan & Kench 2016b, Cuttler et al. 2019). Moreover, reef-derived sediments also contribute directly to the long-term evolution of the reef structure, as well as to shallow- and deep-water sedimentary reservoirs (e.g. lagoons), and coastal landforms (beaches, islands) (Hubbard 1986, Kench et al. 2005, Gischler 2006, Perry et al. 2013a, Morgan & Kench 2016b). Few studies to date have investigated the sedimentary linkages between living reef communities and carbonate-derived landforms (Hart & Kench 2007, Dawson & Smithers 2014, Morgan 2014), and rarely have measured rates of sediment dissolution been incorporated into budgets (e.g. Courtney et al. 2016).

Model summary

This model summarizes the biological (e.g. coral cover and composition, bioerosion), physical (e.g. wave stress, cyclonic activity) and chemical (e.g. carbonate dissolution) processes that influence the availability of carbonate sources on reefs and their conversion into detrital sediment (Figure 7). Reef-derived sediments are composed of the skeletal remains of reef biota, either as eroded fragments of the primary reef framework (e.g. corals, CCA) or directly as the remains of calcifying reef-dwelling organisms upon death (e.g. foraminifera, molluscs, *Halimeda* spp.). Yet, biological productivity by living reef communities does not directly parallel rates of sediment production, as many carbonate sources require the breakdown by external factors before they can contribute to the

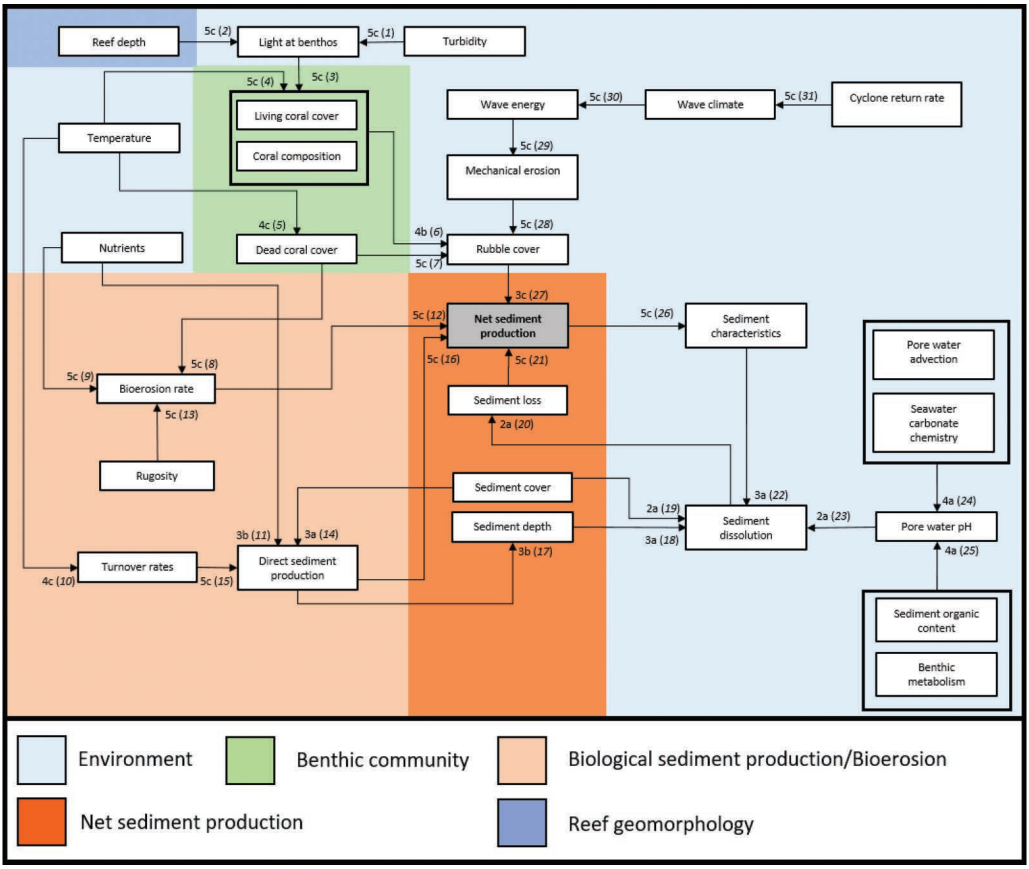

Figure 7 Conceptual model of net carbonate sediment production. This model contains 28 variables and 31 relationships. Variables are grouped into five categories; environment (light blue), benthic community (green), reef geomorphology (medium blue), biological sediment production (light orange) and net sediment production (dark orange). Module output (grey-shaded variable) is net sediment production which represents the gross carbonate sediment production from biological sources (e.g. direct sediment producers, bioerosion) and physical sources (e.g. the breakdown of *in situ* carbonate framework by mechanical erosion) as well as the loss of sediments through dissolution. The bioerosion rate variable is an output from the bioerosion module and represents all variables and relationships in that module. The net sediment produced on the reef then feeds into the carbonate sediment transport and depositional sinks module where sediments are either deposited on the reef system or transported off-reef. Each relationship is provided with a strength (1–5; 5 being the strongest) and confidence score (a–c; c being most confident). Numbers in brackets next to the strength/confidence score relate back to Table 7, which provides details on the relationships with relevant references.

local sediment pool. Here, we identify various biophysical reef processes and describe their influence on net sediment production (Figure 7; Table 7).

The model summarizes both direct and indirect sources of reef-derived sediment production, and loss (e.g. via dissolution), to provide an output of net sediment production. As such, the model focuses on the relationships between key sources of carbonate on reefs (coral cover and composition; out degrees = 1, direct sediment production; out degrees = 3; Figure 7) and the processes that erode (bioerosion; out degrees = 1, physical erosion; out degrees = 1), and remove (sediment dissolution; out degrees = 1) carbonate material. The development of the model highlights the complexities associated with quantifying rates of net sediment production across multiple spatial and temporal scales because of the range of biophysical processes involved. Further, this sub-system model provides a blueprint for including carbonate sediment budgets into census-based carbonate budget studies, which will be critical to improve our understanding on connectivity between reef ecological processes, sediment production and associated landform stability.

Coral cover and composition

Coral cover and composition is the main biological driver of reef-derived sediment because corals are the dominant calcifiers on most reefs, and their structural complexity determines the total source of carbonate framework available for breakdown (Chave et al. 1972, Scoffin 1992, Perry et al. 2012). Moreover, rates and types of sediment supply are derived from the growth traits and skeletal properties of their source organisms (Folk & Robles 1964, Ford & Kench 2012, Perry et al. 2019). Local abiotic conditions (e.g. turbidity, light, temperature, nutrients; # 1–4, 9, Figure 7) can negatively affect coral skeletal properties (e.g. density, micro-hardness), leading to increased rubble generation from hydrodynamic stresses (Risk & Sammarco 1991, Madin 2005, Dunn et al. 2012, Baldock et al. 2014b), or changes in internal bioerosion intensity (Highsmith et al. 1983, Holmes et al. 2000, Hernández-Ballesteros et al. 2013). Mass mortality events (e.g. coral bleaching) create vast amounts of dead coral cover that can be converted into rubble as the framework degrades (Perry & Morgan 2017) or into sand-sized particles following increased herbivory as algal substrates expand (Bellwood 1996, Perry et al. 2020, Taylor et al. 2020). Event-based sediment pulses represent a significant addition of new sediment to reefs (Perry et al. 2020) and have become increasingly more frequent and widespread (Hughes et al. 2018a), but the time lags between coral mortality and sediment generation remain poorly understood.

Bioerosion

Rates of sediment production from bioerosion become significant to local sediment facies when bioeroder activity intensifies (# 12, Figure 7). For example, parrotfish grazing accounted for the production of 85% of island sand (mean grain size of 0.35 mm) in the Maldives because of their high biomass and feeding intensity on reefs (Perry et al. 2015a, Morgan & Kench 2016a). Similar rates and particle sizes are also reported for parrotfish at sites along the Great Barrier Reef (Bellwood 1996). Considerably less is known about sediment production rates by urchin populations, even though individuals also produce sand-sized particles (0.2–0.5 mm) as a by-product of grazing (Hunter 1977, Ogden 1977, Reaka-Kudla 1985, Morgan 2014). Boring organisms (e.g. polychaetes, bivalves, molluscs) typically produce silt-sized particles (<63 µm) that are easily exported off-reef in suspension (Tudhope & Risk 1985). Bioeroding sponges (e.g. *Clinoa* sp.), however, can produce silt-to-sand-sized carbonate chips (15–80 µm) that contribute to local sediment reservoirs where sponge cover is high (Futterer 1974, Rützler & Macintyre 1978, Acker & Risk 1985, Nava & Carballo 2008, Carballo et al. 2017).

Direct sediment production

Direct sediment producers (e.g. *Halimeda* spp., foraminifera) add to detrital sediment pools immediately upon death and are a major source of sediment on some reefs (Kench et al. 2005, Yamano et al. 2005, Hart & Kench 2007, Dawson et al. 2014). In contrast to long-lived corals that are more resistant to breakdown, direct sediment producers have a short lifespan, fast growth and calcification, and high turnover rates (# 15, Figure 7). Although data exist for some key sediment producers (i.e. *Halimeda*) (Freile 2004, Multer & Clavijo 2004, Perry et al. 2016, Castro-Sanguino et al. 2020), limited information on the growth and calcification of benthic foraminifera (Muller 1974, Hallock 1981, Harney et al. 1999, Harris et al. 2015b) and non-articulated calcareous algae is available (Drew 1983, Perry et al. 2016, Perry et al. 2019). More generally, local nutrient conditions and seasonal variability in water temperature and light availability have been shown to influence the growth and calcification of direct sediment producers (# 10, 11; Littler et al. 1988, Teichberg et al. 2013, Castro-Sanguino et al. 2017).

Physical erosion

Physical processes (e.g. wave and currents) drive the production of coarse gravel fragments (>2 mm) and larger dislodged coral clasts on reefs (# 27–31, Figure 7). The greatest physical influence occurs on the reef edge where wave breaking and surging currents increase the physical force on corals and promote damage, breakage and dislodgement (Roberts et al. 1992, Lugo-Fernández et al. 1998a, Brander et al. 2004, Madin et al. 2006). We identify open ocean wave climate as the dominant physical disturbance on reefs (# 29–31). Storm activity (e.g. cyclone/hurricanes) has been documented to cause widespread destruction of coral communities to depths in excess of 20 m (Ogg & Koslow 1978, Highsmith et al. 1980, Edmunds & Witman 1991, Harmelin-Vivien 1994, Alvarez-Filip et al. 2009). These events can produce mass quantities of rubble over large spatial scales (100’s km), resulting in the formation of extensive boulder ramparts on reef flats, and storm ridges at the shoreline, which can persist for decades (Maragos et al. 1973, Baines & McLean 1976, Scoffin 1993, Richmond & Morton 2007). The return rate of storms influences the production of rubble as it controls the frequency of destructive events on reefs.

Sediment dissolution

Carbonate sediments can be lost through chemical dissolution (Eyre et al. 2014). Chemical dissolution of carbonate grains is governed by the aragonite saturation state (Ω_{ar}) of the surrounding seawater. Dissolution occurs when $\Omega_{ar} < 1$, which represents the thermodynamic threshold for aragonite precipitation (i.e. $\Omega_{ar} < 1$ and aragonite dissolves; # 23 & 24, Figure 7). Although overlying seawater in most coral reefs is saturated ($\Omega_{ar} > 1$), sediment pore water Ω_{ar} is related to both the metabolic processes and the composition of overlying seawater that is advected into the sediments (Eyre et al. 2014). Organic matter in sediments can decompose, releasing dissolved inorganic carbon (DIC) into the pore water to decrease pore water Ω_{ar} (Figure 7). For example, the starting Ω_{ar} of the pore water is the overlying seawater that is advected into the sediments; in shallow waters where light reaches the benthos, a strong diel cycle of productivity and associated respiration (organic matter decomposition) exist, controlling dissolution and precipitation (Cyronak et al. 2013, Cyronak & Eyre 2016). When Ω_{ar} becomes sufficiently undersaturated ($\Omega_{ar} < 1$), a point called the carbonate critical threshold (Andersson 2015), carbonate material begins to dissolve (# 20). Further carbonate sediment dissolution is driven by additional organic matter decomposition (# 25). The sediments on most coral reefs are currently net precipitating, with some exceptions in organically enriched reefs (Eyre et al. 2018). Carbonate reef sediments, however, may on average transition from net precipitating to net dissolving by 2050 due to ongoing ocean acidification (Eyre et al. 2018).

Carbonate sediment transport and depositional sinks sub-system

Transitioning from budgets to models

The purpose of census-based carbonate budgets is to quantify the balance of carbonate material in the context of net reef accretion, and therefore, no previous study has comprehensively established quantitative links between reef-derived sediment supply and shoreline evolution. Reef system depositional sinks (lagoons, landforms) can act as large reservoirs of carbonate material, but do not necessarily contribute to reef accretion. Yet, quantifying aspects of reef sediment dynamics is critical for predicting the response of landforms (and other depositional sinks) to changes in both contemporary and future process regimes (e.g. sea level rise, wave energy, sediment generation) (Perry et al. 2011).

The balance of sediment supply, transport and deposition dictates the development of reef-associated landforms (e.g. islands, beaches) and other depositional environments on reefs (e.g. lagoons, channels) (Harney et al. 2000, Kench & McLean 2004, Morgan & Kench 2014, Cuttler et al. 2019). In the few cases, when sediment dynamics have been included within carbonate budgets, it has been within a geological context to account for the retention (e.g. sediment re-incorporation, lagoons/channel storage), and/or loss (e.g. off-reef export), of total detrital carbonate from reefs (Land 1979, Sadd 1984, Hubbard et al. 1990, Harney & Fletcher 2003, Browne et al. 2013). Efforts are underway to understand the processes governing the 'carbonate sediment budget', with a focus on the linkages between reef ecology and landform evolution, in other words, the mechanisms of carbonate sediment generation, transport and deposition (Morgan & Kench 2014, Perry et al. 2015a, Morgan & Kench 2016b, Cuttler et al. 2019). These recent studies have highlighted the important role of large bioeroding organisms (parrotfish, urchins) in generating sand-sized sediment suitable for landform construction and maintenance, and have quantified transport rates and mechanisms of sediment delivery (e.g. bedform migration) to nearby depositional sinks (Morgan & Kench 2014,2016a, Cuttler et al. 2019).

Model summary

This model expands the traditional census-based carbonate budget approach, by incorporating sediment dynamics and shoreline morphodynamics, and capturing the full suite of processes driving sediment supply, transport and deposition in reef environments (Figure 8). Reef-fronted beaches and islands are sedimentary deposits formed primarily through the accumulation of biogenic carbonate sediment. These landforms are intimately tied to the rates of local sediment supply derived from the adjacent coral reef communities (see 'Net sediment production sub-system' section). These

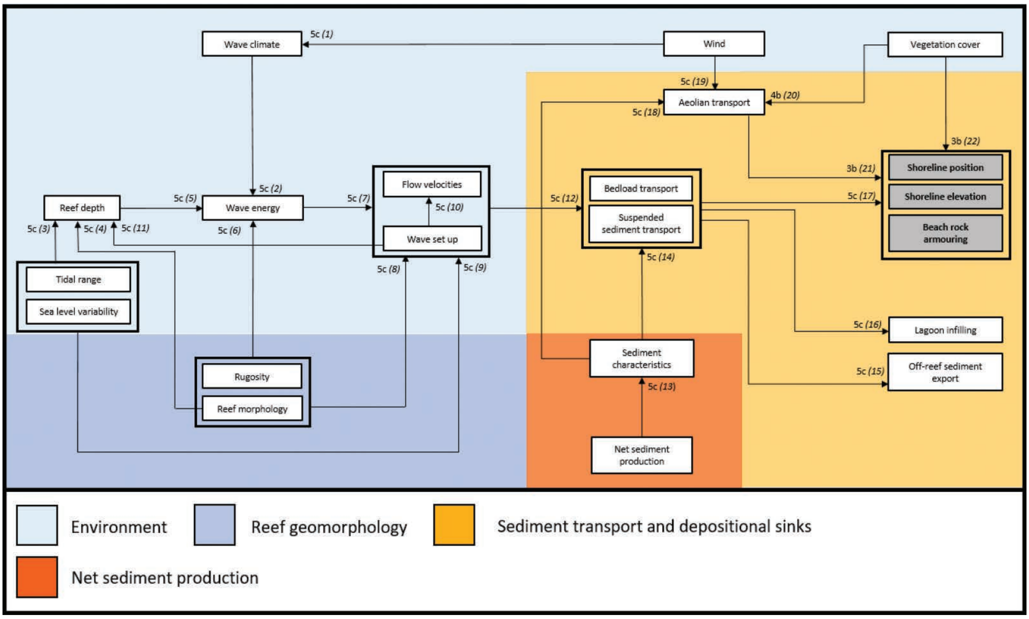

Figure 8 Conceptual model of carbonate sediment transport and depositional sinks. This model contains 21 variables and 22 relationships. Variables are grouped into four categories: environment (light blue), reef geomorphology (medium blue), net sediment production (dark orange), and sediment transport and depositional sinks (yellow). Module outputs (grey-shaded variables) relate to changes in landform morphodynamics. The variable net sediment production is an output from the net sediment production module and represents all variables and relationships in that module. This module captures the processes that mobilize, transport and deposit sediment throughout the reef system, thus representing the links between the ecological processes and landform dynamics. Each relationship is provided with a strength (1–5; 5 being the strongest) and confidence score (a–c; c being most confident). Numbers in brackets next to the strength/confidence score relate back to Table 7, which provides details on the relationships with relevant references.

unconsolidated sedimentary deposits have been shown to be highly dynamic in response to changes in physical forcing (e.g. waves, sea level) and sediment supply, which can cause large-scale modifications to shoreline morphology and elevation. Within many locations throughout the tropics (e.g. atoll reefs), reef-associated landforms provide the only habitable land area for human populations and are of significant ecological value in their support of high levels of terrestrial biodiversity (e.g. seabird populations). Therefore, understanding the processes that deliver reef-derived sediment to the shoreline and govern the formation and morphological stability of these landforms and other depositional sinks across a broad range of timescales (e.g. seasonal to decadal) is of critical importance to the geo-ecological carbonate reef system model.

The model variables are separated into dominant conceptual groups representing: (1) reef hydrodynamics (# 1–11) and sediment supply (# 12–14, 18), and (2) sediment transport and depositional sinks (# 15–17, 19–22; Figure 8; Table 7). Hydrodynamics (wave and sea level variability; out degrees = 6), reef morphology (reef flat width, lagoon and channel geometry, roughness; out degrees = 3) and sediment characteristics (size, shape, density; out degrees = 2; Figure 8) were determined to be the controlling variables of the overall model functionality.

Reef hydrodynamics and sediment supply

Reef hydrodynamics encompasses the wave and water level processes that mobilize and transport reef sediment. Regional wave climate (including extreme events such as cyclone frequency/intensity) determines the incident wave conditions (wave height, period, direction) at a given reef (# 1, 2, Figure 8; Hoeke et al. 2013). Once waves interact with the reef structure, their dissipation and ability to transport sediment is determined by the reef depth (which varies with tidal and non-tidal water levels) and reef morphology (# 3–4, 11). Water depth strongly influences wave breaking (# 5), while reef morphology (i.e. rugosity, fore reef slope, reef flat width) influences wave shoaling, dissipation due to bed friction, and wave setup (the increase in water level that results from wave breaking) (# 6, 8; Gourlay 1996a, Gourlay 1996b, Lowe et al. 2005, Monismith 2007, Lowe et al. 2009a, Buckley et al. 2015, Lowe & Falter 2015, Buckley et al. 2016). Waves generate wave orbital velocities and mean currents (collectively termed 'flow velocities'; # 7, 10, Figure 8) that are responsible for mobilising and transporting sediment (Pomeroy et al. 2015, Cuttler et al. 2019). When no waves are present (i.e. tide-dominated reefs), tidal flows drive the circulation patterns within the reef system (# 9; Lowe et al. 2015, Green et al. 2018).

Sediment produced via the biological and physical erosion of reef communities, or through direct inputs, becomes part of the 'active sediment reservoir' and is available for transport throughout the reef system (see 'Net sediment production' section). Sediment physical characteristics (e.g. shape, size, density) are related to the composition of reef-derived sediments and determine the conditions under which sediment can be mobilized (e.g. fair-weather, storm events) and the mode of transport (bedload, suspended load) (# 12, 14; Sorby 1879, Kench & McLean 1996, Cuttler et al. 2017).

Sediment transport and depositional sinks

Spatio-temporal variability in hydrodynamics drives alterations in sediment transport patterns that lead to the accretion or erosion of depositional sinks (# 15–17, 21, 22, Figure 8). These sinks include (1) off-reef talus deposits, generated by transport down the reef slope or out of channels (# 15; Harney et al. 2000, Morgan & Kench 2016a), (2) lagoon infilling (# 16; Perry et al. 2013a, Harris et al. 2014, Harris et al. 2015a) and (3) shoreline erosion/accretion, which in the context of reef islands is typically observed as changes to island area, height and shape (# 17; Kench & Brander 2006, Beetham & Kench 2014, Mahabot et al. 2016, Cuttler et al. 2019). For landforms, once sediment is deposited on the beach, it can be transported landward via aeolian (wind-driven) transport (# 18–21; Short & Hesp 1982, Sherman & Hotta 1990, Hesp 2002, Aagaard et al. 2004, Bauer et al. 2009) or by storm overwash – an important process for island vertical accretion and sand cay development (# 16; Kench et al. 2008, Woodroffe 2008, Masselink et al. 2020). Furthermore, subaerial sediment can become stabilized through the growth of naturally occurring vegetation (# 22; Hesp 1989, Stephenson & Brander 2003, Jackson & Nordstrom 2011, Charbonneau et al. 2017). Beach sediment can also become cemented *in situ* as 'beach rock', through physical and microbial-mediated chemical processes, which causes the precipitation of calcite crystals within the sediment pore spaces that bind individual sand grains (Vousdoukas et al. 2007). This cementation process can result in a natural armouring of the shoreline and potentially protect the landform from erosion by locking in a specific morphology.

Developing the qualitative geo-ecological carbonate reef system model

Above, we detailed the challenges of transitioning from budgets to models and the development of the individual sub-system models for each module. Here, we present a summary of the shared geo-ecological carbonate reef system model. This qualitative model moves beyond carbonate budgets and crosses the geo-ecological divide by providing links between reef ecology, carbonate system dynamics, reef accretion and landform stability.

To assist in understanding the geo-ecological carbonate reef system model, we developed a high-level overview figure that captures the relationships between the sub-system models through their outputs and critical variables (Figure 1). For example, the *in situ* carbonate production and acute disturbance modules produce outputs that feed into the variable 'total calcification rate'. The bioerosion and carbonate sediment production modules both produce outputs that feed into 'net sediment production', which in turn links to the geo-ecological carbonate reef system model outputs, including 'reef framework density', 'reef accretion' and 'landform morphodynamics'. We identified 'critical variables' according to at least one of three metrics. First, critical variables were those external environmental variables that acted as 'root nodes' (Table 4). External environmental variables were typically identified in only one or two modules, but acted as 'drivers' of a number of pathways, creating a pervasive influence throughout the system. Second, critical variables had high degree centrality with respect to the number of relationships a variable has with others (Table 8, Figure 1). This measure indicates how influential a variable is within the system. Third, critical variables were those that were common to three or more modules (Table 8; Figure 1). For example, living coral cover was included in five of the six modules (see Table 8) and had a total of 13 relationships (across all modules) with other variables. In addition to identifying relationships among sub-system models and the critical variables, we also grouped variables into broad categories (e.g. abiotic and biotic variables) to assist in providing an overview of relationships within the geo-ecological carbonate reef system model.

The value of the geo-ecological carbonate reef system model lies in its identification of *critical variables* that can be quantified, supporting decision-making for resource-limited research of carbonate system dynamics. The overview model accommodates *system complexity* by combining the current knowledge and understanding of the system; assesses *model confidence* through quantifying knowledge strength and confidence ratings; accounts for *environmental influences and acute disturbances*; and provides *flexibility* in terms of what elements of the system are studied while ensuring they can connect back into the whole system. As a result of these features, which we discuss below, we anticipate that the model will provide a blueprint for future research on reefs and associated landforms, with capacity for quantification of the system's response to changing environmental conditions.

Accommodating system complexity

Although data that can be easily collected are more likely to be included in geo-ecological assessments and models, it is nonetheless critical that we seek to represent the complexity of a system. For example, the ReefBudget consists of 33 variables that primarily relate to benthic cover, carbonate

Table 8 Variables listed according to the total level of connectivity (total number of relationships/arrows), number of arrows out (out degrees) and the number of arrows in (in degrees). We also provide a summary of the number of variables included in each module as well as the number of previous census-based carbonate budget assessments that have measured each variable (max 38)

Variables	No. of modules	Total arrows	Arrows out (out degrees)	Arrows in (in degrees)	In situ carbonate production	Acute disturbances	SLR	Bioerosion	Carbonate sediment production	Carbonate sediment transport and sinks	No. of previous carbonate budgets
Seawater carbonate chemistry	4	19	12	7	1		1	1	1		1
Coral composition	5	19	12	7	1	1	1	1	1		36
Light at benthos	5	18	16	2	1	1	1	1	1		5
Flow velocity	3	16	11	5	1			1		1	1
Temperature	5	15	11	4	1	1	1	1	1		4
Degree heating weeks	2	13	9	4	1	1					0
Living coral cover	5	13	6	7	1	1	1	1	1		38
Nutrients	4	11	10	1	1	1		1	1		3
Reef morphology	3	11	10	1			1	1		1	38
Rugosity	5	11	6	5		1	1	1	1	1	30
Reef framework density	3	11	5	6		1	1	1			0
Wave energy	4	10	6	4		1	1		1	1	2
Coral recruitment rate	3	10	5	5	1	1	1				0
CCA cover	3	9	2	7	1	1	1				32
Suitable substrate cover	3	9	2	7	1	1	1				24
Macroborer density	1	9	2	7				1			15
Coral extension rate	2	9	1	8	1	1					27
Coral skeletal density	2	9	1	8	1	1					25
Mechanical erosion	3	8	7	1		1	1		1		1
Sedimentation	2	8	6	2		1		1			9

(*Continued*)

Table 8 (*Continued*) Variables listed according to the total level of connectivity (total number of relationships/arrows), number of arrows out (out degrees) and the number of arrows in (in degrees). We also provide a summary of the number of variables included in each module as well as the number of previous census-based carbonate budget assessments that have measured each variable (max 38)

Variables	No. of modules	Total arrows	Arrows out (out degrees)	Arrows in (in degrees)	In situ carbonate production	Acute disturbances	SLR	Bioerosion	Carbonate sediment production	Carbonate sediment transport and sinks	No. of previous carbonate budgets
Sand/sediment cover	4	8	5	3	1	1	1		1		28
Rubble cover	4	8	4	4	1	1	1		1		23
Macroalgal cover	2	8	3	5	1	1					19
Biocorrosion activity	1	8	3	5				1			16
Microborer density	1	8	1	7				1			16
Turbidity	4	7	6	1	1	1	1		1		4
Dead coral cover	4	7	4	3	1	1	1		1		25
Reef depth	5	7	3	4	1	1	1		1	1	38
OA sensitivity	1	7	3	4	1						0
Temperature sensitivity	1	7	3	4	1						0
Grazer density	1	7	2	5				1			26
Bioabrasion activity	2	7	2	5				1			26
Wave setup	1	7	2	5						1	0
CCA calcification rate	3	7	2	5	1	1	1				7
Chlorophyll-a	2	6	4	2	1	1					1
CCA composition	1	6	3	3	1						0
Net sediment production	4	6	3	3			1	1	1	1	1
Bed load transport	1	6	3	3						1	2
Suspended load transport	1	6	3	3						1	0
Total calcification rate	3	5	2	3	1	1	1				11

(*Continued*)

Table 8 (*Continued*) Variables listed according to the total level of connectivity (total number of relationships/arrows), number of arrows out (out degrees) and the number of arrows in (in degrees). We also provide a summary of the number of variables included in each module as well as the number of previous census-based carbonate budget assessments that have measured each variable (max 38)

Variables	No. of modules	Total arrows	Arrows out (out degrees)	Arrows in (in degrees)	In situ carbonate production	Acute disturbances	SLR	Bioerosion	Carbonate sediment production	Carbonate sediment transport and sinks	No. of previous carbonate budgets
Direct sediment production	1	5	2	3					1		10
Coral calcification rate	3	5	2	3	1	1	1				26
Colonisable substrate	1	5	2	3				1			0
Coral diametre	1	5	1	4		1					10
Coral height	1	5	1	4		1					10
Sediment dissolution	1	5	1	4					1		1
Coral juvenile population	3	4	3	1	1	1	1				0
Sediment characteristics	2	4	3	1					1	1	15
Sediment re-incorporation	2	4	1	3			1	1			1
Pore water pH	1	4	1	3					1		0
Grazable substrate	1	4	1	3				1			0
Aeolian transport	1	4	1	3						1	0
Tidal range	1	3	3	0						1	0
Cyclone duration	1	3	3	0		1					0
Cyclone strength	1	3	3	0		1					0
Wave climate	3	3	1	2		1			1	1	0
Grazer size	1	3	1	2				1			24
Sediment depth	1	3	1	2					1		6
Beach rock armouring	1	3	0	3						1	0
Shoreline position	1	3	0	3						1	0

(*Continued*)

Table 8 (*Continued*) Variables listed according to the total level of connectivity (total number of relationships/arrows), number of arrows out (out degrees) and the number of arrows in (in degrees). We also provide a summary of the number of variables included in each module as well as the number of previous census-based carbonate budget assessments that have measured each variable (max 38)

Variables	No. of modules	Total arrows	Arrows out (out degrees)	Arrows in (in degrees)	In situ carbonate production	Acute disturbances	SLR	Bioerosion	Carbonate sediment production	Carbonate sediment transport and sinks	No. of previous carbonate budgets
Shoreline elevation	1	3	0	3						1	0
Cyclone track	1	3	3	0		1					0
Atmospheric processes	1	3	3	0	1						0
Sea level variability	1	2	2	0						1	0
Wind	1	2	2	0						1	1
Biotic control	1	2	2	0				1			0
Cyclone return rate	2	2	2	0		1			1		0
Reef accretion	1	2	1	1			1				2
Herbivory	1	2	1	1		1					0
Coral size distribution	1	2	1	1		1					10
Turnover rates	1	2	1	1					1		4
Sediment loss	1	2	1	1					1		5
Bioerosion rate	1	3	1	2			1	1	1		22
Pore water advection	1	1	1	0					1		0
Sea level rise	1	1	1	0			1				0
Sediment organic content	1	1	1	0					1		0
Benthic metabolism	1	1	1	0					1		0
Vegetation cover	1	1	1	0						1	0
Lagoon infilling	1	1	0	1						1	0
Off-reef sediment export	1	1	0	1						1	5

Note: Italicized variables are those included in the high-level summary of the geo-ecological carbonate reef system model (Figure 1). These variables are either included in three or more modules, or are key root nodes.

production and bioerosion variables (Perry et al. 2017; Table 1). While this level of complexity is sufficient for estimating rates of *in situ* net carbonate production, it is insufficient for determining how fluctuations in reef health and carbonate production influence reef accretion and/or landform stability over time.

Our geo-ecological carbonate reef system model comprises a total of 80 variables and 265 relationships across six individual but interrelated discipline-specific modules. Of the 80 variables included in the model, 24 are environmental (e.g. light, temperature, seawater carbonate chemistry); 16 relate to sediments (e.g. sediment characteristics and organic content); 14 relate to reef characteristics and benthic cover (e.g. rugosity, living and dead coral cover); 14 to *in situ* carbonate production (e.g. coral and CCA calcification rate); eight to bioerosion (e.g. grazer size and density); and four to landforms (e.g. shoreline position and elevation; Table 6). The diversity of variables provides a more accurate representation of the complexity of these systems.

Of the 80 variables included in our model, only 18 have been reported in the majority (>50%) of census-based carbonate budget studies. These 18 variables represent the bias in existing assessments and models, including benthic cover (e.g. living coral cover, macroalgal cover), grazing rates by urchins and parrotfish, coral growth and reef characteristic variables (e.g. depth, morphology; Table 8). Those variables, such as microborer densities, were less common due to either methodological difficulties or perceptions that it was not as important for carbonate budget estimates.

In addition to accounting for a more comprehensive collection of ecological variables, our model also accounts for the geological environment. These variables represent the ‘geo’ of the geo-ecological carbonate reef system model, which includes 15 new variables that go beyond the reef and relate it to sediment transport and shoreline dynamics. The inclusion of these variables provides the first model to integrate reef ecological change with landform stability. Representing this complexity is essential for developing quantitative models that will more accurately represent reefs and associated landform systems.

Assessing model confidence

One of the main contributions of the geo-ecological carbonate reef system model is an assessment of the existing knowledge base within each of the modules. Differences in confidence ratings between modules were a reflection of the extent of *existing* knowledge. Such assessments are critical in determining where knowledge gaps exist, particularly in terms of what data are available to enable comparisons between sites.

The sub-system models with the highest confidence ratings related to the *in situ* carbonate production module (77% high, 8% low confidence), acute disturbance model (82% high, 3% low confidence) and the carbonate sediment transport and sinks module (86% high, 0% low confidence), reflecting the vast amount of research and understanding associated with coral calcification processes, and physics-based processes central to carbonate sediment transport. In contrast, modules with the lowest confidence ratings included the bioerosion module (62% high, 23% low confidence) and the sediment production module (64% high, 26% low confidence), reflecting unknowns around environmental variables and rates of cryptic boring organisms, and drivers and rates of sediment production and dissolution, respectively. Areas with the lowest confidence rating were largely associated with four areas: CCA cover and calcification rates, boring organism density and activity, sediment dissolution and reef framework density.

An interesting outcome of the modelling process was a correlation between a person’s confidence in their knowledge of a relationship and the perceived strength of that relationship. Modellers rated relationships (influences between variables) in their model based on their perceptions of the strength of those relationships (1 = weak, 5 = strong). Approximately 67% of the total number of relationships were classed as strong relationships and <5% were classed as weak. Weak relationships included the influence of temperature on CCA calcification rates; seawater carbonate chemistry on reef framework density; flow velocity on coral and CCA sensitivity to ocean acidification; environmental drivers of rates of bioerosion; and the influence of sediment dissolution on sediment loss rates. Interesting, of the 25 low confidence relationships, 60% were found to have a low to medium (1–3) strength rating. This correlation points to a bias in what might be considered important within a complex system on the basis of how much data we have on the different variables within that system.

Accounting for environmental influences and acute disturbance events

Environmental influences include both physical (e.g. climate and sea level variables) and abiotic (e.g. seawater carbonate chemistry, light, nutrients) variables. They are necessary to include in any predictive application of the geo-ecological carbonate reef system model because such predictive models ultimately seek to quantify the relationships between environmental variables (cause) and ecological change (effect) (Cacciapaglia & van Woesik 2020, Lange et al. 2020). For example, of the 31 critical variables identified, the majority (19) were environmental variables, 11 of which were (physical) external drivers (Figure 1). The 11 external drivers included atmospheric processes (light, temperature) and wind, wave climate and sea level variables, cyclone-related variables, and landform vegetation cover (Figure 1). These variables were typically only present in one module and acted as 'root nodes'.

One of the most important contributions of the geo-ecological carbonate reef system model is the inclusion of the acute disturbance module. This module contains 63 relationships that connect 36 variables that describe the influence of these events on carbonate production, including variables that specifically relate to disturbance events such as degree heating weeks, cyclone characteristics and mechanical erosion. The acute disturbance module provides a comprehensive blueprint for future carbonate production assessments that seek to assess how these large events influence carbonate production over time (e.g. during the recovery period). The blueprint can be used to support researchers in making decisions around which variables should, and can, be quantified with available resources to estimate current and/or future carbonate production.

The variables and relationships of the acute disturbance module are thus important to capture for modelling changes in carbonate production. Existing census-based carbonate budget assessments typically only provide a 'snap-shot' of present-day carbonate production rates. Few assessments have conducted repeat measurements through time to enable an estimate of change in carbonate production and reef budgetary state in response to changing conditions (Manzello et al. 2018); and pre- and post-disturbance event assessments (Perry & Morgan 2017, Lange & Perry 2019). Yet, it is these events (e.g. bleaching and cyclones), which are predicted to increase in frequency and severity in coming years (Carrigan & Puotinen 2011, Hughes et al. 2017) that are most likely to have large-scale effects on carbonate production. Importantly, we currently lack data on how net carbonate production will change during and following these events. As such, current estimates of the influence of acute events on reef carbonate production and growth are potentially inaccurate, creating the need to develop a predictive quantitative model.

Given that future climate change will likely change ocean conditions (e.g. high temperatures, lower pH, lower light, more frequent and intense cyclones; Hoegh-Guldberg & Bruno 2010, Hughes et al. 2017), it is imperative that physical and abiotic variables are included in geo-ecological carbonate reef system modelling. To provide environmental context, we encourage researchers to include in future carbonate studies site-specific data (in-water) on light, temperature, seawater carbonate chemistry, sediments and nutrients, and wave energy and current velocity. In the absence of direct *in situ* measurements of these variables, there are some readily available data sources (e.g. global wave hindcasts, satellite-derived measures water quality and temperature) that could be (relatively) easily incorporated into future quantitative models that seek to predict ecological change with environmental change. But it should be noted that these data sources operate over larger spatial scales

(>100 m) so likely do not reflect changes in processes at the reef habitat scale. Finally, to quantify cyclone impacts more accurately within geo-ecological carbonate reef system models, we need to also include variables that influence coral breakage thresholds, such as the strength of the substrate upon which colonies are attached (Madin 2005) and intrinsic coral properties (e.g. coral morphology, coral size, coral porosity; Baldock et al. 2014a). These data would allow us to improve modelling of cyclone impacts on coral communities.

Achieving model flexibility

One of the main strengths of our modular approach is that it provides flexibility for future researchers working on part (or all) aspects of the entire geo-ecological reef system. For example, if the focus of the research was on fluctuations in coral and CCA calcification rates with environmental change, researchers could include data on variables and relationships identified in the *in situ* carbonate production module. If researchers were interested in understanding how changes in benthic cover and coral community characteristics (e.g. coral size distributions), following a bleaching event, influenced total calcification rate, they could use the acute disturbance event module. If researchers were aiming to predict reef accretion with future climate change impacts, they could include all models except the carbonate sediment transport and sinks module. The flexibility of the overall geo-ecological qualitative model could also prove critical for future quantitative modelling because a lack of data in one module does not limit the development and application of other modules.

Towards a quantitative geo-ecological carbonate reef system model

Above we detailed how each of the modules of the geo-ecological carbonate reef system model was developed and integrated into the geo-ecological carbonate reef system model. We now turn our attention to current knowledge gaps and related future research directions for each sub-system module. Identifying data needs is critical in quantifying relationships within each module, and thus the overall model, providing the opportunity to develop predictive capacity. In other words, the development of a quantitative model requires both a comprehensive qualitative model and empirical data that describes the relationships of the qualitative model. Below we discuss modelling challenges related to our current knowledge and understanding within each of the sub-system models across changing spatial and temporal scales, and briefly consider the feasibility of developing a quantitative model given current knowledge gaps and computational issues. Lastly, we identify future research directions that would aid the development of a predictive geo-ecological carbonate reef system model.

In situ *carbonate production*

The *in situ* carbonate production model includes 28 variables and 61 relationships (Figure 3). Modellers were highly confident in the majority (77%) of relationships in the model, which reflects the either well-studied or commonly assumed nature of many of the relationships. Well-established relationships were often those between environmental variables. Examples include reef depth affecting light at benthos and the variety of physiochemical controls on seawater carbonate chemistry (e.g. calcification, photosynthesis, atmospheric CO_2 and temperature; Figure 3). Lower confidence ratings were often those relationships *between* environmental and ecological variables, such as the influence of nutrients, temperature and seawater carbonate chemistry on CCA cover (Figure 3).

Relationships with low confidence ratings highlight the need to improve our understanding of the influence of dominant environmental variables on coral and CCA cover, and calcification rates. For example, the influence of wave characteristics on flow on reefs and water velocity has been shown to affect the sensitivity of corals to ocean acidification in some laboratory experiments (Comeau et al. 2014a, 2019b), but we have inadequate knowledge (relationship rated as '2a'; Figure 3) on how strongly this relationship might apply across different coral species or reef environments. We also have inadequate knowledge of the relationships between seawater carbonate chemistry and species composition (relationship rated as '1b'; Figure 3). For instance, ocean acidification has differential effects on calcification among coral species in laboratory studies (Comeau et al. 2017a, 2019a), which theoretically could lead to changes in species composition assuming that the more resilient species flourish while the abundance of more sensitive species declines. Moreover, changes in species composition have been previously reported along pH gradients (Barkley et al. 2015), indicating the role of ocean acidification in structuring coral reef communities. Evidence to date therefore suggests that a relationship should exist, but more studies are required to quantify the relationship.

Understanding (and modelling) the effects of thermal stress and temperature sensitivity (Figure 3) on CCA calcification rates (rated as 'a') and percent cover (rated as 'b') is challenging given that there is inadequate knowledge about the bleaching thresholds of CCA. This lack of knowledge is partly due to the challenges of maintaining CCA in aquaria, in addition to the minimal field-based data available for documenting CCA responses to thermal stress events (Cornwall et al. 2019). Moreover, the identification of CCA species based solely on morphology is challenging (Gabrielson et al. 2018), and many species may have been incorrectly ascribed, resulting in a lower confidence of species-specific responses to different environmental variables.

Quantifying temporal trends in coral and CCA calcification is important for characterising reef maintenance, reef function and the potential for structurally extensive coral reef development. Yet, inadequate knowledge is available relating to long-term (i.e. decadal) changes of coral calcification rates for those taxa that are morphologically complex and/or lack annual density banding (e.g. key reef-building acroporids). With respect to CCA, fewer studies have quantified calcification rates or investigated the response of calcification rates to environmental variables. Furthermore, we have a relatively limited understanding on how short-term acute disturbance events impact the longer-term (>5 years) rates of calcification for both coral (i.e. reef-building taxa) and CCA.

To improve the development of a quantitative carbonate production model, the primary focus area for future research should be the characterisation of long-term (e.g. decadal) changes in coral and CCA calcification rates for multiple taxa across different reef environments (Table 9). An increased understanding of the complex interplay between organism morphology, organism metabolic activity and the degree of mass transfer variability would also provide a clearer framework for modelling these interactive effects. Specifically, future research directions should include

1. The influence of temperature, thermal stress and temperature sensitivity on CCA calcification rates, percent cover and species composition, both geographically and over time, particularly following disturbance events.
2. The individual and combined effects of water flow velocities, nutrients and OA sensitivity on CCA and coral calcification rates and percent cover
3. The different calcification rate responses to temperature of coral taxa from a range of locations
4. The long-term (interannual to decadal) quantifiable changes in coral and CCA calcification rates for key species.

Acute disturbance events

The acute disturbance events model includes 36 variables and 63 relationships, of which 82% were rated with high confidence and 3% with low confidence. Areas of high confidence included the direct and indirect effects of cyclones on the abiotic environment (e.g. waves and water quality);

Table 9 Summary of research questions and knowledge requirements for developing a quantitative model

Module	Research question	Why gap exists	Research needs
In situ carbonate production	1. What is the influence of temperature and thermal stress on coralline algae calcification, % cover and species composition both geographically and over time, particularly following repeated disturbance events?	Logistical difficulties (e.g. challenges in maintaining CCA in aquaria because they often bleach in the control tanks); Lack of knowledge and/or understanding (e.g. generally limited field-based data before/after thermal stress events)	Requires understanding of temporal and geographical changes in CCA growth and % cover across latitudinal gradients, and in response to thermal stress events and for a range of taxa
	2. What are the individual and combined effects of water flow velocities, temperature, light and OA on CCA and coral calcification rates?	Logistical difficulties; lack of knowledge and/or understanding	Requires controlled aquaria studies to better understand both the individual and interactive effects
	3. Why do coral taxa from a range of locations show different calcification rate responses to temperature (i.e. why some corals show a positive or curve-shaped temperature-growth relationship while others do not)?	Lack of knowledge and/or understanding	Further exploration of physiological acclimation/adaptation mechanisms (e.g. photo-physiology and bio-calcification) is required to decipher why some corals show a positive or Gaussian-shaped temperature-growth relationship while others do not, particularly for coral species with distributions that extend to tropical and temperate zones
	4. What are the drivers of long-term (interannual to decadal) changes in coral and CCA calcification rates for key species?	Logistical difficulties; lack of resources (time)	Requires long-term growth rate studies for key taxa, such as the reef-building corals (particularly branching taxa) and CCA that are important for binding the reef substrate
Event (acute)-driven disturbances	1. How does stress (during and following) from acute disturbance events influence rates of carbonate production (and loss)?	Site access	Account for temporal and spatial variability in species sensitivity and recovery to disturbance in stress vs unstressed environments (e.g. revised bleaching thresholds for turbid reefs)
	2. What are the long-term temporal dynamics of benthic components after an acute disturbance event?	Site access	Requires integrating decadal changes in the size structure and species composition of calcifiers after disturbance but also projecting the fate of carbonate material produced by the disturbance, with consideration of possible interactions with calcifier recovery rates in space and time

(*Continued*)

Table 9 (*Continued*) Summary of research questions and knowledge requirements for developing a quantitative model

Module	Research question	Why gap exists	Research needs
Event (acute)-driven disturbances (cont.)	3. How do interactions between various benthos influence response of community carbonate production to acute disturbances?	Lack of knowledge and/or understanding	Requires laboratory experiments on interactions between benthic calcifiers to understand how loss/gain of one calcifier after acute disturbance may have flow on effects for other calcifiers
Coral reef response to sea level rise	1. How do we rectify the varying temporal scales of geological and ecological processes operating on reefs?	Methodology limitations; lack of knowledge and/or understanding	Requires long-term ecological studies (e.g. multi-decadal or longer) to understand how short-term dynamics (seasonal to annual) relate to longer-term processes
	2. Can we increase the spatial coverage and temporal resolution of geological reconstruction of coral reefs?	Methodology limitations	Advances in high precision U-Series dating on multi-reef core transects, in regions with well-constructed sea level curves, can provide high spatial resolution of past reef evolution with the change in benthic composition over time. This can be combined with emerging research on the inclusion of rare earth elements and bioeroders to detail the paleo oceanographic and environmental conditions during coral reef development
	3. What are the key hydrodynamic and oceanographic processes that drive rates of carbonate production, erosion and incorporation into the reef framework over decadal timeframes?	Methodological limitations	Requires a wider spatial (and longer term) deployment of *in situ* data loggers to capture oceanographic and environmental conditions across a number of different reef habitats and types. These data should be combined with data from carbonate budgets and reef geological studies (using high precision dating)
	4. Can we develop probabilistic models that can quantify uncertainty among processes that drive reef change?	Lack of knowledge and/or understanding	Requires the application of statistical and/or machine learning to start applying uncertainties to carbonate budget outputs and reef accretionary models. This will provide an important measure of model confidence
Bioerosion	1. What are the critical environmental controls on biocorroding organisms diversity, density and activity?	Lack of knowledge and/or understanding; organism traits	Requires long-term detailed studies that combine site-specific (habitat) environmental data with differences in micro/macroborer abundance and activity data
	2. How does reef framework factors such as substrate density influence bioerosion rate?	Lack of knowledge and/or understanding; organism traits; methodological difficulties	Requires an assessment of reef framework composition with bioerosion rate, potentially using complementary data from reef cores and ecological surveys

(*Continued*)

Table 9 (*Continued*) Summary of research questions and knowledge requirements for developing a quantitative model

Module	Research question	Why gap exists	Research needs
Bioerosion (cont.)	3. How do variations in bioabrader composition, abundance and activity relate to changes in gross sediment production and reef building processes?	Lack of knowledge and/or understanding; organism traits; methodological difficulties	Requires long-term studies that accurately quantify bioerosion rates with an assessment of where the carbonate removed ends up (e.g. in the reef framework or off-reef)
Net sediment production	1. What are the impacts of climate change (e.g. increasing temperature, OA) on sediment production regimes?	Organism trait; methodological issues	Requires new quantitative methods to measure sediment production by a range of reef calcifiers to determine how large-scale disturbance events will alter the magnitude and rate of sediment supply from reefs. Further information also required on how environmental change will influence organism growth, calcification and turnover rates
	2. Do currently used estimates of direct sediment production accurately represent true sediment production over space and time?	Organism trait; methodological issues	Developing new field survey methods for quantifying the abundance of direct sediment producers. Methods should be established for a wide range of sediment-producing organism and focus of relatively rapid field approaches for documenting reef sediment production, and their growth and calcification rates
	3. Can we better quantify the lag times between sediment production and landform deposition?	Organism trait; methodological issues; lack of understanding and/or knowledge	Establish quantitative methods to track sediment from living reefs to landforms. Requires a detailed reconstruction of sediment transport pathways on reefs, an overview of sediment chronology and the interpretation of mixed old and new sediment assemblages within detrital reservoirs
	4. Can we quantitatively assess the influence of carbonate dissolution on sediment production and existing sediment reservoirs?	Organism trait; methodological issues	Provide assessments on the factors that influence sediment dissolution on reefs, their overall impact to detrital carbonate sinks and how reef conditions will change in the future under varying climate scenarios
Carbonate transport and sinks	1. How do common empirical sediment transport models perform for biogenic sediments?	Lack of knowledge and/or understanding	Establishment of entrainment relationships for biogenic sediment at the individual component scale as well as bulk sediment scale
	2. What are the key mechanisms and rates of sediment transport in reef systems?	Lack of knowledge and/or understanding	Increased observations of sediment transport across various sub-reef environments (fore reef, reef flat, lagoon) to determine transport rates and mechanisms of sediment to depositional sinks

(*Continued*)

Table 9 (*Continued*) Summary of research questions and knowledge requirements for developing a quantitative model

Module	Research question	Why gap exists	Research needs
Carbonate transport and sinks (cont.)	3. What are drivers of reef-fringed shoreline dynamics from seasonal to decadal timescales?	Lack of knowledge and/or understanding	Increased observations of reef-fronted shoreline dynamics at intermediate timescales (seasonal to decadal) to determine the relative roles of physical processes (waves, water levels) and sediment supply in maintaining reef-fronted coasts
	4. What is the role of vegetation in the accretion and erosional stabilisation of coral reef island landforms?	Lack of knowledge and/or understanding	Account for the role of vegetation type in geomorphological development of islands through the use of *in situ* species abundance surveys and remote sensing LiDAR technologies. This should target role of vegetation colonisation in short to long-term accretion, stability and erosional protection. There is a lack of knowledge regarding the interaction of climate processes (wind and metocean) with vegetation and how this affects long-term stabilisation of reef islands
All modules	Can we upscale local processes to more meaningful units (e.g. entire reef complex and sedimentary landforms) without losing accuracy?	Time, money and expertize	Role for earth observation approaches that draw on satellite and UAV imagery to generate spatially continuous estimates of carbonate dynamics across the range of sub-environments around reef platforms

specific interactions between benthic components (e.g. higher sediment cover reduce suitable substrate cover for CCA); and the importance of species-specific coral traits (e.g. skeletal density and extension rates) to assess carbonate production. Low confidence relationships reflect the difficulty in predicting community responses to spatially and temporally variable stress exposure (Figure 4).

The variable, and potentially interactive, nature of disturbance events creates model uncertainty and emphasizes the need for an improved understanding of how inherent environmental conditions interact with disturbance regimes to shape coral community structure at specific locations (e.g. Morgan & Kench 2017, Safaie et al. 2018, Sully & van Woesik 2020). For example, recent studies have reported that turbidity reduces coral bleaching relative to nearby clear-water reefs during thermal anomalies (Sully and van Woesik 2020, Oxenford & Vallès 2016, Morgan & Kench 2017). These studies suggest that reduced exposure to high solar radiation associated with turbidity can decrease bleaching and mortality levels; however, once turbidity reaches a certain threshold, the effect of both stressors can become cumulative (Fisher et al. 2019). When cyclones and bleaching events occur simultaneously, potential exists for interactive effects that can lead to both positive and negative impacts on carbonate production. For example, a moderate cyclone may counteract bleaching events by cooling water temperature through cloud shading, rain, wave action mixing warm surface layers with cool deeper waters and turbid run-off also reducing solar radiation (Carrigan & Puotinen 2014, Oxenford & Vallès 2016). Alternatively, reductions in reef structural complexity caused by severe cyclones (Fabricius et al. 2008, Roff et al. 2015a) are typically larger after bleaching events because dead coral skeletons have a weaker resistance to shear stress (Williams et al. 1999); or the turbidity from wave action and riverine run-off may place even greater stressors on the bleached corals, thus having a negative impact (Wooldridge 2009). These complex interactions among stressors are location and event specific, highlighting the need for site-specific observations pre- and post-disturbance to ensure appropriate modelling of net carbonate production over time.

Understanding cyclones and bleaching impacts on carbonate reef system models demands a thorough understanding of site-specific processes due to their complex (and potentially interactive) interactions with the coral reef ecosystem. Reef vulnerability and recovery from disturbance differ among coral communities, based on their specific physical and ecological environment (Moustaka et al. 2019, Evans et al. 2020) and the patchiness of acute disturbance events (e.g. cyclones and warming; Fabricius et al. 2008). This patchiness leaves some living corals in deeper or sheltered locations that can help recovery on the damaged sections of reef (Halford et al. 2004). Furthermore, extensive coral mortality is not always followed by rapid coral recovery but instead can lead to community shifts (i.e. macroalgal-dominated), which are difficult to anticipate (e.g. Hughes 1994, Diaz-Pulido et al. 2009, Graham et al. 2015, Roff et al. 2015a). Predicting these dynamics is challenging because it requires capturing complex processes (e.g. competition for space, grazing, ecological facilitation) that typically operate at small spatial and temporal scales (e.g. within habitats and at monthly intervals; Bozec et al. 2019). Ultimately carbonate reef system models need to include long-term dynamics of coral cover *under* stress regimes to improve assessment of recovery capacity from future disturbances, particularly given the predicted increase in frequency of cyclones (Elsner et al. 2008) and bleaching events that will likely outpace the rate at which systems can respond to any positive effects of disturbance events.

In summary, to improve the development of a quantitative carbonate model, key areas for further research include (Table 9):

1. The quantification of carbonate production in stressed versus unstressed conditions, accounting for species-specific responses
2. The integration of long-term (multi-annual) dynamics of benthic components after disturbance to project the fate of net carbonate production under different scenarios of stress regimes
3. The assessment of how interactions between various benthos influence responses of community carbonate production to acute disturbance events.

Coral reef response to sea level rise

The coral reef response to sea level rise model includes 27 variables and 54 relationships that detail the complex interactions that drive net carbonate production and coral reef accretion. Of the 54 relationships, 67% had high confidence, 30% had moderate confidence, and 4% had low confidence. Relationships with high confidence included the relationship between sea level rise and reef depth (including the associated change this imparts on reef hydrodynamics), and the processes driving the recruitment of new corals and the pathways that lead to interannual changes in coral composition and cover. Areas of low confidence largely relate to relationships influencing reef accretion such as coral composition, reef framework density and sediment incorporation (Figure 5).

This sub-system model attempts to bridge the gap between ecological and geological processes that operate on different spatial and temporal scales. A challenge here, therefore, was to provide links between these two areas of coral reef research without introducing substantial errors that override any useful result. For example, extrapolation from short- to long-term scales will introduce errors associated with multiple cycles of short-term processes and interpolation from long to short-term scales will overlook important processes that act in the short term. Such errors will influence the values of carbonate production and erosion and the residual accretion rate of the reef. The geologic record can be used to mitigate potential errors associated with interpreting rates of reef accretion (and carbonate accumulation) and changes in benthic assemblages over shorter-time scales (i.e. years). One approach is to apply high precision radiometric dating (i.e. sub-annual to sub-decadal resolution) to coral cores extracted along transects or in high spatial density (e.g. Roff 2020). By taking multiple samples from several reef cores, these data sets are approaching temporal timescales that are captured using the census-based methods, although they only provide an assessment of production and not carbonate loss. Despite recent advances in dating precision, connecting ecological and geological understanding to annual and interannual scales is still a long-standing challenge and crucial knowledge gap in both perspective and knowledge (Woodroffe 2008, Hubbard 2015).

Uncertainty also continues to exist over the hydrodynamic and oceanographic processes that lead to the generation of different benthic cover types, such as rubble, and reef rugosity (Madin et al. 2014). Gross accretion rates of primary reef calcifiers are well known over short-term scales but the role of other processes such as the production, erosion and incorporation of carbonate material into coral reef framework is still poorly understood. While understanding these processes presents substantial challenges, methods are continually advancing that may bridge the gaps in knowledge, with this model providing a guide to the processes that are essential to driving reef response under rising sea levels.

Census-based carbonate budgets and the conversion of net carbonate production to reef accretion rates rely on a number of assumptions (outlined in the ‘Developing the qualitative model subsystems’ section). At present, the effects of these assumptions on model outputs (e.g. reef accretion rate) are unknown. Understanding these effects, however, is critical for providing confidence in results and quantifying uncertainty. As such, future carbonate budgets should seek to describe the impact of underlying assumptions by providing confidence ranges. Furthermore, the incorporation of a probabilistic approach to census-based carbonate budgets will also help manage the uncertainty introduced by the assumptions of the carbonate budget. Such approaches are commonly used when providing forecasts for complex systems (e.g. Cowell et al. 2006; Vitousek et al. 2017), and we consider a necessary future step to increase the relevance and importance of carbonate budget approaches as tools for coral reef managers and researchers.

In summary, to facilitate improved descriptions of reef change on the scales of decades to centuries and move towards a quantitative geo-ecological carbonate reef model, future research should include (Table 9):

1. Long-term (decadal-scale) studies across different reef environments and habitats that capture both ecological and reef geomorphic changes as a means of linking the varying temporal scales that these processes operate across. This can combine traditional (e.g. diver surveys) and advanced (e.g. drone flights) approaches to mapping ecological communities with advanced approaches to mapping change to the physical structure of coral reefs (e.g. drone, lidar and structure-from-motion surveys).
2. High precision radiometric dating on coral reef core transects to provide higher temporal and spatial resolution on coral reef accretion and reconstruction of benthic community composition.
3. A wider spatial range of *in situ* logging of oceanographic (e.g. waves, tides and currents) and environmental conditions (e.g. temperature and light) in different reef environments and habitats.
4. The application of numerical models that incorporate a wider range of processes (e.g. Salles et al. 2018) and, importantly, uncertainties between the processes that drive reef change via probabilistic approaches and statistical/machine learning (e.g. Pall et al. 2020).

Bioerosion

The bioerosion model includes 23 variables and 34 relationships, of which only 62% were rated with high confidence and 23% with low confidence. Although each relationship is supported by empirical evidence in at least one species or location, ‘exceptions to the rule’ apply to almost all relationships and many environmental drivers show both positive and negative effects, depending on the species (e.g. sedimentation positively influences some macroboring species but negatively impacts others). Areas of low confidence related to synergistic effects of environmental variables on internal reef bioerosion. More broadly, limitations to modelling bioerosion relate to difficulties in estimating temporal variability in bioerosion due to its non-linearity over time, complex feedbacks and missing or contradictory data. Furthermore, limited data and knowledge exist on rates of bioerosion sediment production and sediment re-incorporation processes (Figure 6).

Bioerosion is highly variable across geographies and among reef zones (across which population densities and environmental influences will naturally vary). This paucity of knowledge not only concerns species biogeography (e.g. greater influence of urchins in the Caribbean), but also in environmental responses – with nutrients found to increase microboring on Caribbean reefs (Carreiro-Silva et al. 2009), but not on Pacific reefs (Vogel et al. 2000). In particular, there has been limited consideration of regional variability of reef framework properties (e.g. density, rugosity) on rates of bioerosion. As such, spatial differences in bioerosion and our understanding of its patterns and processes remain ongoing challenges.

Temporal changes are also a challenge to capture: bioerosion can naturally fluctuate daily (e.g. parrotfish grazing pressure) and seasonally (e.g. Browne et al. 2019), as well as rapidly with large changes in abundance driven by environmental drivers such as pollution events (sponges), diseases (urchins) or habitat changes like coral loss (microborers). Over short timescales (weeks to years), bioerosion shows ecological succession (i.e. is not stable, but also does not necessarily increase proportionally or linearly with time; Kiene 1988, Tribollet 2008a, Schönberg 2015), with freshly exposed substrates showing differential removal rates over weeks to months as microborers and later macroborers colonise, weaken and change the framework (Chazottes et al. 1995). Given these successional changes, long-term studies that track changes in bioerosion rates with environmental and habitat differences (e.g. suitable substrate and reef framework density) are needed to provide a more accurate estimate of 'average' bioerosion required for modelling.

In addition to the short-term challenges of quantifying bioerosion, another major limitation is the calculation of bioerosion itself. 'Net bioerosion' only describes the redistribution of material and not export from the system: removal of material may depend on the grain size produced by the boring organism (could be related to organism size, e.g. urchin test size), habitat factors (e.g. porosity of the substrate) and local conditions (e.g. flow). While bioeroders are important in breaking down reef structure (Hutchings 1986, Eakin 1992, 1996), they also perform numerous other roles critical to the healthy functioning of a reef, such as the recycling and redistribution of reef-produced calcium carbonate. Sediments that are re-incorporated back into the reef framework play a critical role in maintaining reef structure and are therefore an important component of reef building processes (Davies 1983, Perry 1999, Mallela & Perry 2007). Relating carbonate degradation by bioeroder activity to subsequent sediment export or deposition is difficult, but these data are necessary to understand sedimentary processes on coral reefs.

In summary, to improve the development of a quantitative carbonate model, we need more data on bioeroder (across all taxa) responses to interacting (and multiple) environmental variables (e.g. temperature, pH, nutrients, light), from both field and experimental studies. Knowledge gaps that currently limit bioerosion estimates relate primarily to understanding (Table 9):

1. The environmental controls (including interaction of multiple effects) on internal (macro- and microborers) organism diversity, density and activity
2. The influence of reef framework factors such as substrate density and complexity on bioerosion rate
3. The rates of sediment production and re-incorporation from bioabraders and quantifying the role of these sediments for longer-term processes, such as reef development and accretion.

Net carbonate sediment production

The net sediment production model comprises 28 variables and 31 relationships. Experts rated 64% of the relationships in the model as high confidence and 26% as low confidence. The high confidence relationships were associated with physical mechanisms (e.g. wave energy) derived from established physics-based principles of fluid mechanics (Brander et al. 2004, Lowe et al. 2005), or relationships between co-dependent environmental variables, such as the influence of seawater turbidity on light at the benthos (Figure 7; Cooper et al. 2007, Fabricius et al. 2016, Morgan et al. 2020). Despite the perceived strength and confidence of the model overall, a paucity of quantitative data that sufficiently characterize rates of sediment production between calcifying taxa, reef settings and geographic regions remains. Relationships classified as low confidence mostly relate to chemical processes (e.g. seawater carbonate chemistry, pore water advection, sediment organic content) involved in the dissolution of existing carbonate sediments (Eyre et al. 2014). The quantitative importance of these relationships to sediment reservoirs remains unclear.

Differences in the temporal variability of sediment production processes on reefs (i.e. minutes to centuries) challenge the incorporation of sediment production into carbonate models and our understanding of how net sediment production will vary with climate change. The challenge arises primarily due to the potential time lags between organism death and the creation of suitably sized sediment for transport, or re-incorporation into the reef framework. For example, physical processes (waves) may create coral rubble instantaneously during a cyclone, but the breakdown of coral rubble into sand-sized particles under normal wave conditions can take decades (Ford & Kench 2012). In contrast, bioerosion processes (e.g. internal boring, grazing) can produce significant quantities of sediment from coral rubble and the reef framework over ecological timescales (Perry & Morgan 2017, Cuttler et al. 2019, Taylor et al. 2020). Similarly, direct sediment producers can rapidly generate sediment on timescales related to their lifecycle (Hallock 1981, Perry et al. 2016, Perry et al. 2019).

Spatial variations in sediment yield observed between reef habitats (e.g. reef crest versus lagoon) and different geographic settings (Smithers 1994, Yamano et al. 2005, Perry et al. 2011, Morgan & Kench 2016b) also influence model confidence. For example, foraminifera species (e.g. *Calcarina*, *Baculogypsina* and *Amphistegina*) often dominate Pacific Ocean reef sediments (Langer & Lipps 2003; Fujita et al. 2009; Dawson et al. 2014), whereas gastropod tests and coral grains provide the bulk of material in the Torres Strait (Hart & Kench 2007), and *Halimeda* grains have high relative abundance on many Caribbean reefs (Folk & Robles 1964). Using spatial interpretations of sediment reservoirs to assess an organism's biological productivity, however, is not straightforward because their relative abundance within sediments may be disproportionately higher to their live cover on reefs (Yamano et al. 2000). This challenge arises because the skeletal properties (e.g. shape, density, porosity) of specific organisms (e.g. foraminifera) may make them more transportable and widespread on reefs (Yamano et al. 2000, Dawson et al. 2014), or more resistant to abrasion enabling higher rates of preservation in the sedimentary record (Ford & Kench 2012). Differences in carbonate composition (e.g. percentage Mg-calcite) also determines how susceptible grains are to chemical dissolution (Eyre et al. 2014, Perry et al. 2016).

In summary, to improve the development of a quantitative carbonate model, areas for future research include (Table 9):

1. The improved understanding of the role of climate change in reef sediment production
2. A deeper understanding of the spatial and temporal dimensions of direct sediment production
3. The quantification of lags between organism mortality and sediment production
4. The examination of the influence of carbonate dissolution on existing sediment reservoirs.

Carbonate sediment transport and depositional sinks

Our carbonate sediment transport and depositional sinks model comprises 21 variables, with 22 relationships (Figure 8). The model describes the main physical drivers (waves, currents, sea level) and mechanisms of sediment transport (mobilisation, transport, deposition) to determine the fate of sediments (landforms, lagoons, off-reef deposits). Within our module, 86% of the relationships were classified with the highest confidence rating. This confidence level reflects the physical basis of the relationships (e.g. reef hydrodynamics; Lowe & Falter 2015) and the wealth of existing knowledge from siliciclastic coastal environments (e.g. sediment transport processes; Aagaard et al. 2013). Three relationships (# 19–21; Figure 8) received more moderate confidence ratings due to the limited quantitative understanding of aeolian (wind-driven) processes across coastal geomorphology, both generally (Houser 2009, Houser & Ellis 2013, Hesp & Smyth 2016) and in reef settings (Hilton et al. 2019).

The direct physical relationships that underlie this model are present across the range of spatio-temporal scales, such that our confidence ratings are likely to be somewhat insensitive to varying spatial or temporal scales. For example, the sediment carrying capacity of a given current is proportional to its speed; this relationship is relevant whether applied over seconds to years, or metres to kilometres. Although we have high confidence in the existence and strength of these relationships across multiple temporal and spatial scales, the ratings do not necessarily reflect our ability to quantify or model these processes in reef environments.

Challenges remain in quantifying carbonate sediment transport rates and linking these processes to the morphodynamics of depositional sinks. Sediment transport formulae are empirical relationships that relate parameters of the overlying flow (i.e. current speed) to sediment characteristics (i.e. grain size, density) to predict sediment entrainment and transport (Soulsby & Whitehouse 1997). These empirical equations have been developed using siliciclastic beach sediment or idealized particles, which tend to be approximately spherical and have a relatively uniform density. Reef-derived sediments, however, are often irregularly shaped and of variable density, thus violating the underlying assumptions of empirical relationships that rely on siliciclastic sediments, and questioning the applicability of these equations to carbonate settings (Kench & McLean 1996, Cuttler et al. 2017, Riazi et al. 2020). Similarly, given the diverse composition of carbonate sediment and the potential for the composition to evolve through time (i.e. as the relative abundance of sediment contributors changes), a need exists to develop quantitative relationships for how individual components are transported (Paphitis et al. 2002, Smith & Cheung 2005, Rieux et al. 2019). Finally, predicting sediment transport in reef environments is further complicated by the presence of the coral canopy, which strongly modifies the near-bed flows (Lowe et al. 2008) and raises questions about the most applicable velocity measurement to use for sediment transport (Pomeroy et al. 2017). Therefore, the complexities of carbonate settings require a new approach to predict sediment entrainment and transport.

In addition to inadequate quantification of relationships for the transport of carbonate sediment, inadequate data exist for disentangling drivers (e.g. storm versus fair-weather conditions) and mechanisms (e.g. bedform migration, transport through complex bathymetry) of sediment transport processes. Previous use of sediment traps enables single point measurements of transport averaged over time (Storlazzi et al. 2009, Browne et al. 2013, Morgan & Kench 2014), but only offers limited insights into the temporal variability of transport (i.e. how transport rates vary based on changes in waves or sea level). To investigate the temporal variability of sediment transport, previous research has relied on acoustic or optical sensors to measure both suspended sediment and bedload transport (Storlazzi et al. 2004, Vila-Concejo et al. 2014, Pomeroy et al. 2015, Cuttler et al. 2017, Pomeroy et al. 2018, Cuttler et al. 2019). Much of this work, however, has been carried out at a small spatial (order 1 m) and temporal (weeks to one year) scales, and it remains a challenge to upscale this knowledge into models that can be applied at an entire reef scale and/or over long timescales (seasonal to decadal).

Similarly, we see a lack of research directly linking sediment supply and transport rates to depositional sink morphodynamics (Harris et al. 2014, Morgan & Kench 2014, Harris et al. 2015a, Cuttler et al. 2019). Most previous work on shoreline dynamics in reef settings has focused on the event scale (Mahabot et al. 2016, Duvat et al. 2017b, Cuttler et al. 2018) or decadal scale (Ford 2013, Kench et al. 2015, Duvat & Pillet 2017, Kench et al. 2018), whereas lagoon infilling or off-reef export has been observed over short-term experiments (weeks to season; Harris et al. 2014, Morgan & Kench 2014). Thus, there is limited understanding of depositional sink morphodynamics over intermediate timescales (seasonal to interannual; Kench & Brander 2006, Cuttler et al. 2020) as well as how the timescales of morphodynamic development relate to temporal variability in sediment supply and transport processes. Finally, for subaerial sinks (islands, beaches), vegetation cover likely plays a significant role in the construction and stabilisation of landforms. Understanding the biophysical feedbacks between vegetation dynamics (species abundance, biomass, density) and aeolian transport processes under changing met-ocean conditions is critical in identifying long-term landform stability and resilience.

In summary, to improve the development of a quantitative carbonate model the future research directions include (Table 9):

1. The development of carbonate-specific sediment transport formulations that account for variable sediment composition and characteristics
2. The increase of observations of sediment transport rates and processes, including transport through complex bathymetries
3. The quantification of depositional sink morphodynamics (especially shorelines) over intermediate timescales
4. The investigation of the role of vegetation in reef-fronted shoreline stability.

Quantitative modelling feasibility

The development of the quantitative reef geo-ecological carbonate reef system model will require considerable effort across several integrating disciplines (e.g. ecology, geology, statistics, data science) as well as computational knowledge and power. The qualitative model presented here represents, to the best of our knowledge, all the known organisms, drivers and relationships that are part of the geo-ecological carbonate reef system, but mathematically accounting for all these relationships might not yet be possible. The main reasons that could limit quantitative model development include (1) a lack of data that describe some of the identified relationships; (2) issues around resolving and integrating processes that operate at different spatial and temporal scales; and (3) compounding errors that result in a non-meaningful output. A complete assessment of how the quantitative model may be developed is beyond the scope of the study, but creating six sub-system models that are targeted (i.e. more discipline specific), incorporate processes that (for the most part) operate at the same timescales and can be run independently allows parts of the model to be developed separately despite possible roadblocks in other areas. When all (or some) of the sub-system models are complete, they could be integrated using a loosely coupled system model (Giri et al. 2019), which also allows for the use of different software (e.g. among the different sub-system models) that work across different spatial and temporal scales.

Summary

Overall, the variables and relationships in the models for each sub-system module of the geo-ecological carbonate reef system model do not necessarily represent single, stable cause–effect relationships. Instead, they represent, to the best of our knowledge, the weight of evidence of carbonate reef system variables and their relationships to one another over the coming decades. As we increase our knowledge of these variables and relationships, the model will evolve and increase in its predictive capacity and accuracy. Importantly, the data in the literature do not necessarily enable reliable quantification of each of the relationships in the qualitative model, for many of the reasons outlined above, limiting immediate opportunities for prediction.

Identifying relationships and associated knowledge gaps is critical in improving our understanding of complex interactions that exist within all facets of the geo-ecological model. Here, we identified common knowledge gaps (among modules) for future research directions that include (1) tracking long-term (interannual to decadal) processes, (2) capturing interactions between ecological components and environmental controls (including interactions of multiple effects), (3) measuring changes in net carbonate production during stressed environmental conditions and (4) developing a deeper understanding of the spatial and temporal dimensions of carbonate production and sediment dynamics. These knowledge gaps exist largely due to methodological constraints (e.g. quantifying direct sediment production) and resource requirements (e.g. long-term studies that capture ecological and geological changes).

A growth in the use of both GIS and earth observation technology provides promise for addressing some of these knowledge gaps. These technologies can generate continuous measurements of critical variables (e.g. turbidity, coral cover, cyclone duration and strength, island vegetation cover), providing high spatial and temporal resolution data during stressed and unstressed environmental conditions. Furthermore, localized rates of carbonate production (i.e. for a patch reef) can be upscaled to geomorphically meaningful units, such as entire coral reefs and, by extension, sedimentary landforms, such as reef-associated landforms (Hamylton 2014). However, a critical part of this approach will be to ensure appropriate ground-truthing at relevant spatial and temporal scales, which could be incorporated into ongoing, local monitoring programs where this level of information can be easily collected.

The wider application of all approaches outlined here may help link the ecological and geological processes that feature in most carbonate budgets and models that attempt to forecast reef response with climate change impacts. No single approach, however, will be capable of addressing all issues associated with describing or forecasting coral reef change on the scale of decades. Improvements can only be made by using multi-disciplinary methods over multiple spatial and temporal scales, which are likely only possible via collaboration and knowledge sharing across disciplines.

Contributions and conclusion

We have provided the first comprehensive method and model for understanding geo-ecological carbonate reef systems. This work provides three major contributions to the field. First, we have provided a novel method for individual elicitation of mental models and shared development of a qualitative complex system model. Second, we have generated a qualitative geo-ecological carbonate reef system model. Third, we have identified a number of critical future research pathways. We briefly touch on each of these contributions, before providing some concluding thoughts.

A novel method for developing a shared qualitative model of a complex system

The novel elicitation modelling method was developed specifically for modelling complex systems, such as carbonate reef systems that are governed by complex and interacting biological, physical and chemical processes. Method development enabled a structured approach in identifying variables and their relationships to one another, which form the geo-ecological carbonate reef system model. Relationships were evaluated by considering our confidence in the existence of the relationship, as well as the relative strength of that relationship. The method supported a modular approach to model development, providing opportunities to explore both similarities and differences within expert-generated models. The extensive literature review that accompanied and followed model development led to the identification of knowledge gaps within the model. This information is critical in working towards the development of a quantitative model.

A qualitative geo-ecological carbonate reef system model

The most significant contribution of this work is a complex system model that links the carbonate reef system (the focus of previous carbonate budgets) to carbonate sediment production (sediment budgets) and associated landforms. As such, we have moved beyond carbonate budgets to provide the first qualitative model that crosses the geo-ecological divide. Census-based carbonate budgets provided the framework on which to build the geo-ecological carbonate system model. By evaluating previous field-based studies that quantified (part of) the carbonate reef budget, with additional related literature that focused on specific aspects of carbonate sediment systems, we were able to identify strengths and limitations within carbonate budgets. The model partly addresses these limitations through accommodating system complexity, assessing model reliability and accounting for environmental influences. We also highlight where additional data, knowledge and methodological testing are required to further address these limitations and improve our capacity to estimate carbonate production. Furthermore, by developing our qualitative model using a modular approach, the model provides flexibility for future researchers working on part (or all) of the carbonate reef to landform system.

Pathways for carbonate reef system research

This review provides a number of critical resources for researchers working within (and across) a number of disciplines related to carbonate reef systems (e.g. ecology, sedimentology, biogeochemistry, oceanography, coastal morphology, conservation). These resources can be classified into three broad areas: (1) planning new research projects (1–5), (2) planning *in situ* data collection (6–8) and (3) developing quantitative models (9–11; Table 10). New research projects (e.g. PhD or post-doctoral project) require an extensive literature review (knowledge and associated methods), which are provided here together with a list of targeted research questions and related research requirements

Table 10 A summary of resources provided through the extensive literature review and model development

No.	Resource
1	Extensive reference list
2	Summary of past census-based carbonate budget studies
3	A comprehensive list of variables and definitions
4	Reliable understanding that underpins management actions
5	Future research questions/directions
6	Overview of current methods for census-based studies
7	Assessment of associated limitations per sub-system module
8	Identification of critical variables
9	Individual conceptual sub-system modules
10	Reef-system carbonate model high-level overview
11	Semi-quantitative evaluation of model confidence

Note: Resources are grouped into three categories that include planning new research projects (white), planning *in situ* data collection (light grey) and developing quantitative models (dark grey).

(Table 9). The overview of methods used in carbonate budget studies, with their related limitations and the identification of critical variables, provides a solid foundation from which to design a well-considered data collection plan. For those researchers focused on developing predictive models, we anticipate that the conceptual sub-system models (together with our assessment of model confidence) will provide a blueprint for a quantitative model that incorporates one or more of the sub-system models.

Concluding comments

We need to improve our capacity to predict coral reef and associated landform responses to future climate change. More reliable predictions of ecological response to physiochemical changes are critical for developing appropriate management and mitigation strategies that seek to protect and preserve these complex systems. Importantly, a multi-disciplinary approach is required to assess and resolve differences in the spatial and temporal scales over which ecological, physical and chemical processes operate. Quantitative models that capture system complexity and bridge the geological-ecological divide will play an increasingly important role for predicting future changes. Our qualitative geo-ecological carbonate reef system model provides an important first step towards the development of these predictive models. As such, we anticipate that this qualitative model will be of significant value to both the scientific and conservation communities.

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A COMPARATIVE REVIEW OF MACROMEDUSAE IN EASTERN BOUNDARY CURRENTS

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Abstract The productive eastern boundary current (EBC) systems provide significant sources of global marine protein and have been subject to intense research over the last 50 years. Yet large jellyfish, which are present in all four major systems, have seldom been included in otherwise comprehensive reviews. This undoubtedly reflects their lack of intrinsic commercial value, and the consequently slow pace of knowledge generation. We attempt to redress that imbalance here and to consolidate disparate information on the macromedusae of EBC systems. With the exception of the Canary Current system, which supports a generally low biomass of mostly subtropical taxa,

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jellyfish assemblages in the Benguela, Humboldt and California Current systems are dominated by cool water taxa that can occur at high abundances. While there are large gaps in knowledge, which are highlighted, it is clear that jellyfish can play significant ecological roles in each system. Although there may be strong similarities in faunal composition among the different systems, there are pronounced differences in population responses to the environment and in system resilience and these are reviewed and discussed.

Keywords: Biogeography; Coastal Upwelling; Cnidaria; Ecology; Ecosystem; Fisheries; Medusozoa.

Introduction

The four main eastern boundary current (EBC) systems are located along the western coastlines of continents bordering both the Pacific (California, Humboldt) and Atlantic (Canary, Benguela) Oceans. They are characterized by very high productivity and short food chains, and are collectively responsible for >20% of global capture fisheries (Ryther 1969, Schwartzlose et al. 1999, Rykaczewski & Checkley 2008), contributing significantly to regional employment and local economies (Ommer et al. 2009). All four systems are characterized by wind-driven coastal upwelling: upwelled water delivering new nitrogen into the euphotic zone over generally narrow continental shelves (Barber & Smith 1981). They are regarded as naturally eutrophic systems, and the abundant nitrate fuels productive phytoplankton communities dominated by large cells (principally diatoms), whose energy and materials in turn feed into largely herbivorous zooplankton (calanoid copepods and euphausiids) and/or omnivorous filter- and particulate-feeding small fishes, principally clupeoids (Chavez & Messié 2009). Any mismatch between cycles of phytoplankton production and consumption results in sedimentation, leading to bottom waters with often hypoxic characteristics (Grantham et al. 2004). It has been suggested that these ecosystems are characterized as having a “wasp-waist” structure in which low species diversity at middle trophic levels can strongly impact the structure of the entire ecosystem by influencing the biomass of both its predators and prey through bottom-up and top-down controls (or “middle-out” trophic controls), respectively (Cury et al. 2000 *cf* Fréon et al. 2009).

Given their pivotal role in food security, upwelling ecosystems have been and continue to be, the subject of extensive research. Whilst much of this is specific to individual EBCs as it pertains to the regional management of local resources, the four systems generally share substantial organisational structure, with greater similarities among the systems that share ocean basins (e.g. the two Pacific and the two Atlantic EBCs). In their analysis of the wasp-waist structure of the four EBC systems, Fréon et al. (2009) subdivided each into four (latitudinally and bathymetrically) arguing that shelf and offshelf areas function slightly differently and that each system has a natural internal boundary separating water with colder and warmer temperate affinities. Despite some simplifying assumptions in their approach, Fréon et al.’s (2009) analyses demonstrate greater similarities between the composition and structure of the Pacific EBCs, relative to the two Atlantic Ocean EBCs (Fréon et al. 2009) (but see Figure 1). While each system has a number of endemic species (genera and families), a surprising number of taxa are shared between systems (Table 1). Sardines (*Sardinops*), anchovies (*Engraulis*), and chub and horse mackerels (*Scomber* and *Trachurus*, respectively) immediately come to mind. However, these common taxa are not confined to coastal pelagic and large migratory species, as they also include many members of the plankton, including jellyfish (Table 1). At the time that Fréon et al. (2009) undertook their analyses, jellyfish were deliberately excluded owing to a lack of information. Yet, as we outline below, jellyfish can be conspicuous components of EBC systems and there are some strong commonalities between them.

Our understanding of jellyfish populations in EBC systems is meagre and, at times, contradictory. Whilst jellyfish populations naturally undergo intra-annual fluctuations in abundance that reflect the interaction of species-specific responses to the environment (Fernández-Alías et al. 2020) and processes of aggregation and accumulation at frontal regions and in embayments

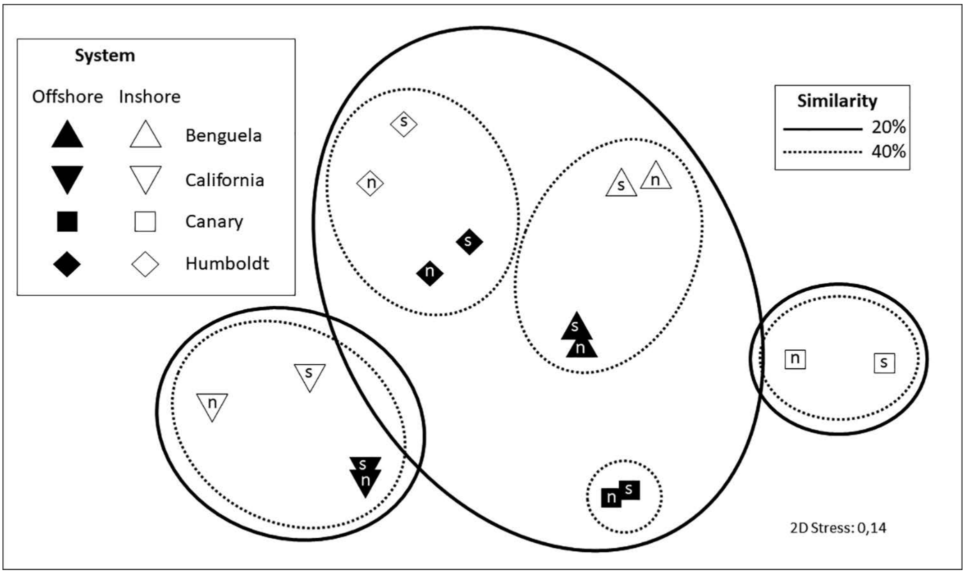


Figure 1 Non-metric multidimensional scaling plot showing the similarity (Bray Curtis Index, presence absence) between the generic composition of sub-systems within the four major EBC systems considered here. Data restricted to smaller functional groups only (plankton, cephalopods and small pelagic fishes); reanalysed from Fréon et al. (2009) using PRIMER software. Key to EBC systems and subsystems (inshore, offshore) provided; n, northern; and southern, s.

Table 1 Number of genera found in one, two, three or all four of the EBC systems considered here, by functional group

Functional group	Unique to one EBC system	Shared between two EBC systems	Shared between three EBC systems	Shared between four EBC systems	Total number of genera
Baleen Whales	2	–	1	1	4
Cephalopods	7	5	–	1	13
Chaetognaths	2	–	–	4	6
Copepods	6	3	3	2	14
Demersal fish	34	2	–	1	37
Diatoms	9	3	3	1	16
Dinoflagellates	6	4	2	1	13
Dolphins and toothed whales	3	7	4	2	16
Euphausiids	–	–	3	2	5
Inshore large pelagic fish	7	4	1		12
Medium-sized pelagic fish	–	1	–	2	3
Mesopelagic fish	13	3	–	–	16
Offshore large pelagic fish	1	–	1	2	4
Pinnipeds	7	–	1	–	8
Seabirds	18	9	2	2	31
Sharks and rays	11	3	5	10	29
Small pelagic fish	7	–	1	1	9
Macromedusae	*Rhizostoma*	*Aurelia*	*Chrysaora, Aequorea*	*Pelagia*	5

Source: Data reanalysed from Fréon et al. (2009).

Note: Genera considered are those that contribute towards 90% of the biomass in each functional group.

(Graham et al. 2001), there is some evidence to suggest that at the global level, jellyfish populations are increasing monotonically in some systems. Without attempting to explain the drivers, Condon et al. (2013) have suggested that jellyfish populations undergo 20-year oscillations in size at the global scale and that we are presently in an upward phase. That said, at a regional-scale their dataset indicates that populations in the California Current have declined since records began, whilst those in the Benguela and the Humboldt systems have neither increased nor decreased (Condon et al. 2013). These results differ from those of Brotz et al.'s (2012) global analysis of jellyfish populations in large marine ecosystems (LMEs) using "soft" data. The latter authors have suggested that there have been recent increases in the Benguela and California Current systems, but a decrease in the Humboldt system. The data used by Brotz et al. (2012) required the assignment of a confidence level to assessed trends, and these were regarded as "high" for the Humboldt and Benguela systems but (perhaps surprisingly) "low" for the California Current system. Nothing substantive is known about changes in the long-term dynamics of jellyfish populations in the Canary Current EBC. Although our understanding of jellyfish has increased in the last few decades (e.g. Gibbons & Richardson 2013), this increase in focused research and knowledge has not been evenly spread across the world's ecosystems, and surprisingly little has actually been conducted in EBC systems, despite their obvious importance.

What are jellyfish?

Jellyfish are organisms whose body tissues comprise >95% water (Lucas & Dawson 2014) and include representatives from three phylogenetically very distinct taxa (Giribet & Edgecombe 2020): Ctenophora, Cnidaria and Chordata (Thaliacea). Salps, pyrosomes and doliolids (Thaliacea) are strictly epipelagic filter feeders, pumping water across mucous nets that are fine enough to trap bacteria and micro-phytoplankton. They play an important role in the biological carbon pump, turning surface production into fast-sinking faecal pellets and marine snow. Salps, pyrosomes and (especially) doliolids have complex life cycles involving an alteration between sexual and asexual generations, with sexual individuals being hermaphroditic. By contrast, ctenophores are strictly carnivorous, either by capturing mesozooplankton prey on colloblast-laden surfaces or by engulfing (usually) other ctenophores whole. They are hermaphroditic and are capable of reproducing at a small size. Whilst a few taxa are benthic, most ctenophores are pelagic and can be found in all layers of the ocean from the surface to the bathyal.

The phylum Cnidaria comprises three subphyla, only one of which includes pelagic, free-living members: Medusozoa (Kayal et al. 2013). As their name suggests, medusozoans typically (and ancestrally) display an alteration of generations (metagenesis) between a (usually) benthic polyp that reproduces asexually and a free-swimming medusa that reproduces sexually (sexes are generally separate). That said, the medusa phase may be lost in some taxa, whilst the sessile polyp phase may be lost in others. All cnidarians are carnivorous, capturing prey on nematocyst-laden surfaces in a variety of ways, although some shallow water taxa also contain photosynthetic zooxanthellae. Like ctenophores, pelagic cnidarians can be found in all oceans and at all depths, although taxa that have retained a metagenic life history are generally more common in shallow water over continental shelves.

Despite their differences, the three distinct taxa share an ecological commonality: they all have members whose populations have the potential to increase very rapidly and can strongly influence energy flow within the ecosystems in which they occur (Lucas & Dawson 2014). Although all three taxa are found in EBC systems, thaliaceans are generally (e.g. Thiriot 1978), but not always (Martin et al. 2017, Miller et al. 2019), uncommon in nearshore waters. Our knowledge of ctenophores in upwelling ecosystems is limited, perhaps because of their fragility and reluctance to fix and preserve well, although more robust species such as *Pleurobrachia* can be found in abundance in enclosed embayments (e.g. Gibbons et al. 2003). Medusozoans, however, can be abundant.

The subphylum Medusozoa comprises three classes with medusoid members: Hydrozoa, Cubozoa and Scyphozoa. The medusa phase, when present, differs widely in size among the different classes, with those of scyphozoans generally being larger than those of cubozoans, which in turn are larger than those of hydrozoans, with some exceptions. Of the three classes, scyphozoans are certainly more conspicuous in EBC systems, although ecological information about the other two is relatively scant.

The possession of a metagenic life cycle confers a distinct advantage to jellyfish that is otherwise denied to species with a holopelagic life style (including forage fish), because polyps allow populations to persist in an area when surface advection may export medusae or when environmental conditions no longer favour the survival of medusae. Polyps and medusae can survive in waters with a low concentration of dissolved oxygen, and when food densities decline to the point of starvation, some medusae (and polyps) may metabolise body tissues and shrink before regrowing again when the ambient food environment improves. Jellyfish do not require light in order to feed on mesozooplankton (unlike particulate-feeding fishes), and their often-large size, when combined with their low carbon content, makes them no less efficient than fish when feeding (Acuña et al. 2011). Indeed, their growth rates resemble those of some clupeoid fish (Palomares & Pauly 2009).

In the preceding paragraph, we have deliberately drawn comparisons between jellyfish (principally scyphozoans) and (small pelagic) fishes because both are effectively members of the same trophic guild. Both have the ability to feed on the young of each other and themselves (Irigoien & De Roos 2011) and both feed at a broadly similar trophic level. Significant research has been conducted on the dynamics of pelagic fish populations in EBC systems for intuitive reasons, such as their tremendous commercial fisheries role and their great importance to many higher trophic-level predators. Population shifts between anchovy and sardine (the dominant two species) have been recorded in most systems (Schwartzlose et al. 1999, Checkley et al. 2009), and there is evidence to suggest that these are likely caused by climate variability, but may also be secondarily affected by competition, predation and fishing (Chavez et al. 2003, Tourre et al. 2007).

Scope of this review

A considerable amount of research has been conducted on the environment and the exploitable living resources of EBC systems, for obvious reasons. Although this work has been reviewed and synthesized extensively (e.g. Benguela – Shannon et al. 2006, Humboldt – Thiel et al. 2007, Canary – Arístegui et al. 2009, California – Checkley & Barth 2009), none of these contributions have incorporated jellyfish in a meaningful way, despite the fact that they can be abundant in all systems at some time. Part of the reason for their exclusion reflects a lack of knowledge, which in turn reflects their commercial value: fisheries laboratories often lack the resources to devote to studying anything that does not contribute directly to the economy. As a consequence, the research that has been conducted on jellyfish has tended to be done by scientists from outside national laboratories, often with external international support, or by interested government biologists when the opportunity arises. The nature of the beast is such that chance plays a big role in jellyfish science, and as such the knowledge acquired has taken time to accumulate to the point that syntheses can be made. However, we believe that the time is ripe for a first review of knowledge of jellyfish in three of the four major EBC systems, and we attempt to do that here.

We have structured our review as follows. For each EBC system, which approximates an LME *sensu* Sherman & Alexander (1986) and not a regional sea (Sheppard 2019), we briefly recapitulate salient features of the biophysical environment in order to contextualize the species observed. The emphasis is on brief, as all systems have been the subject of previous reviews (see above). We then provide an overview of the jellyfish species present, their distribution in space and time, and summarize key biological processes. We look at the ecological role these organisms play within the EBC systems as predators and prey, their interactions with local economies and how they have been included in ecosystem models. We have taken this more functional approach, rather than a species-by-species account, as we believe it is easier to compare across taxa and it allows readers to make their own generalizations. We have deliberately confined our review to information that has been generated within the four EBC systems dealt with here: knowledge about any EBC species that has been created from outside the EBC systems has not been considered. Whilst we acknowledge that this may not satisfy all readers, it should be remembered that a species' ecology is likely context dependent (e.g. Swift & Dawson 2020). It should also be noted that we frequently refer to seasons in the text, and we do this without consistent reference to boreal or austral for comparative purposes. In the Benguela and Humboldt EBC systems, spring is regarded as September–November, summer as December–February, autumn as March–May and winter as June–August.

We conclude the review by attempting to put our observations in a phylogenetic context, by synthesising ecological knowledge across systems and by highlighting gaps and constraints. This has not been an easy task as different questions have been asked of jellyfish in the four EBC systems, and not all have been equally studied. Specifically, data for the Canary Current system are very patchy, and our account in this regard is based largely on qualitative and anecdotal data. However, we have taken the decision to include this scant knowledge for the sake of completeness and to highlight the issues faced by jellyfish scientists in developing countries. We stress at the outset that some of the data used here have yet to see the light of day in the peer-reviewed literature and some of the analyses use published data in a way that differs from the original.

The Benguela ecosystem

Description

The Benguela ecosystem spans the western coastline of southern Africa, from southern Angola and the seasonally shifting Angola:Benguela front in the north (~17°S) to the southernmost extension of the Agulhas Bank at ~37°S (Hutchings et al. 2009). The landmass is orientated approximately N–S for the most part, although along the south coast of South Africa, it has a W–E orientation (Figure 2). The continental shelf is broad over the western part of the Agulhas Bank, in the area of the Orange River cone and off central Namibia (Walvis Bay); it is narrowest at Cape Point, Cape Columbine, Lüderitz and Cape Frio (Figure 2). The seabed is for the most part composed of soft sediments, and rocky substrata are largely restricted to headlands at the aforementioned capes and peninsulas and inshore islands. Offshore, the sediments are largely of biogenic origin, whilst inshore they are predominantly terrigenous (Rogers & Bremner 1991).

Unlike all other EBCs, that of the Benguela is bounded to the north and south by warm subtropical waters: the Angola Current in the north and the Agulhas Current in the south (Figure 2). The position of the Angola:Benguela front is dynamic and shifts seasonally to reflect the relative intensities of upwelling in northern Namibia and the Angola Current (Shannon 1985); interannual changes reflect ENSO events and zonal wind stress in the equatorial Atlantic (Florenchie et al. 2003). Occasionally, large quantities of warm, oxygen-poor water flow into the northern region (Rouault et al. 2007, Rouault 2012). The Agulhas Current, which tracks the edge of the Agulhas Bank and retroflects eastward at ~39°S, may similarly influence the Benguela ecosystem through eddies, rings and filaments that are shed into the South Atlantic (Lutjeharms 2006).

The interaction between the South Atlantic high and the continental low-pressure systems results in onshore winds, which, owing to the orientation of the landmass, its orography and deserts, favour coastal upwelling (Shannon 1985). Upwelling is, for the most part, seasonal, being maximal in spring and early summer and is most intense at the aforementioned capes and peninsulas (Shannon 1985). It is particularly strong and relatively aseasonal at Lüderitz (~26°S) in southern Namibia, and upwelling here effectively divides the system into northern and southern sub-systems (Shannon 1985). Circulation in the northern Benguela is less dynamic than in the south owing to the wider shelf there, and a double-circulation cell is seen off central Namibia (shelf break and continental slope) that effectively traps water over the shelf (Barange et al. 1992).

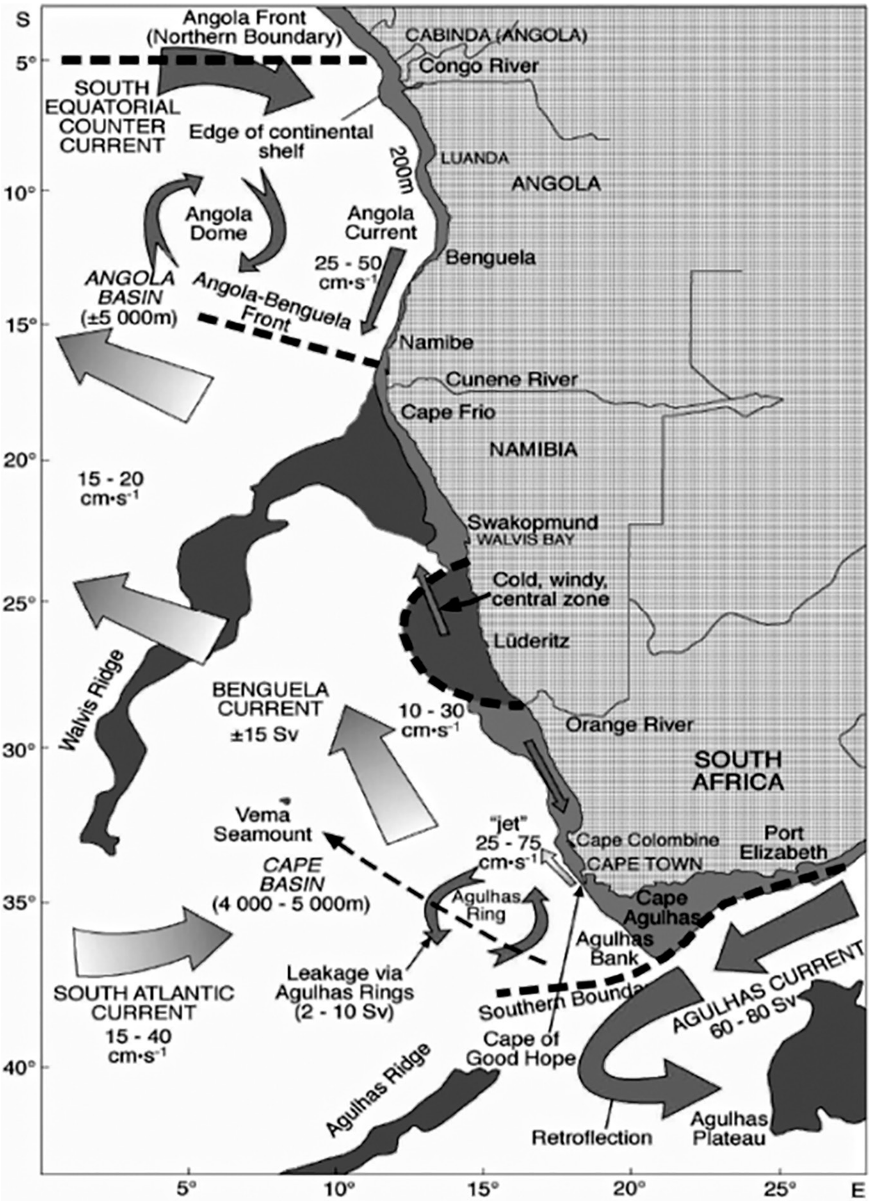


Figure 2 Map of the Benguela upwelling ecosystem showing positions of major coastal centres and dominant oceanographic features (BCLME, accessed from http://www.bclme.org).

The northern Benguela ecosystem is characterized by low concentrations of dissolved oxygen, especially in the north (Chapman & Shannon 1985). This is driven by a combination of factors including the southward movement of warm, oxygen-poor water in the Angola Current and the upwelling of low-oxygen water following upwelling at Cape Frio, as well as thermal stratification and the decay of *in situ* production (Monteiro & van der Plas 2006). While low-oxygen water can be found in the southern Benguela, its appearance is driven solely by the decay of *in situ* production (Monteiro & van der Plas 2006), and although it never approaches the areal extent witnessed off Namibia, its impacts in nearshore embayments may be significant (Pitcher et al. 2014).

Upwelled water is cold and nutrient-rich, and when introduced onto the shelf, it fuels massive phytoplankton production, especially downstream of upwelling centres (Shannon & Pillar 1986, Pitcher et al. 1992). Phytoplankton assemblages are initially dominated by diatoms, but these give way to dinoflagellates and smaller cells in space and time as nutrients are progressively stripped from surface waters (Pitcher et al. 1992). Periods of calm following upwelling events may lead to the outbreak of red tides, typically in enclosed embayments, which are particularly common during autumn in the south (Pitcher et al. 2014). Phytoplankton biomass tends to be greater in the northern than southern Benguela, owing to the more sluggish circulation there, although self-shading leads to lower production rates (Brown et al. 1991). Spring peaks in phytoplankton biomass are observed in both the southern (Hutchings et al. 2009) and northern (Louw et al. 2016) Benguela, although there is significant variability throughout the year.

Although the diversity of zooplankton assemblages in the Benguela ecosystem is typically low, and increases to the northern and southern boundaries of the system, biomass is high (Gibbons & Hutchings 1996). Zooplankton assemblages are dominated by large copepods and euphausiids (Hutchings et al. 1991), which tend to display ontogenetic diel vertical migration (DVM) and which have life cycles that take advantage of vertical changes in both cross-shelf water movement and the food environment (Pillar et al. 1992, Verheye et al. 1992). Most of the dominant copepods are herbivorous (Mauchline 1998, Verheye et al. 1992), whilst the euphausiids are omnivorous (Pillar et al. 1992). Seasonality in the biomass of zooplankton can be observed, and peaks in both the northern (Bode et al. 2014) and southern (Hutchings et al. 2009) Benguela may occur several months after that of phytoplankton. In the northern Benguela, zooplankton biomass peaks reflect the positions of the shelf break and the continental slope (Bode et al. 2014). Verheye et al. (1998, 2016) have noted long-term increases in the abundance of copepods in the southern and northern Benguela, respectively, over the period 1950–2010, which they attribute to a decrease in the biomass of pelagic fishes (see below).

Owing to its high productivity, the Benguela ecosystem supports valuable commercial fisheries for both pelagic and demersal species. Whilst the latter are more economically valuable, the former constitute the lion's share of the landings (FAO 2016). In the region, three species dominate the pelagic fish biomass: the sardine *Sardinops sagax* and the anchovy *Engraulis encrasicolis*, with the round herring *Etrumeus whiteheadii* coming in as a poor third (Roel & Armstrong 1991).

In common with other EBC systems, stocks of anchovy have tended to alternate with sardines as targets of the commercial fishery off South Africa (van der Lingen et al. 2006), in part reflecting bottom-up changes driven by climate and in part top-down changes driven by exploitation (van der Lingen et al. 2006). At present, sardine populations in the southern Benguela are estimated to be comparatively small and their centre of distribution has shifted eastwards (effectively) out of the Benguela (Watermeyer et al. 2016). However, sardines have historically comprised the major part of the pelagic fish fauna off Namibia (Shackleton 1987), where phytoplankton populations are enormous (Brown et al. 1991). At the end of the 1960s, the population size was estimated to be ~10 million t (Boyer 1996) and landings approached 1.5 million t, but following overexploitation, their populations crashed. It was thought, at the time, that anchovies and juvenile horse mackerel were direct competitors with sardines for resources and in an attempt to rebuild the sardine population, fisheries directed their efforts at the former species (Butterworth 1983, Shelton 1992). Unfortunately, however, this only resulted in the further decline of both anchovy and sardine populations: declines that to this day have not been reversed and the meagre quota is rarely filled (Mereghetti 2017).

Owing to the fact that small pelagic fishes occupy such a pivotal position in upwelling ecosystems, populations of some top predators off Namibia, especially seabirds, have declined to endangered levels (Crawford 2007, Crawford et al. 2008) in recent years. Fur seals (*Arctocephalus pusillus*) now regularly experience periods of starvation and mass mortality (Sibeene 2006). At the same time that small pelagic fish stocks collapsed, however, populations of bearded gobies (*Sufflogobius bibarbatus*) and jellyfish (see below) as well as horse mackerel (*Trachurus capensis*) have increased (Venter 1988, Boyer & Hampton 2001). Building on Bakun & Weeks (2006), Roux et al. (2013) have summarized these changes to the ecosystem, which are closely tied to increased flows of material and energy to the benthos, and which appear to be maintained by jellyfish.

Macromedusae

Species composition

Pagès et al. (1992) have detailed the medusozoans to be found within the Benguela upwelling ecosystem, and Pagès (1992), and Pagès & Gili (1991a, 1991b, 1992) have described cross-shelf, alongshore and vertical changes in assemblages and linked their observations to changes in the environment. The vast majority of the species are hydrozoans measuring less than 5 cm in diameter (Pagès et al. 1992).

Of the macromedusae considered here, seven Discomedusae, two cubozoans and one hydrozoan can be collected in the Benguela, and these are illustrated in Supplementary Figure 1. *Eupilema inexpectata* and an as yet undescribed species of *Drymonema* are restricted to the SW Cape; *Rhizostoma luteum* occurs in the nearshore waters of the Agulhas Bank and along the west coast of South Africa and into Namibia south of Lüderitz. This species is not generally very common in the Benguela, although it may occasionally be stranded in relatively high numbers at Groen River (30.83°S, 17.57°E; Supplementary Figure 2) and in smaller numbers at Lüderitz.

The cubozoan *Carybdea murrayana*, previously recognized as *Carybdea branchi* (Straehler-Pohl 2020), is common around Cape Town and is known to extend northwards as far Walvis Bay. It is seasonally abundant in very shallow waters and can be problematic for those swimming and diving in kelp beds. This species has never been caught in waters deeper than 50 m depth, although interestingly, the type specimen was recovered during the Challenger Expedition from waters off Sierra Leone, at a depth of 400 m. To our knowledge, there are no records of it being collected along the west coast of central Africa. *Chirodropus gorilla* is a large cubozoan that is routinely caught in pelagic and demersal trawls off Namibia, though never in abundance. Even though it is primarily an offshore species, it is regularly stranded during summer and autumn at Lüderitz in southern Namibia (sometimes in hundreds on one day: Grobler unpublished data), and occasionally also at Walvis Bay. This west African species is found from southern Namibia to the Gulf of Guinea.

None of the aforementioned species will be discussed further. All the remaining species of Discomedusae belong to the family Pelagiidae: *Chrysaora fulgida*, *Chrysaora africana*, *Chrysaora agulhensis* and *Pelagia noctiluca*. The hydrozoan is *Aequorea forskalea*.

Although *Chrysaora fulgida* had been synonymized with *Chrysaora hysoscella* by Pagès et al. (1992), it is regarded as a Benguela endemic, occurring from the western Agulhas Bank in the south to southern Angola in the north (Ras et al. 2020). *Chrysaora agulhensis* is a newly recognized species that is very closely related to *Chrysaora fulgida* (Ras et al. 2020); it is endemic to the Agulhas Bank and occurs from just north of Cape Town in the West to Port Elizabeth in the East (Figure 3A). Stiasny's (1939) arguments for considering that *Chrysaora africana* be synonymized with *Chrysaora fulgida* were long-held (Morandini and Marques 2010), but recent evidence suggests it is indeed distinct (Bayha et al. 2017, Ras et al. 2020). *Chrysaora africana* occurs from southern Namibia northwards to the Gulf of Guinea.

Pelagia noctiluca can be found around the entire region from Port Elizabeth in the SE to southern Angola in the NW (Figure 3B), whilst *Aequorea forskalea* occurs throughout the Benguela ecosystem (Pagès et al. 1992; Figure 3C, F): both species are regarded as having circumglobal distributions. Recent work suggests that local populations of *Pelagia noctiluca* are distinct from, and basal to, those in the North Atlantic and Mediterranean basins (Miller al. 2012), and elsewhere (Ale et al. 2019). The data presented by Ale et al. (2019) indicate that material from the SE Atlantic is more closely related to that from the SE Pacific (and not the North Atlantic), and they hint that it may not be *Pelagia noctiluca, sensu* Forskål. More taxonomic work is needed too on the identity of *Aequorea forskalea* (previously considered locally as *Aequorea aequorea*; Pagés et al. 1991), despite

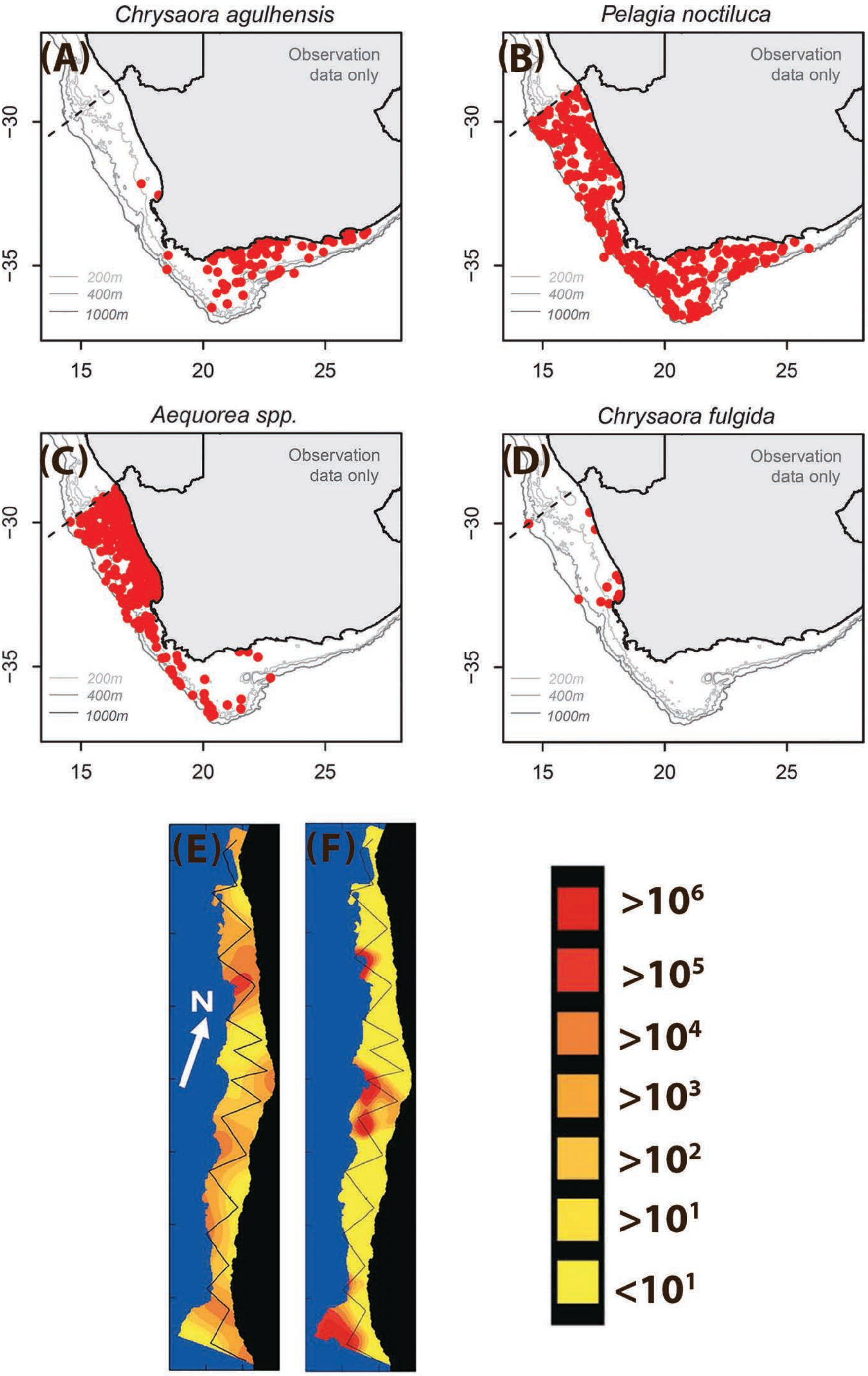


Figure 3 Distribution of *Chrysaora agulhensis* (A), *Pelagia noctiluca* (B), *Aequorea* sp. (C) and *Chrysaora fulgida* (D) from specimens collected by observers aboard eight annual research surveys conducted in South African national waters between January and May each year over the period 2011–2020. Data collected by SAEON Egagasini Biodiversity Unit in collaboration with the national Department of Forestry, Fisheries and Environment: Offshore Resources Research. Also shown is the distribution of *Chrysaora fulgida* (E) and *Aequorea* sp. (F) off Namibia in 2003 – colour scale is density, tonnes per nautical mile^2 (from Lynam et al. 2006).

the data of Dawson (2004: Figure 1, pp. 253), as the distribution maps for this species in WORMS exclude the Benguela region (Schuchert 2020).

Distribution

Space There are few data that describe in detail the distribution of *Chrysaora agulhensis* or of *Pelagia noctiluca*, over and above that provided above. Unpublished observations indicate that *Chrysaora africana* is thinly distributed in strictly coastal waters, but that it is regularly present in the harbour at Walvis Bay. Pelagic trawl catches from the RV Dr. Fridtjof Nansen show that *Chrysaora africana* can be found in very small numbers in more offshore waters of the northern Benguela to a depth of ~100 m and that it is more frequently encountered in the north of the region than elsewhere.

Most of our information about the distribution of macromedusae in the region applies to *Chrysaora fulgida* and to a lesser extent *Aequorea forskalea*: the dominant species in the (especially northern) Benguela ecosystem (Lynam et al. 2006). While both species are patchily distributed (Sparks et al. 2001) across the Namibian shelf and can be found together in pelagic trawl catches, their centres of abundance differ, with the latter tending to be found offshore (Fearon et al. 1992, Buecher et al. 2001, Sparks et al. 2001), and further north of the former (Fearon et al. 1992). Unpublished data collected by Grobler indicate that *Aequorea forskalea* is commonly recorded at Lüderitz, both stranded and in pelagic trawls, which agrees with the observations of Lynam et al. (2006; Figure 3F). In their two-year long study of gelatinous zooplankton in the Walvis Bay lagoon, Skrypzeck & Gibbons (2021) failed to collect any specimens of *Aequorea forskalea* (or any other species of *Aequorea*),[1] suggesting that polyps of this species are not located in shallow water, although *Chrysaora fulgida* was abundant. Differences in distribution of medusae may thus be linked, in part, to the distribution of polyps, although the two medusae clearly have differences in environmental optima, with *Aequorea forskalea* preferring warmer water than *Chrysaora fulgida* (Fearon et al. 1992, Sparks et al. 2001). That said, patterns may be reinforced by interspecific interactions (Sparks et al. 2001, Ras et al. 2020; see below). Results from data collected off Lüderitz during regular sampling of beach-stranded jellyfish (2008–2020) and during trawls conducted as part of oceanographic surveys (2008 to 2012) indicate that in southern Namibia, *Aequorea forskalea* is present off Lüderitz throughout much of the year (see below).

In their analysis of Namibian commercial and research catches over the period 1992–2006, Flynn et al. (2012) noted that the greatest numbers of jellyfish were observed at depths less than 200 m and between 20 and 24°S (Figure 4). It should be stressed that the data did not allow Flynn et al. (2012) to distinguish between species of jellyfish in their analyses, which were simply based on their presence or absence in trawl catches. The accumulation of jellyfish off Walvis Bay likely reflects the prevailing oceanography, which serves to concentrate, and retain, pelagic biota over the continental shelf there (Barange & Boyd 1992, Barange & Pillar 1992).

Unfortunately, similar information is not available for the southern Benguela, despite South Africa's more sophisticated economy and infrastructure. At the time of writing, jellyfish are not routinely recorded by either the commercial or research fishing fleets. That said, records of the incidence and identity of jellyfish in research catches have recently started to be collected in a project being driven not by the relevant fisheries department but by the Department of Science and Technology. Figure 3 provides a summary of this scant information to date, for the relevant species.

Information on cross-shelf changes in the size of *Aequorea forskalea* has not previously been reported. Off Lüderitz, however, the results from 17 midwater trawls conducted between 2008 and 2012 (covering all four seasons) suggest that juvenile *Aequorea forskalea* (<5 cm central disc diameter) tend to be found close inshore (62% of eight trawls at 2–5 nautical miles [nm] from shore) and rarely at 10 nm from shore (20% of five trawls), being entirely absent offshore (none were found in four trawls at 30 and 50 nm from shore: Figure 5A). Although these small size *Aequorea forskalea* generally contributed a small proportion (<15%) of the total sample size of most trawls, they

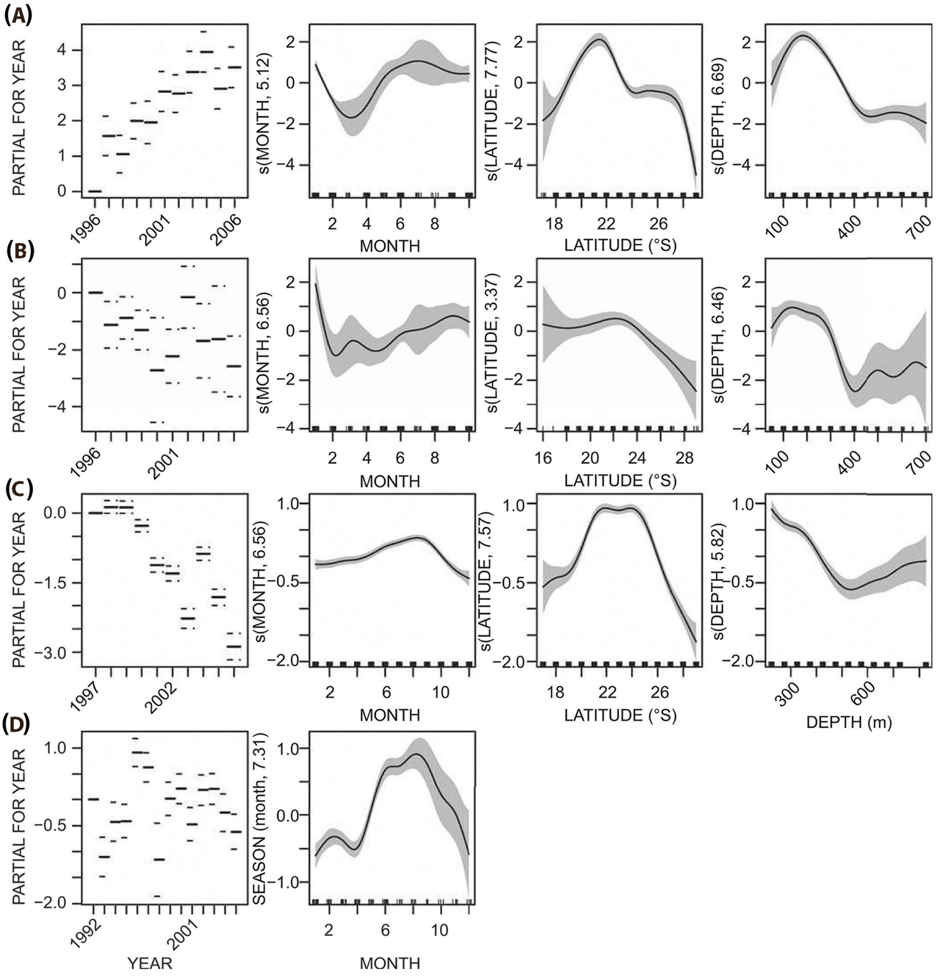


Figure 4 Term plots showing the response, the proportion of occurrence jellyfish, against predictors year, month (seasonality), latitude and depth for separate GAMs computed on jellyfish data collected off the coast on Namibia. Data from research cruises aboard the RV Dr. Fridtjof Nansen (1996–2006) for (A) demersal ($r^2 = 49.2\%$, $n = 1\ 539$) and (B) pelagic samples ($r^2 = 48.8\%$, $n = 316$), and from commercial fisheries for the (C) demersal fleet (1997–2006) ($r^2 = 46.9\%$, $n = 10\ 218$) and (D) the pelagic fleet (1992–2007) ($r^2 = 56.1\%$, $n = 110$). The y-axis is a relative scale, with positive y-values on the plots indicating a positive effect of the predictor on the response and a negative y-value indicating a negative effect. Shaded regions represent standard errors (from Flynn et al. 2012).

contributed 38% and 50%, respectively, to two trawls (September and July 2011) at 5 nm from shore. Small specimens of *Chrysaora fulgida* appear to be found inshore of large specimens in the northern Benguela (Fearon et al. 1992, Buecher et al. 2001). Unpublished data from the RV Dr. Fridtjof Nansen cruise conducted in August 2003 also indicate that smaller specimens of this species may be found off northern Namibia and that average size increases southward to Walvis Bay: an observation in agreement with that of Fearon et al. (1992).

Populations of both *Chrysaora fulgida* and *Aequorea forskalea* are primarily epipelagic (Flynn et al. 2012), certainly off Namibia, but individuals can be found throughout the water column (Flynn et al. 2012). Using data obtained from almost 40 submersible dives, Sparks et al. (2005) suggest that *Aequorea forskalea* might deepen their centre of abundance in the water column with increasing sea

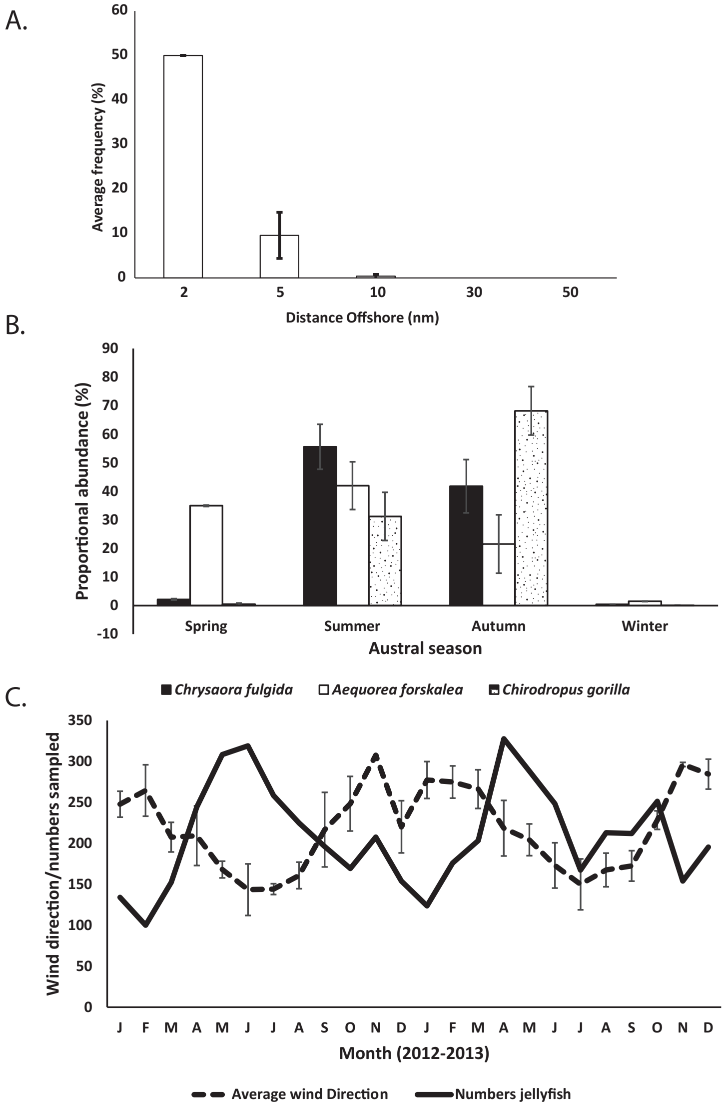


Figure 5 Average frequency (percent of catches; SE) of *Aequorea forskalea* measuring less than 5 cm bell diameter caught in midwater trawls off Lüderitz between 2008 and 2012 ($N = 17$), (A). Seasonality in the stranding of three species of regional macromedusae at Shearwater Bay, Lüderitz, based on routine observations of between 5 and 60 minutes duration (numbers dependant) collected daily from January 2014 to June 2020; data expressed as annual percentages (SE) (B). Number of stranded *Chrysaora fulgida* recorded (and sampled) each month during a 60-minute survey of Walvis Bay lagoon over the period January 2012–December 2013; average wind direction (SE) also shown from data collected using the AANDERAA anemometer at the Pelican Point lighthouse, measured at 10-inute intervals ($N = 17{,}544$; focal plane 35 m, measurement height to 39 m) (C).

surface temperature (SST), arguing that this could serve to limit offshore advection in the Ekman layer and thereby maintain themselves over the shelf. These authors supported this by indicating that individuals in nearshore waters have been found closer to the surface than they were further offshore (Sparks et al. 2005). *Aequorea forskalea* does not appear to demonstrate any size gradient with depth. However, in the case of *Chrysaora fulgida*, larger individuals are found in deeper than shallower water, offshore (Buecher et al. 2001).

Space-time Data regarding temporal changes in abundance of either *Chrysaora agulhensis* or *Pelagia noctiluca* are few. Unpublished data supplied by the community scientist Peter Southwood indicate that the latter is reported around Cape Town throughout the year, being most commonly found in winter. It is likely to be a mid-shelf species that gets moved into near coastal waters with changes in prevailing winds. As noted previously, personal observations indicate that medusae of *Chrysaora africana* are persistently present in small numbers off central Namibia. It is also been observed at Lüderitz, albeit rarely, and 26 specimens were recovered stranded on 14 of 624 sampled occasions between 2011 and 2016; all were immature, with an average diameter of 11.2 cm (±2.8 cm standard deviation), and all but one specimen were recovered in summer and autumn (Grobler unpublished data).

Information on interannual changes in the distribution or biomass of jellyfish in the region is restricted, and certainly nothing exists for the southern Benguela. Whilst there is no pattern of consistent change in the populations off Namibia in recent time (Flynn et al. 2012; Figure 4), there do appear to have been increases since the early 1970s, despite the lack of hard baseline data. Venter (1988) makes the first reference to this increase stating “The abundant occurrence and wide distribution of jellyfish off the coast of South West Africa (Namibia) is a well-known phenomenon, especially after the dramatic decrease in pelagic fishing in 1972” Venter 1988, pp. 56). As Fearon et al. (1992) noted and Roux et al. (2013) stressed, if jellyfish were as common prior to the early 1970s as they are now, they should have been reported in the otherwise comprehensive studies of Hart & Currie (1960) or Stander & De Decker (1969), but they were not, implying that they were not a major component of the system at that time. Ephyrae of *Chrysaora fulgida* dominate gelatinous zooplankton communities in Walvis Bay lagoon (Skrypzeck & Gibbons 2021). However, NONE were caught, or at least reported upon, by Unterüberbacher (1964) “from the regular plankton collections made in Walvis Bay over the period 1959–1962, though he did note the presence of other, similarly sized jellyfish in his samples…[again suggesting]…that large jellyfish populations were not a feature off Namibia at the time” (Skrypzeck & Gibbons 2021, pp. 10).

On the intra-annual scale, jellyfish are reported throughout the year in the northern Benguela (Venter 1988, Fearon et al. 1992), but appear to peak in abundance over the shelf during late winter through to mid spring (Flynn et al. 2012; Figure 4). We should be cautious in our interpretation of the latter, because they could reflect processes of physical aggregation linked to seasonal oceanographic forcing (Barange & Boyd 1992, Barange and Pillar 1992), rather than population processes *per se* (Graham et al. 2001), especially given that most of the data were collected over the shelf.

Unpublished data show that *Chrysaora fulgida* can be found throughout the year in the shallow waters off Walvis Bay and Lüderitz (Figure 5B, C). This species is more commonly stranded at Lüderitz between late spring and early autumn, with the highest numbers usually found during the period December to March. Although it is rarely present on beaches during winter and early spring (June – October) (Figure 5B), it can be caught during inshore trawl surveys off Lüderitz at that time, indicating that the species is present throughout the year along the southern part of Namibia’s coast too. The data from Walvis Bay indicate that the presence of large medusae may be related to prevailing winds from the SE and that westerlies are associated with reduced numbers (Figure 5C). Unpublished data collected from Lüderitz by Grobler indicate that most jellyfish strandings there are also linked to coastal winds from the SW. These observations suggest that their (inshore) presence may be linked to upwelling and tentative support for this comes from new evidence provided by Skrypzeck et al. (2021) using stable isotopes of $\delta^{15}N$ and $\delta^{13}C$ (Figure 6). These authors show that the $\delta^{15}N$ signatures of the large, sexually mature medusae encountered in Walvis Bay lagoon are lower than those of ephyrae and small medusae, but are statistically indistinguishable from large specimens collected offshore (Figure 6). The high $\delta^{15}N$ of inshore specimens is matched by primary producers there with very different $\delta^{13}C$ values (macroalgae and marine angiosperms), suggesting a reliance by production on new nitrogen: offshore populations being sustained by recycled nitrogen (Skrypzeck et al. 2021).

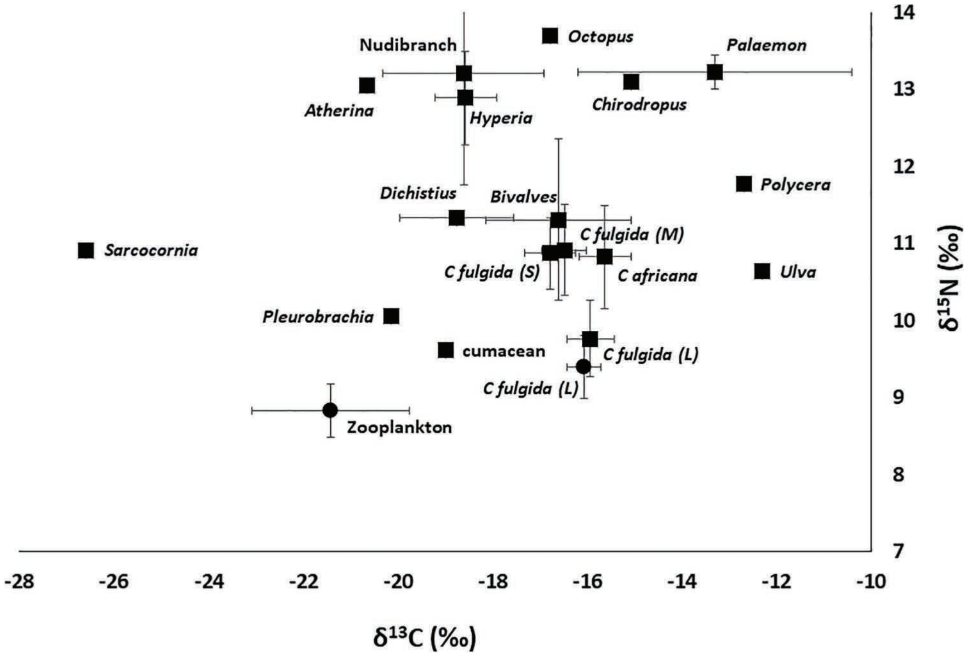


Figure 6 Isotopic biplot (δ^{13}C and δ^{15}N, mean values ±95% confidence intervals) of organisms collected in Walvis Bay (circles), and waters further offshore (squares). Data for *Chrysaora fulgida* subdivided by size class: L ≥300 mm, M <300 mm, ≥100 mm; S <100 mm. From Skrypzeck et al. (2021).

Although there are no data regarding the structure of populations in the case of *Aequorea forskalea*, those of *Chrysaora fulgida* appear to comprise a wide size range of individuals throughout the year (Buecher et al. 2001; Figure 7A). That said, proportionally more small individuals are recovered during summer than winter (Buecher et al. 2001). Although the data on which these observations are based were derived from area-integrated trawl catches taken at depths greater than 50 m (Buecher et al. 2001), they are supported, in part, by measurements of randomly sampled individuals ($n = 5508$) collected in Walvis Bay lagoon at approximately bi-weekly intervals over the period January 2012 to February 2014 (Figure 7B). Although all size classes were represented during spring and summer, small (<20 cm diameter) individuals dominated the samples (see "Reproduction" section, below) and larger individuals (>50 cm diameter) were missing in autumn and winter (Figure 7B). Off Lüderitz, populations of stranded *Chrysaora fulgida* included both juveniles and adults during all months when they were found on beaches (Figure 7C), but the largest contribution by juveniles <15 cm diameter occurred between summer and autumn (December to April).

Quantitative information on temporal changes in the abundance or distribution of either *Aequorea forskalea* or *Chrysaora fulgida* in the southern Benguela is entirely missing. That said, populations of the latter species may become more obvious in nearshore waters during autumn, as dense aggregations have forced the temporary shutdown of Koeberg nuclear power station just north of Cape Town during May 2005 and March 2020 (see below).

There is no firm evidence to indicate that either species displays DVM (Flynn et al. 2012), although no detailed studies using tags have been undertaken (as Fossette et al. 2016).

Biomass, growth and mortality

Biomass For reference purposes, information on the relationships between bell diameter and mass and other gross morphological variables of the common medusae found in the Benguela Current

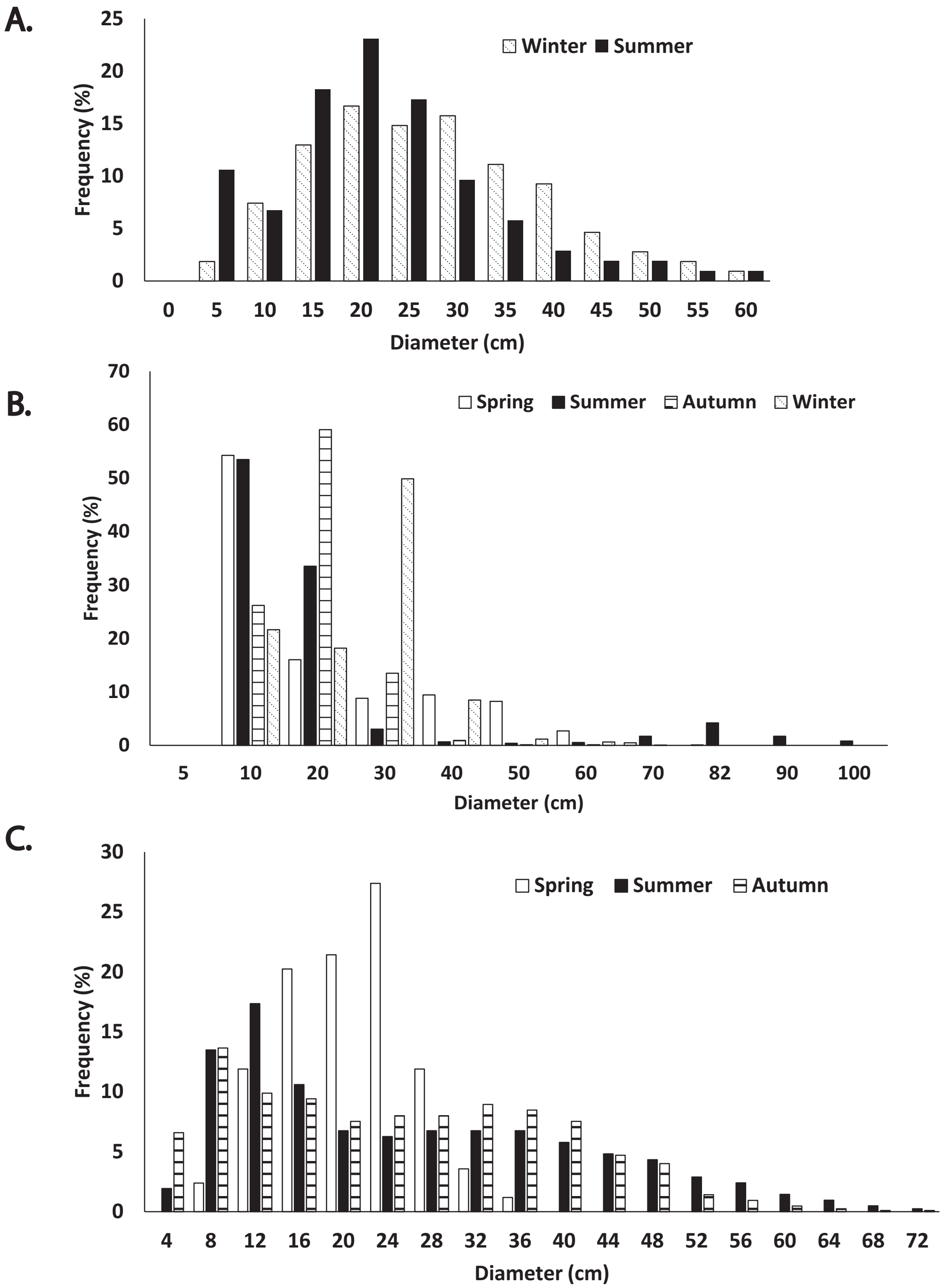


Figure 7 Seasonal changes in the size distribution of *Chrysaora fulgida* sampled in waters offshore of Walvis Bay (A) and in Walvis Bay lagoon (B), and stranded on the lagoon beaches at Lüderitz (C). Data in (A) from Buecher et al. (2001) and data in (B, C) from samples measured during the sampling of stranded material as described in Figure 5 (above).

system are shown in Supplementary Table 1. Information on carbon and nitrogen content of different tissues can be found in Supplementary Table 2.

Unfortunately, there are no empirical estimates of jellyfish biomass in the southern Benguela and the few we have from the northern sub-region vary significantly with the method of data collection. The South West Africa Pelagic Egg and Larvae Surveys (SWAPELSs) were conducted over the period January 1982 to February 1989 and comprised a series of routine stations extending latitudinally from 17°30′S to ~29°S, and offshore to a distance of 65 nm. Paired Bongo nets with a mouth opening of 57 cm diameter, fitted with 300 and 500 µm meshes, were used to collect zooplankton samples in the upper 50 m, and although they were not specifically designed to target jellyfish, the latter were nevertheless captured. Using these data, Fearon et al. (1992) estimated that the average biomass of jellyfish off Namibia during the 1980s was 40.5 million t: 10.8 million t *Aequorea forskalea* and 29.7 million t *Chrysaora fulgida*. Fearon et al.'s (1992) estimates were generated by extrapolation and using line-integration methods and were accompanied by estimates of standard error and coefficient of variation. The latter ranged between 0.42 and 0.46 for *Chrysaora fulgid*a and *Aeqourea forskalea*, respectively, and 0.33 overall. There was significant intra-annual and inter-annual variability in estimates, which also changed latitudinally (Fearon et al. 1992).

Plankton nets are not an ideal method for collecting information on the biomass of relatively large animals. Using data collected from pelagic fishing trawls and applying the swept area methods, Sparks et al. (2001) estimated that there were 4.9 million t of jellyfish off Namibia from a survey conducted off Walvis Bay during winter 1999. This total was broken down as 3.1 million t of *Aequorea forskalea* and 1.8 million t of *Chrysaora fulgida*. The data used by Sparks et al. (2001) were collected along a **single** cross-shelf transect, and mean data were scaled up to the total shelf area (179,000 km^2), assuming both species were homogeneously distributed. No estimates of variation were provided. The greater relative biomass of *Aequorea forskalea* than *Chrysaora fulgida* estimated by Sparks et al. (2001) contrasts with the findings of Fearon et al. (1992), which reflects (in part) differences in the location of the sampling areas.

Although large fishing nets are a better tool for sampling large jellyfish than small plankton nets and have been widely employed elsewhere to determine jellyfish biomass (e.g. Brodeur et al. 2008a), it needs to be remembered that small individuals will pass through meshes, while larger animals may get extruded owing to their gelatinous nature. Multi-frequency hydroacoustics can be used to quickly assess the biomass of pelagic organisms over large areas, if appropriate target strengths have been determined and discriminatory algorithms have been developed. Brierley et al. (2001) pioneered the use of this tool in the region using vessel-mounted echosounders at 18, 38 and 120 kHz during an experimental survey on board the RV Dr. Fridtjof Nansen in 1999. These authors were able to distinguish targets attributable to *Chrysaora fulgida* and *Aequorea forskalea*, suggesting that "a simple multifrequency approach…could be used to discriminate between echoes from jellyfish and some commercially important pelagic fish" (Brierley et al. 2001, pp. 55). The multi-frequency hydroacoustic tool was further improved during another experimental campaign in 2001: an additional transducer (200 kHz) was added to the echosounder, studies on single jellyfish targets of different sizes were conducted, and issues around zooplankton backscatter were corrected (Brierley et al. 2004, 2005). Finally, during August 2003, a shelf-wide survey was conducted that was aimed specifically at determining jellyfish biomass, and Lynam et al. (2006) published the results in a widely cited paper. It was estimated that (in 2003), "the biomass of jellyfish was 12.2 million t (99% by mass *Aequorea forskalea*, mean jellyfish density 361 t·nm^{-2}, standard error 22 t·nm^{-2}), and that the total biomass of fish was 3.6 million t (Cape horse mackerel 1.1 million t, mean 33 t·nm^{-2}, SE 1.5 t·nm^{-2}; Cape hake 1.7 million t, mean 50 t·nm^{-2}, SE 2.3 t·nm^{-2}; clupeoids 0.8 million t, mean 23 t·nm^{-2}, SE 1.0 t·nm^{-2})" (Lynam et al. 2006, R493). Unfortunately, the 2003 survey has not been repeated, primarily because regional fisheries vessels lack the echosounders, expertize and budget needed.

Table 2 Von Bertalanffy growth parameters *of Chrysaora fulgida* and *Aequorea forskalea* in the northern Benguela ecosystem

Species	*n*	$L_{\min}$ (cm)	$L_{\max}$ (cm)	L_∞ (cm)	W_∞ (g)	K (yr^{-1})	*C*	*M*
Aequorea forskalea	3396	4	10	11.1	141	0.87	0.50	2.09
Chrysaora fulgida	2240	7.5	62.5	68.2	10 725	4.30	0.25	4.83

Source: From Palomares and Pauly (2009).

Growth, mortality and longevity There are no empirical estimates of growth rate or mortality for any species of medusae within the Benguela ecosystem. However, using the length frequency data published by Brierley et al. (2001) and Buecher et al. (2001), Palomares & Pauly (2009) derived estimates for these parameters for *Chrysaora fulgida* and *Aequorea forskalea* (Table 2) using a variety of methods, including Wetherall plots (Wetherall 1986). These authors adjusted the von Bertalanffy growth curve parameters to account for seasonality, following Somers (1988), by setting the winter point as July (Palomares & Pauly 2009). The winter point represents the month when water temperatures are lowest and growth is assumed to be at its minimum: it determines the timing of the first sinusoidal growth oscillation. As Palomares & Pauly (2009) stress, the use of Wetherall plots does not generate values of mortality (Z, where $Z = M$, as $F = 0$: Z = total mortality, F = fisheries mortality and M = natural mortality), but rather values of mortality relative to K (growth coefficient) which should be considered heuristic.

The estimates of L_∞ (maximum size) derived by Palomares & Pauly (2009) for *Chrysaora fulgida* are some 12 cm smaller than the maximum size observed in the field, where W_∞ (maximum weight) may exceed 20 kg (unpublished data). Whilst Pagés et al. (1991) recorded specimens of *Aequorea forskalea* with a maximum diameter of 27.5 cm, which differs by about 16 cm from the L_∞ derived of Palomares & Pauly (2009), this discrepancy likely reflects differences in the measures used. The latter authors used the diameter of the thickened central lens, which gets recovered from trawls and which was recorded by Buecher et al. (2001) and Brierley et al. (2001), whilst the measurements of Pagés et al. (1991) also included the more delicate marginal umbrella. Brierley et al. (2004) calculated that the relationship between central lens and total diameters (Supplementary Table 1B), and if the L_∞ value estimated by Palomares & Pauly (2009) is so adjusted, material differences with the observations of Pagés et al. (1991) disappear.

Attempts to age Discomedusae from field specimens are fraught. Size is an unreliable indicator of age, given that individuals may grow rapidly when provided with abundant food at optimum temperatures, but will shrink (not starve to death) when environmental conditions deteriorate (Arai 1997). The statoliths of cubozoans can be used to age individuals, in much the same way that otoliths can be used to estimate the age of bony fish, owing to the fact that the basanite crystals (calcium sulphate hemihydrate) are consolidated (e.g. Heins et al. 2018). Statoliths are sectioned and polished and then (daily) rings counted using light or scanning electron microscopy (e.g. Gordon & Seymour 2012). In the case of scyphozoans, however, the statoliths comprise a loose accumulation of individual crystals (Heins et al. 2018 and references therein), which makes ageing outside controlled experimental environments difficult. The maximum age of *Chrysaora fulgida* in captivity exceeds 18 months.

Beach-stranded material at Lüderitz suggests that cohort progression could perhaps be used to analyse the growth of juvenile *Chrysaora fulgida* (Figure 8). Although caution should be exercized in the interpretation of these data, preliminary results of the two cohorts that were observed over the period February–March 2011, indicate that growth rates were similar in each (Figure 8) and that they were rapid.

Reproduction

Sexual reproduction No studies on the reproduction of *Pelagia noctiluca* or *Aequorea forskalea* have been conducted in the region. *Pelagia noctiluca* in the central and northern Adriatic Sea and

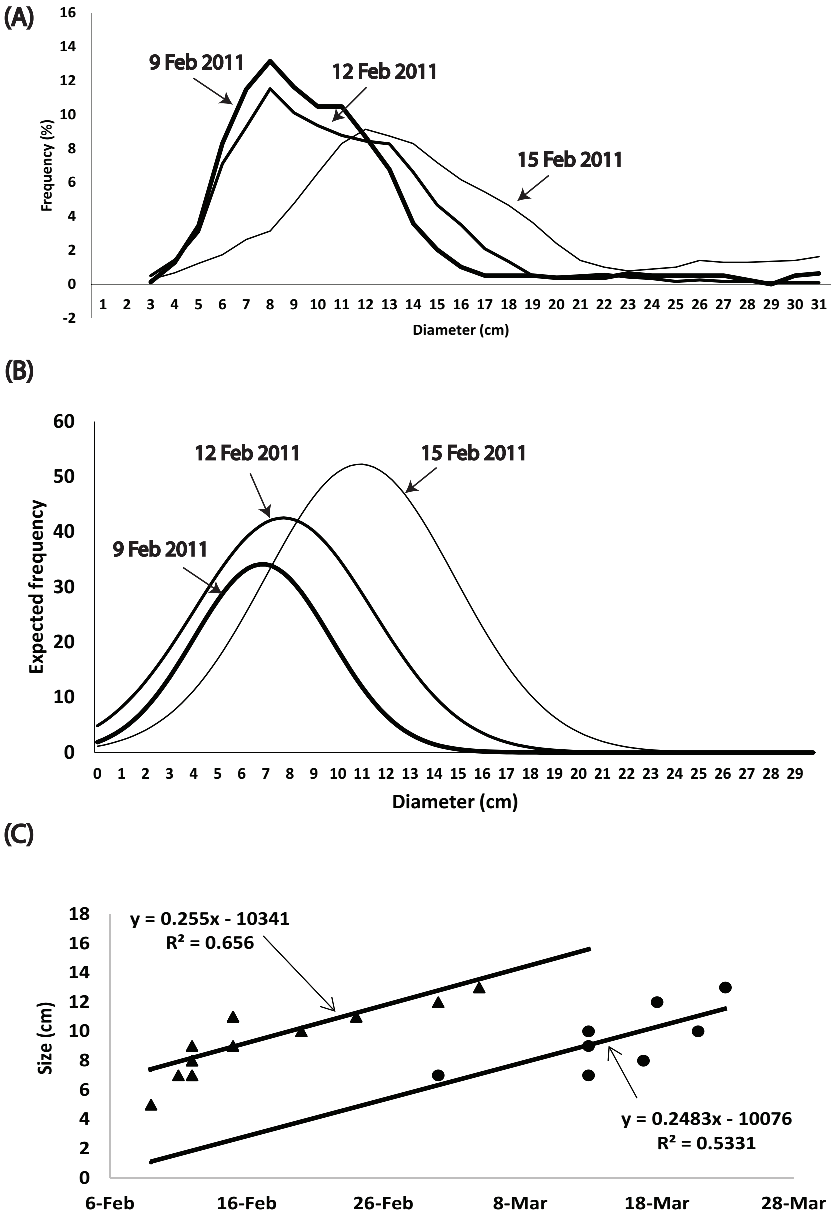


Figure 8 The size structure of beach-stranded specimens of *Chrysaora fulgida* at Lüderitz lagoon observed on three occasions over the period 9–15 February 2011 (A); changes in the average size of stranded *Chrysaora fulgida* from two cohorts measured in Lüderitz lagoon during February and March 2011 (B). Data are random samples of stranded jellyfish (Grobler unpublished).

in the Strait of Messina appear to reproduce throughout the year as oocytes of all maturity states can be found each month (Rottini Sandrini & Avian 1991, Milisenda et al. 2018). This contrasts with the situation in the North Atlantic (Russell 1970).

While there is little information regarding reproduction in *Chrysaora agulhensis*, like *Chrysaora fulgida* and *Chrysaora africana*, the species is known to be dioecious (Ras et al. 2020). Unfortunately, the sex of an individual *Chrysaora* from the region can only be determined by histological examination. Our knowledge of the sex ratios in populations of any species of *Chrysaora* (or indeed any Discomedusae for that matter) is almost entirely missing, although detailed observations conducted in Walvis Bay suggest that the sex ratio for *Chrysaora fulgida* there is ~1:1 (F:M) (Skrypzeck 2019).

Our understanding of gonad development and reproductive maturity of macromedusae in the Benguela ecosystem is entirely restricted to *Chrysaora fulgida* and to a lesser extent *Chrysaora africana*.[2] From the work recently conducted in Walvis Bay (Skrypzeck 2019), it would appear that the pattern of gametogenesis in both the species is similar to that displayed by other Discomedusae (Eckelbarger & Larson 1988, Eckelbarger 1994, Schiariti et al. 2012). Synchronous oocyte development is observed in *Chrysaora fulgida* and group-synchronous development in *Chrysaora africana*. The oocytes of *Chrysaora africana* are slightly smaller than those of *Chrysaora fulgida*, and they have a slightly different shape. The gonads of both species appear to have specialized gastrodermal structures (less conspicuous in *Chrysaora africana*), and there is a close association between the developing oocytes and the gastrodermis (Skrypzeck 2019).

Reproduction of *Chrysaora fulgida*, at the population level, occurs throughout the year: it appears to be aseasonal, at least for some parts of the population. Whilst individuals may mature at a relatively small diameter (M 22.5 cm; F 36 cm), they may also only mature at a larger size (up to M 73.4 cm; F 77 cm). Populations off central Namibia therefore appear to display reproductive heterogeneity, with individuals dancing to their own rhythm. Off Walvis Bay, sex-indeterminable medusae of *Chrysaora fulgida* dominate nearshore samples throughout the year and sexually mature medusae are relatively uncommon (see Figure 9A, Table 3). By contrast, off Lüderitz in southern Namibia, the majority of adult *Chrysaora fulgida* stranded in late summer and autumn have well-developed gonads, which indicates that some parts of the population may display reproductive seasonality. Histological evidence suggests that individuals are semelparous, although there is the possibility that some females may spawn over a protracted period: a partially spent individual (~38 cm diameter) has been observed.

Chrysaora africana seems to mature at ~20 cm diameter, and reproduction at the population level appears to be strongly seasonal, with a peak in autumn and winter (Figure 9B, Table 3). Females seem to be able to reproduce in a serial fashion over a more protracted period of time before dying: individuals display restricted iteroparity (Skrypzeck 2019). Most of the *Chrysaora africana* recorded in the nearshore waters of Walvis Bay are mature, although immature individuals can be found in all seasons (Skrypzeck 2019).

Asexual reproduction While *Pelagia noctiluca* is holoplanktonic, and so produces no polyps, the balance of species is metagenic. That said, no polyps of any Discomedusae have ever been observed *in situ* in the Benguela region. However, it is likely that they will be attached to hard substrata (Lucas et al. 2012), which for the most part occur in shallow water (Rogers & Bremner 1991). However, the benthic polyps of both *Chrysaora africana* and *Chrysaora fulgida* have been described from cultures (Ras et al. 2020), and they essentially resemble others of the genus (Morandini & Marques 2010). Ziegler & Gibbons (2018) noted that asexual reproduction in the polyps of *Chrysaora fulgida* includes lateral budding by means of stolons, the production of podocysts,[3] strobilation (see below) and lateral budding (*sensu* Adler & Jarms 2009). The latter of these methods was the most prevalent way by which new polyps were generated, and although most polyps produced lateral stolons, few of these developed buds (Ziegler & Gibbons 2018). Asexual polyp production appears to be positively impacted by food (concentration and feeding frequency) and temperature over the range 12–20°C (Ziegler & Gibbons 2018). Although podocysts were formed in low numbers at all temperatures, more were produced at lower than higher food densities; no podocysts were produced by starved polyps (Ziegler & Gibbons 2018).

To return to the medusa phase of the life cycle, the asexual polyp, under species specific environmental conditions of food, temperature and/or salinity, will undertake the process of strobilation to release ephyrae (Raskoff 2003, Treible & Condon 2019). Strobilation by polyps of *Chrysaora*

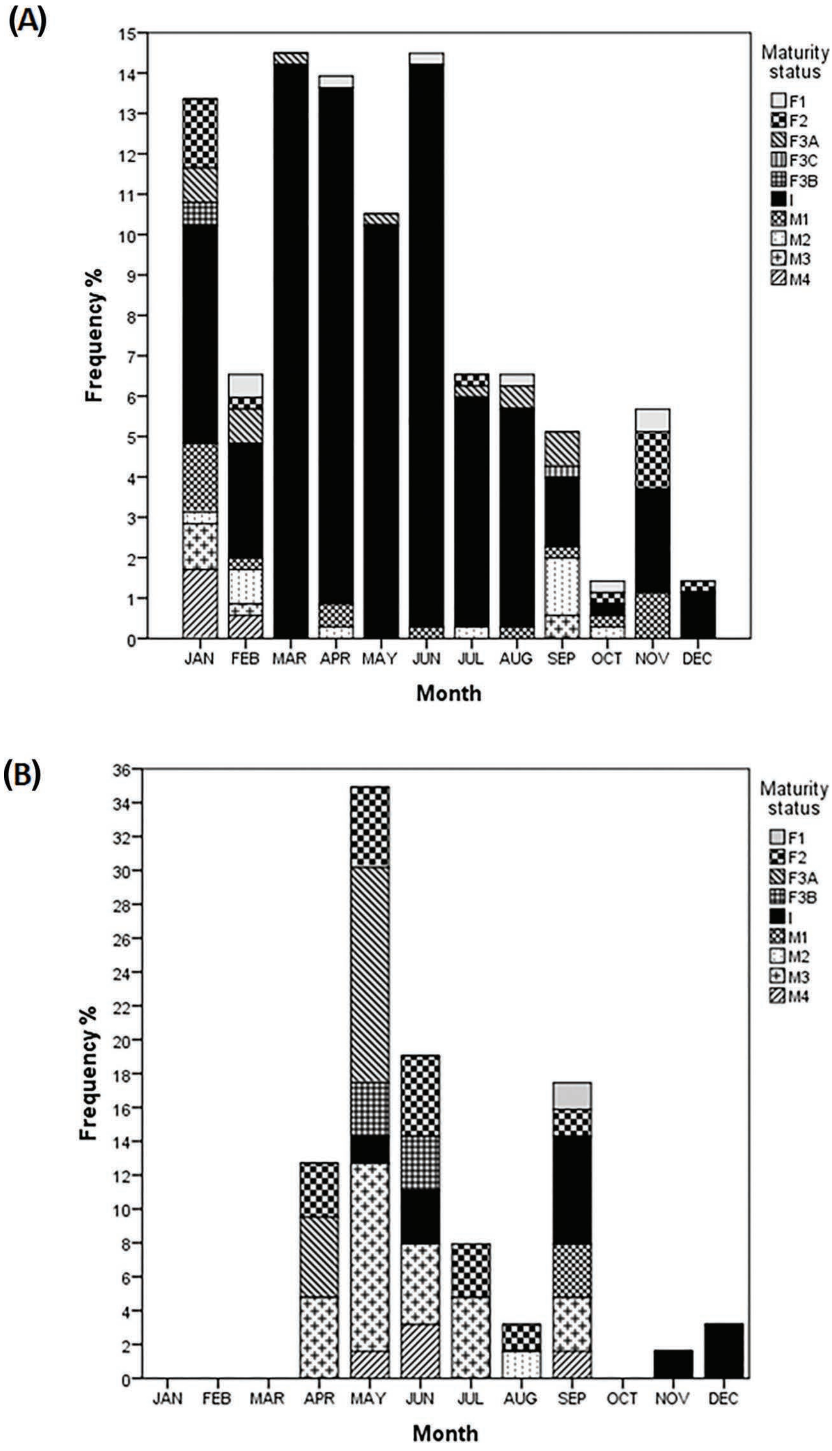


Figure 9 The average frequency (%) of different gonad maturity statuses of female (F1–F3C), sex-indeterminable (I) and male (M1–M4) *Chrysaora fulgida* and *Chrysaora africana* among stranded medusae at Walvis Bay; January 2012–February 2014. See Figure 6 for details of sampling, and Table 3 for information on maturity status descriptions (adapted from Skrypzeck 2019).

Table 3 Description of the maturity statuses of *Chrysaora africana and Chrysaora fulgida*, as determined from histological measurements of specimens caught in Walvis Bay lagoon (adapted from Skrypzeck 2019).

Maturity Status	Description
I	Sex-indeterminable, no gonad development
F1	Unripe female, predominance of ≥50% pre-vitellogenic oocytes
F2	Unripe female, predominance of >50% early vitellogenic oocytes to mid vitellogenic oocytes and <15% of late vitellogenic to released stage oocytes
F3	Ripe female, ≥15% of late vitellogenic to released stage oocytes. To be categorized into - • Ripe/ovulating gonad **(F3A)**, or • Disintegration of gonad structures **(F3B)**, or • Partially spent gonad **(F3C)**
M1	Unripe male, <70% of sperm follicles contains spermatozoa
Mripe	Ripe male, ≥70% of sperm follicles contains spermatozoa. To be categorized into -: • Individual sperm follicles visible that contains spermatozoa **(M2)**, or • Sperm follicles clustered or merged, spermatozoa may or may not be released into subgenital sinus, and/or sperm follicles merged into highly condensed spermatozoa areas **(M3)**, or • The disintegration of follicle walls, gastrodermis and subgenital sinus **(M4)**

fulgida was observed by Ziegler & Gibbons (2018) in the laboratory, but only rarely and only at 12°C. The number of ephyral discs produced ranged from five to eight (Ziegler & Gibbons 2018). We should be cautious in our treatment of these data because the experiments were only conducted for a period of 30 days under a constant set of environmental conditions; strobilation was not the subject of the study. More extensive but hitherto unpublished work by Krish Lewis at the Two Ocean's Aquarium demonstrates that polyps of *Chrysaora fulgida* can be readily maintained at temperatures between 12 and 20°C, but that strobilation is stimulated when polyps are exposed to a temperature of 11°C for a period of 14 days, after which the temperature is raised to 14°C (fed to satiation daily, under 12-hour light). Under these conditions, up to 42 ephyral discs per polyp may be observed (average 30) and individuals may re-strobilate at a reduced rate some four to six weeks later. By contrast, strobilation of *Chrysaora agulhensis* is achieved when the temperature is raised from a two-week exposure at 14°C, to 18–20°C, the number of ephyrae in this case averaging 23 per polyp (29 maximum) (Krish Lewis, Two Oceans Aquarium; unpublished data).

Skrypzeck (2019) has recently detailed the morphology and development of the ephyrae of *Chrysaora fulgida* and *Chrysaora africana* from field collections in Walvis Bay lagoon, noting that the two species are readily distinguishable *in situ*. These observations imply that the polyps of both species are present in the immediate area, perhaps on the infrastructure associated with the industrial harbour there, or with associated maritime activities (Skrypzeck 2019). Using these descriptions, Skrypzeck & Gibbons (2021) chronicled the structure of gelatinous zooplankton assemblages over the period January 2012 to December 2013, changes in which appear to be driven primarily by bottom temperature and day length.

The data presented by Skrypzeck & Gibbons (2021) indicate that ephyrae of *Chrysaora africana* may appear in the water column as early as mid-June and persist until early October, but peak in abundance at the end of winter (August). In the case of *Chrysaora fulgida*, newly released ephyrae also first make an appearance in the plankton during mid-winter (July), soon after the lowest bottom temperatures are recorded. They peak in abundance in late winter and spring (August/September/October) and have disappeared by the start of summer (December) (Figure 10A). While more developed ephyrae first occur in the water column at the end of winter (August) and have all but vanished by mid-summer (January), they may make periodic appearances during late summer (February to May) as juveniles. In other words, the recruitment of ephyrae to the plankton off Walvis Bay is not continuous throughout the year, but is a protracted six-month affair.

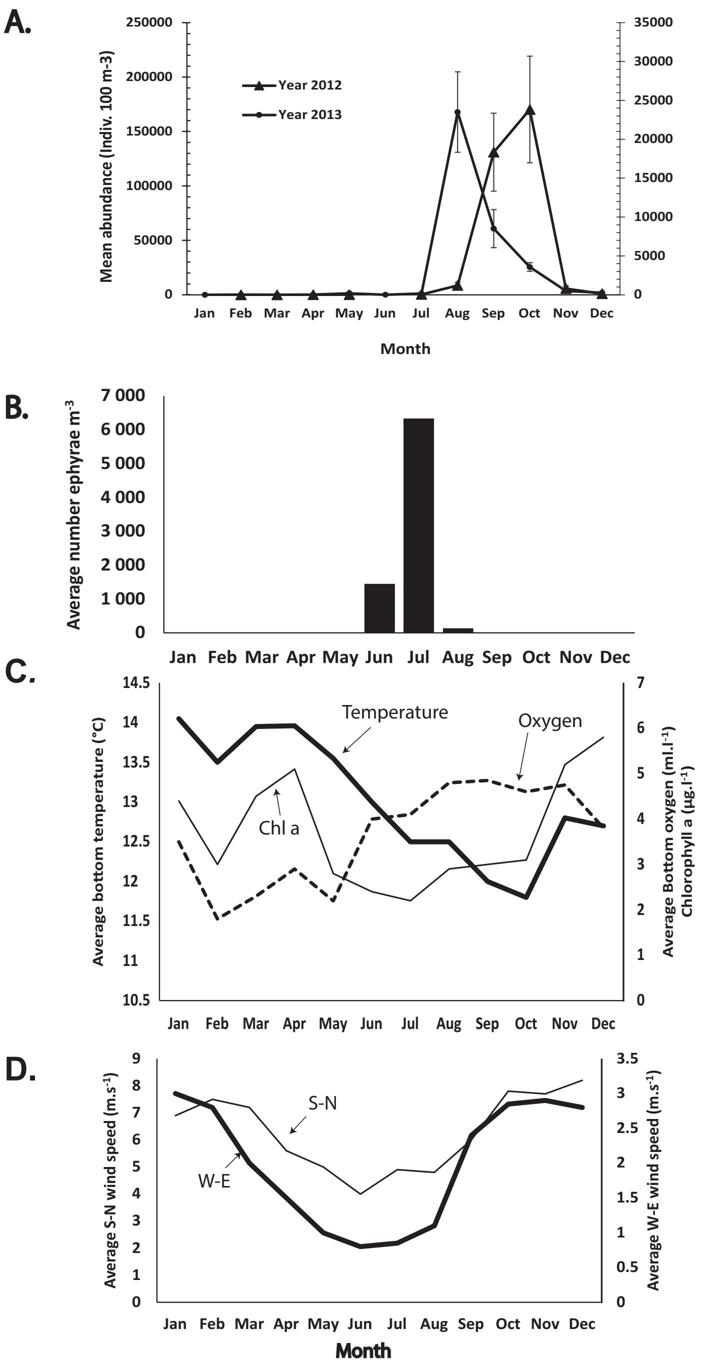


Figure 10 Average monthly abundance (SE) of ephyrae of *Chrysaora fulgida* in Walvis Bay lagoon during 2012 (left *y*-axis) and 2013 (right *y*-axis) (A); monthly average number of ephyrae m^{-3} at three inshore stations at Lüderitz, collected as part of zooplankton samples during routine oceanographic surveys (B), with accompanying environmental data (C, D). Data in B - D derived from hourly (wind speeds) or weekly (ephyrae, oxygen Chl a) observations averaged across months and years, 2010–2013, ephyrae; 2010–2018, bottom temperature and oxygen; 2008–2017, Chl a; 2011–2017 wind speeds). (A) from data in Skrypzeck & Gibbons (2021), (B - D) from Grobler (unpublished).

Interestingly, it would appear from unpublished data that ephyrae of *Chrysaora fulgida* may first appear in the water column at Lüderitz during April and persist only until September (Figure 10B) (Grobler unpublished data). In other words, the release period at ~26°S is some two months in advance of that at ~23°S (Walvis Bay), although again it may occur over a protracted period of time. The nine-year time series of data collected in the inshore waters of Lüderitz (only a part of which is shown in Figure 10B) indicates that ephyrae are most abundant during winter (when upwelling winds off Lüderitz are weakest), and are least common during spring and summer (October to February), when upwelling winds are strongest (Figure 10D). This is unlike the situation at Walvis Bay, where the strongest upwelling winds occur during September. Ephyrae were most prevalent at Lüderitz when bottom water temperatures were in the range 11–12.6°C (though they were seen in waters at 14°C or more) and when bottom dissolved oxygen levels were high (between 3 and 6 $mL{\cdot}L^{-1}$) (Figure 10C). Winter periods off Lüderitz are also characterized by frequent storms and high swell conditions, with increased turbulence and sediment loads in the water column. Thus, the highest abundance of ephyrae in the inshore waters of Lüderitz occurs under the combined conditions of lowest upwelling strength, high bottom dissolved oxygen, low bottom temperatures and increased turbulence (due to high winter swells).

While ephyrae of Discomedusae are rarely encountered in plankton samples from the southern Benguela, Helm and Gibbons (2008) did note what appear to be ephyrae of *Chrysaora* between St. Helena Bay and Lambert's Bay during spring 2000. Unfortunately, because zooplankton samples are not collected regularly around South Africa, it is not possible to comment further. That said, the data demonstrate that polyps are present in the region and, given that bottom water temperatures are coldest off the west coast of South Africa during spring (Shannon 1985), they imply that strobilation is probably initiated as elsewhere.

The data provided by Skrypzeck & Gibbons (2021) indicate that Stage 0 and Stage 1 ephyrae[4] of *Chrysaora fulgida* appear together in plankton samples in the lagoon at Walvis Bay (July), suggesting that there is a very short development period from the former to the latter. Stage 2 ephyrae appear for the first time in August and persist until December, implying a development time of approximately one month from Stage 0 to Stage 2 (total body diameter 2.07 ± 0.48 mm – 14.24 ± 4.03 mm), at an ambient temperature of 13.2°C. "Interpretation of [the] data with regard to subsequent ephyral development is complicated by the fact that the more advanced stages (Stage 3–5) were pooled and recorded in samples throughout the year, albeit at very low densities. Two hypotheses can be invoked to explain this observation: (1) small numbers of polyps may be strobilating throughout the year, either inside or outside the lagoon, (2) the further development of ephyrae within Walvis Bay lagoon is variable and potentially slow. Neither of these can be discounted but as there appear to be two peaks in relative abundance of the older stages (Stage 3–5) each year (late winter and early spring; autumn), it is possible that ephyrae released early in the season mature quickly, whilst those released at the end develop more slowly. This is not unlikely given that growth rates of ephyrae will vary with the quantitative and qualitative food environment (e.g. Båmstedt et al. 2001), as well as with temperature (e.g. Widmer 2005)" (Skrypzeck & Gibbons 2021, p. 80).

The densities of Stage 0, and especially Stage 1, ephyrae of *Chrysaora fulgida* recorded in the lagoon at Walvis Bay by Skrypzeck & Gibbons (2021) were exceedingly high: maximum densities of Stage 1 ephyrae greater than 4672 m^{-3} were observed in one sample collected during October 2012. By contrast, the densities of the more advanced stages (Stage 3–5) only attained a maximum of 8 m^{-3}, again collected during October 2012. Two things become obvious from these data. First, despite its lagoonal nature (Skrypzeck & Gibbons 2021), advection to the outside, nearshore environment is effective. And second, given that the densities observed are higher than those that have been observed for any other species of jellyfish to date, potential contributions to adult populations are enormous, in the absence of mortality.

Interactions with other species and human activities

Diet

There has only been one explicit and published study on the diet of macromedusae in the Benguela region and that is of *Chrysaora fulgida* in the Walvis Bay lagoon (Flynn & Gibbons 2007). The data presented by the latter authors should be treated with some level of caution as only 55 individuals were examined; they were caught using a fine mesh dip net at the surface in September 2003 (Flynn & Gibbons 2007). The diet was diverse, and although it was dominated by branchiopods and copepods, it included dinoflagellates and carideans and, interestingly, the adults and larvae of benthic species (in abundance). Numbers of the latter were greater by night than by day, although whether this reflected the vertical migration of predator (downwards) or prey (upwards) is unknown (Flynn & Gibbons 2007). The shallow nature of the lagoon (<8 m depth) may explain both the high numbers of benthos and the very low numbers of fish larvae recorded.

Indirect evidence of feeding comes from an examination of stable isotope ratios (^{13}C:^{12}C and ^{15}N:^{14}N) and fatty acids. Whilst not exactly revealing in details, a reanalysis of the data collected by van der Bank et al. (2011) from the edge of the inner shelf (~180 m) off Walvis Bay in 2008 shows that there are differences in the isotope signatures of both common species (Figure 11A, Supplementary Table 3). The $\delta^{15}N$ of *Chrysaora fulgida* (9.43 ‰ ± 0.92: $n = 48$) was significantly ($F = 20.40$. $p < 0.0001$) lower than that for *Aequorea forskalea* (10.72 ‰ ± 1.70: $n = 39$), as too was the $\delta^{13}C$ ($F = 10.96$. $p < 0.005$; –15.38‰ ± 1.05, –14.67‰ ± 0.92, respectively). These differences are supported by a multivariate analysis of fatty acids (Analysis of Similarity, ANOSIM global $R = 0.62$, $p = 0.001$) (Figure 11B), with the key differences between the two species shown in Supplementary Table 4. While *Chrysaora fulgida* and *Aequorea forskalea* are clearly different from the other dominant zooplankton in the area, they are also very obviously different from each other.

Parasitism

Hyperiid amphipods are well known as parasites/predators of a variety of gelatinous zooplankton, including salps, ctenophores and scyphozoans (Laval 1980). *Hyperia medusarum* is routinely collected from specimens of *Chrysaora fulgida* across the shelf off Namibia, and their distribution among hosts tends to display a negative binomial distribution. While amphipods are found in all tissues, there is a tendency for loads to be greater in the gonads (Buecher et al. 2001); they are also more common on animals with full stomachs (Flynn & Gibbons 2007). If we accept that the relatively low infestation rates observed by Buecher et al. (2001) reflect the loss of parasites following the trawl capture of jellyfish, there is a significant increase in infestation with increasing animal size (mass/diameter) (Brierley et al. 2004, Flynn & Gibbons 2007). However, evidence to suggest that increased parasite loads are associated with an altered body condition is contradictory (Flynn & Gibbons 2007 *cf* Brierley et al. 2004). Interestingly, parasite loads do not appear to materially impact on hydroacoustic backscatter, with the lion's share of the signal coming from the jellyfish and not the amphipods (Brierley et al. 2004).

Predation

Direct evidence of predation on jellyfish by other organisms in the Benguela is scant. That said, a hitherto undescribed species of *Drymonema* from the south-western Cape region of South Africa has been photographed eating *Pelagia* (Supplementary Figure 3A). Like other species of *Drymonema*, this animal is episodic in appearance and uncommon (Malej et al. 2014), so its impact on wider jellyfish populations is likely to be limited. In captivity, this species will readily feed on a variety of scyphozoans, including *Chrysaora fulgida* and specimens of *Aurelia*, but not the cubozoan *Carybdea murrayana* (Krish Lewis, Two Oceans Aquarium, Cape Town; personal communication).

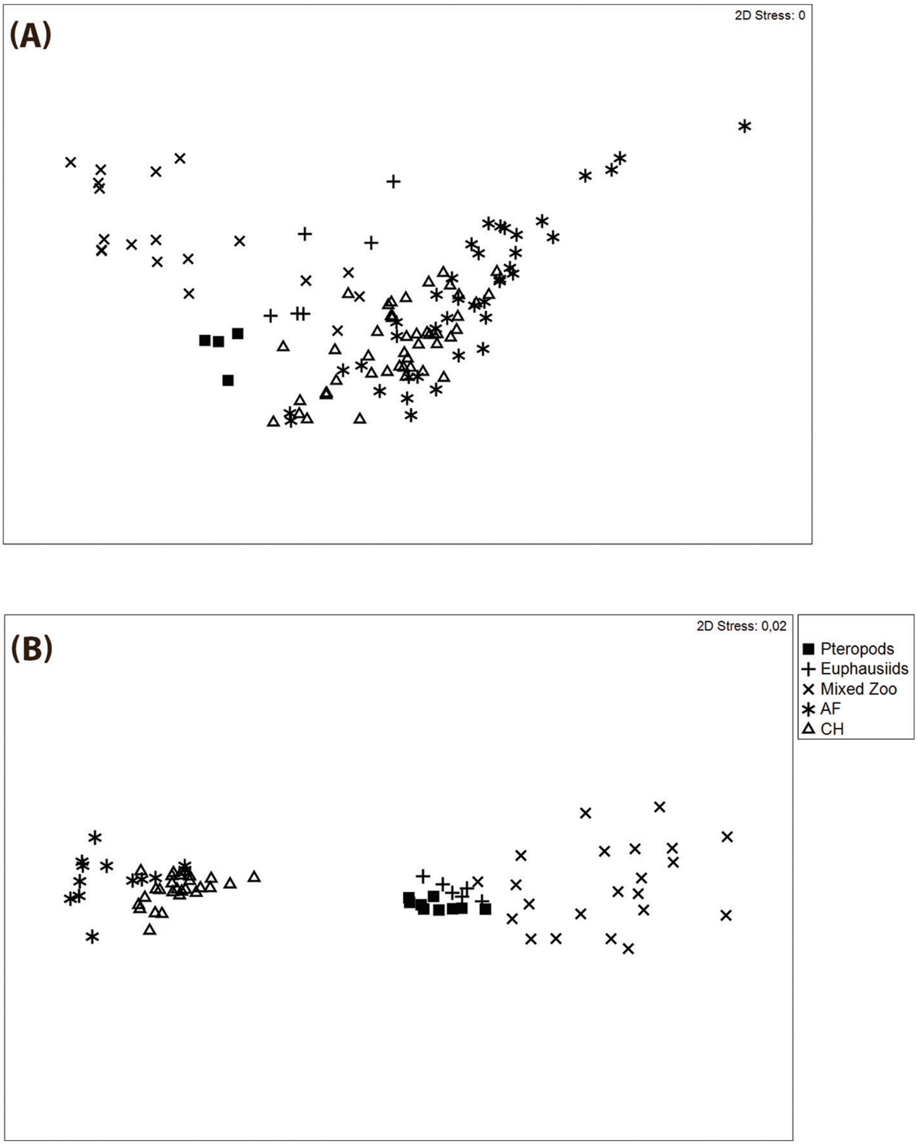


Figure 11 Non-metric MDS plots showing the similarity (Euclidean distance) in the stable isotope composition (^{13}C:^{12}C and ^{15}N:^{14}N) (A) and fatty acid content (B) of planktonic organisms sampled off the coast of Namibia in April 2008. Isotope data were normalized, and fatty acid data were $\log_{10}(x + 1)$ transformed, prior to the construction of similarity matrices. All analyses computed using PRIMER7. Data extracted from van der Bank et al. (2011); fatty acid details shown in Supplementary Table 4.

The near-mutually exclusive, cross-shelf distribution of *Aequorea forskalea* and *Chrysaora fulgida* off Namibia has been remarked upon by several authors (Fearon et al. 1992, Buecher et al. 2001, Sparks et al. 2001). While the two species appear to favour slightly different environments (Sparks et al. 2001), the differences in distribution could reflect (in part) intraguild predation, because species of both genera are known to eat other gelatinous organisms (Feigenbaum & Kelly 1984, Purcell 1991). Species of *Chrysaora* are widely cultured in public aquaria, and growth to exhibition size is greatly improved by providing them with a diet that includes chunks of jellyfish of

Table 4 Seasonal changes in the percentage of catches of each of the dominant pelagic fish in the northern Benguela that also contained jellyfish (a); the percentage of total catch weight represented by catches that also contained jellyfish (b) and the ratio of catch weight with jellyfish vs. catch weight without jellyfish (c). Annual data also shown

Species		*Sardinops sagax*	*Engraulis encrasicolis*	*Trachurus capensis*	*Etrumeus whiteheadi*	*Sufflogobius bibarbatus*
Number trawls		**6045**	**1642**	**6330**	**2624**	**429**
a. Percent catches w jellyfish	Autumn	21	20	11	18	78
	Winter	37	52	38	54	65
	Spring	29	27	50	47	100
	Summer	15	20	10	17	60
	Annual	**26**	**33**	**12**	**24**	**70**
b. Percent biomass catches w jellyfish	Autumn	32	16	8	16	88
	Winter	38	59	32	42	90
	Spring	39	20	23	25	100
	Summer	15	2	10	26	58
	Annual	**34**	**44**	**9**	**25**	**69**
c. Catch wt w jellyfish / Catch wt wo jellyfish	Autumn	1.72	0.78	0.67	0.87	2.02
	Winter	1.59	0.66	0.29	0.38	n/a
	Spring	0.98	0.08	1.02	1.76	0.90
	Summer	1.06	1.34	0.76	0.62	4.55
	Annual	1.45	1.62	0.72	1.03	**0.97**

Source: Data collected over the period 1992–2006 and extracted from Utne-Palm et al. (2010).

another species (Widmer 2008a). *Chrysaora fulgida*, like the other species of *Chrysaora* found in some EBCs, has elaborately folded, voluminous oral arms basally (Supplementary Figure 1), which Bayha and Dawson (2010) have suggested might be an adaptation for medusivory. Interestingly, however, the stable isotope data published by van der Bank et al. (2011) show that *Aequorea forskalea* has higher values of $\delta^{15}N$ than *Chrysaora fulgida* in the waters offshore of Walvis Bay, although whether this reflects predation of the former on the latter or on a different resource base is unknown. Personal observations reveal that meta-ephyrae of *Chrysaora africana* readily consume ephyrae of *Chrysaora fulgida*.

What van der Bank et al.'s (2011) analysis does show, however, is that jellyfish represent a significant source of food for the bearded goby *Sufflogobius bibarbatus*, *Aequorea forskalea* being important for large gobies, whilst *Chrysaora fulgida* is similarly valuable for smaller fish. Although it is unknown whether the jellyfish eaten by the bearded goby are alive or dead at the time of consumption, the former is assumed (see below).

Beach-stranded jellyfish are quite quickly consumed by a variety of marine and terrestrial scavengers including whelks of the genus *Bullia,* as well as ghost crabs (*Ocypode cursor* Supplementary Figure 3B), whilst sea anemones will devour smaller species that drift too close to the seabed (Supplementary Figure 3C). Observations of beach-stranded jellyfish at Lüderitz have revealed a variety of coastal seabirds feeding on both *Chrysaora fulgida* and *Chirodropus gorilla*. Although the gonads of both these jellyfish species are the main target (Supplementary Figures 3D, E), smaller birds like sanderlings (*Calidris alba*) are attracted to the associated hyperiid amphipods (Supplementary Figure 3F).

Associations with fish

Approximately 70% of the pelagic catches (69% by biomass) of the bearded goby *Sufflogobius bibarbatus* made by the fishing industry off Namibia over the period 1990–2007 (n = 11324) also included jellyfish (Utne-Palm et al. 2010; Table 4). Either the bearded goby and jellyfish have a very similar distribution across the shelf, at the scale of the catch, or the bearded goby chooses to associate with jellyfish. Unlike most gobies, *Sufflogobius bibarbatus* has retained a swim bladder and displays DVM (Utne-Palm et al. 2010). It has been hypothesized that when bearded gobies move up into the water column at night in order to "re-oxygenate" their blood and digest their stomach contents (they have spent daylight in hypoxic bottom water, feeding and avoiding predators), they may deliberately associate with jellyfish (Utne-Palm et al. 2010). This strategy would serve to reduce predation pressure, as choice chamber experiments seem to suggest that bearded gobies are indifferent to the presence of jellyfish (*Chrysaora fulgida*), whilst some potential predators (*Trachurus capensis*) actively avoid them (Utne-Palm et al. 2010). At the same time that gobies use jellyfish as refugia, they may also be using them as a food source.

The data shown in Table 4 reveal that there is little in the way of microscale overlap in the distribution of *Trachurus capensis* and jellyfish. And less than 25% of small pelagic fish catches (anchovy, sardine and red-eye round herring) are also caught with jellyfish suggesting either a deliberate attempt at avoidance of jellyfish by skippers or a real difference in microscale pelagic habitat use. Unsurprisingly, there were no differences in the weight of goby catches with or without jellyfish, but interestingly, catches of sardine and anchovy were almost 50% bigger when they co-occurred with jellyfish (Table 4). This level of overlap between jellyfish and small pelagic fishes is one of the main reasons why applications to fish for jellyfish off Namibia have been rejected: the risk of a significant sardine or anchovy by-catch is incompatible with efforts to regrow pelagic fish stocks.

A spatial and dietary overlap between jellyfish and small pelagic fishes in other EBC systems (see below) has led to concerns that competition between the two groups may occur. The isotopic comparisons generated by van der Bank et al. (2011) suggest that *Aequorea forskalea* feed at the same trophic level as anchovy and small horse mackerel ($\delta^{15}N \approx 12‰$; Iitembu et al. 2012), whilst *Chrysaora fulgida* feed at the same trophic level as sardine ($\delta^{15}N \approx 9‰$; Iitembu et al. 2012). Anchovy and small horse mackerel feed predominantly on meso- and macro-zooplankton (James & Findlay 1989, Kadila et al. 2020), whilst sardine will switch between phytoplankton and mesozooplankton, depending on ambient prey densities (van der Lingen 1994, van der Lingen et al. 2006).

Using historical fisheries and survey data (1991–2011), Tjizoo (unpublished) noted a spatial separation of *Chrysaora fulgida* and horse mackerel off Namibia: the former occurring mostly in cool water (<15°C) off central Namibia, while the latter were more common in warmer waters further north. Data seem to suggest that horse mackerel are more broadly distributed over the shelf relative to *Chrysaora fulgida*, which is confined to waters less than 100 m bottom depth. As adult horse mackerel adopt to mesopelagic and demersal zones with maturity (Barange et al. 2005), *Chrysaora fulgida* only overlap spatially with juvenile horse mackerel that inhabit coastal epipelagic zones. Isotopic data indicate pronounced trophic overlaps between *Chrysaora fulgida* and juvenile horse mackerel, as they feed at the same trophic level (2.5). It has been suggested that this difference in environmental preference allows the spatial co-existence of horse mackerel and *Chrysaora fulgida* in the northern Benguela ecosystem.

Fisheries and human activities

Estimates of pelagic fish biomass in South Africa and Namibia are usually derived from multi-frequency hydroacoustic surveys. Despite the fact that acoustic target strength estimates have been determined for *Chrysaora fulgida* and *Aequorea forskalea* (Brierley et al. 2001, 2004, 2005) and that algorithms have been developed to discriminate between jellyfish and pelagic fishes, these tools are not regularly employed by fisheries management authorities.

Research trawls off central Namibia regularly capture *Chrysaora fulgida* in such quantities that repairs to nets are required. And this after trawls of short duration. And "as noted by Venter (1988), the high biomass of jellyfishes in the late 1970s had become a nuisance to fishermen and interfered with fishing operations in the region by clogging and damaging nets" (Roux et al. 2013, pp. 253).

Whilst jellyfish have yet to cause any blockages of the intake pipe for the desalination plant just north of Swakopmund in Namibia, *Chrysaora fulgida* has forced the temporary closure of the nuclear power plant at Koeberg, just north of Cape Town in South Africa. The plant, which is operated by ESKOM, is the only nuclear power station on the African continent and first became operational in mid-1984. At full capacity, the plant can deliver 1940 MW to the national grid, its two pressurized water reactors requiring 80 m^3 seawater s^{-1} to do so. Although the plant is provided with a specially constructed intake basin, this became inundated by extensive jellyfish blooms in May 2005 and March 2020, which blocked the drum filters causing temporary shutdowns to power generation.

Macromedusae in ecosystem models

A number of foodweb models have been constructed in the Benguela region since the late 1990s, generally distinguishing the southern Benguela off South Africa and the northern Benguela off Namibia and southern Angola due to the perception that many commercial fish stocks were distinct between the two sub-regions and because of different fisheries management history and regimes. With the exception of the models presented in Heymans et al. (2004) which combined jellyfish in a single "zooplankton" group, the other models contained an aggregated "*gelatinous zooplankton*" functional group. However, the parameterization of the models around the jellyfish functional group was made through untested assumptions due to a complete lack of data or estimates on the most important parameters concerning this group (biomass, growth, diet, consumption rates, predation, survival, etc.). It should also be noted that some of these early models (Heymans 1996, Heymans and Baird 2000a,b) erroneously assumed a jellyfish diet dominated (84.1%) by phytoplankton, which resulted in a misrepresentation of this functional group in the foodweb. It is now accepted that most of the biomass of gelatinous zooplankton in the region is composed of *Aequorea forskalea*, *Chrysaora fulgida* and other planktivorous carnivores.

The next series of foodweb models were also designed using the ECOPATH approach (Christensen & Pauly 1992) and were constructed similarly for the southern and northern Benguela. These models were aimed at highlighting gaps in knowledge about some potentially important functional groups and describing the trophic flows around the main commercially exploited fish stocks. The overall intention was to use these models to open the way for a possible multispecies approach of fisheries management in the Benguela region (Jarre-Teichmann et al. 1998, Shannon & Jarre-Teichmann 1999). In the absence of empirical data on jellyfish in either sub-systems, those models assumed a jellyfish biomass of one million t in the southern Benguela and five million t in the northern Benguela. These assumptions of wet mass were then converted to carbon (assuming 98%–99% water content and a conversion factor of 0.4 for dry mass to carbon). The diet was partitioned equally between phytoplankton, detritus (bacteria), micro- and mesozooplankton (25% each). Production over biomass (for tissue) was assumed to be half that of the estimate for macro-zooplankton, while other parameters were assumed to be similar to that of macro-zooplankton. With very little information on predators of jellyfish in the Benguela region, the inevitable conclusion of these modelling exercises showed that jellyfish seem to have a relatively unimportant role, with a very low "ecotrophic efficiency", in the trophic flows of those two sub-systems. However, the potential competitive interactions with small pelagic fishes (sardine and anchovy in particular) were highlighted in both studies, as well as caution regarding the interpretation of these preliminary results, due to the very high level of uncertainty surrounding the assumed parameters concerning the jellyfish functional group.

By using both ECOPATH models built for different time periods and dynamic simulations within the models (ECOSIM, Walter et al. 1997), as well as more up-to-date information about jellyfish, we have highlighted some possible important changes in the northern Benguela foodweb since 1970 (e.g. Roux & Shannon 2004, Watermeyer et al. 2008). In comparison with other EBC systems, the structure of the present northern Benguela ecosystem is exceptional, being characterized by a very low biomass of small pelagic fish and a very high biomass of jellyfish (Moloney et al. 2005, Shannon et al. 2009). These studies have emphasized an increase in pelagic-benthic coupling in the northern Benguela, by comparing both with other EBC systems and that of the northern Benguela prior to the sardine collapse. The structural change that accompanied the collapse of small pelagic fish collapse and the increase in jellyfish biomass was a probable redirection of flows away from predators in the pelagos (marine mammals, seabirds and predatory fish) to the benthos and detritus. This led to a drop in the efficiency of the major trophic pathways supporting the dominant commercial fisheries. These possible changes in the trophic structure of the northern Benguela have been supported by most time series of trophodynamic indicators (e.g. Cury et al. 2005). It must be noted that the linkages between jellyfish and other functional groups in these models were still not well understood, and there was a wide uncertainty in the parameterization and dynamics of the models with regard to jellyfish (Roux & Shannon 2004, Shannon et al. 2009).

A more recent study by Roux et al. (2013) supports the hypothesis that the overfishing of sardine resulted in the collapse of the stock in the northern Benguela, which triggered an increase in jellyfish in this system. This comparative study of the southern and northern Benguela combined commercial fisheries data, trophodynamic indicators, predator diet and energetic information, as well as foodweb modelling outputs over more than four decades (Roux et al. 2013). The resulting changes in the foodweb structure were found to be profound and indicated a possible alteration to the wasp-waist trophic control structure of the ecosystem. In the latter, abundant populations of small pelagic fishes as the main and efficient energy conduit from producers to higher trophic levels and exert a top-down trophic control on producers (plankton) and a bottom-up trophic control over higher trophic levels (e.g. Cury et al. 2000, Shannon et al. 2000, Cury & Shannon 2004). The altered state of the northern Benguela ecosystem, which includes a dominance of jellyfish in biomass on the other hand, seems to be characterized by an increased pelagic-benthic coupling, an increased flow to detritus and a reduced efficiency of energy transfer towards higher trophic levels.

Based on our present understanding of the regional ecosystem, jellyfish could have been a major contributing factor in the dramatic changes observed in the northern Benguela, together with the sardine stock (e.g. Roux et al. 2013). However, there are many gaps in the basic data that prevent us from fully understanding the trophic interactions that led to these changes. Priority should be given to refining both biomass estimates (and investigating possible seasonal variability) and the basic parameters to be used in foodweb models (diet composition, growth parameters, consumption and assimilation rates, predation, survival, etc.). Incorporation of these missing data in foodweb models should allow a better understanding of the role of jellyfish in the foodweb and the past and present changes in their dynamics. The likely results are expected to be essential for an improvement in the scientific advice aimed at an application of an ecosystem approach to fisheries management in the region.

The Humboldt ecosystem

Description

The Humboldt Current System is the most productive eastern boundary upwelling system in terms of fish productivity and is one of the most productive ecosystems in the world ocean; it supports one of the largest single-species fisheries (Peruvian anchovy *Engraulis ringens*) (Chavez et al. 1999, 2008, Pennington et al. 2006). The system is the equatorward flowing, eastern portion of the basin-scale southeast Pacific anticyclonic gyre. The Humboldt Current system extends from southern Ecuador and the Galapagos Islands (~1°S), where cold upwelled waters are limited by warm tropical waters of the equatorial front, to southern Chile (~42°S) where water masses are bounded by the West Wind Drift (Thiel et al. 2007). The Humboldt Current system is bounded by the meridionally oriented coastline of South America and a narrow continental shelf (Figure 12).

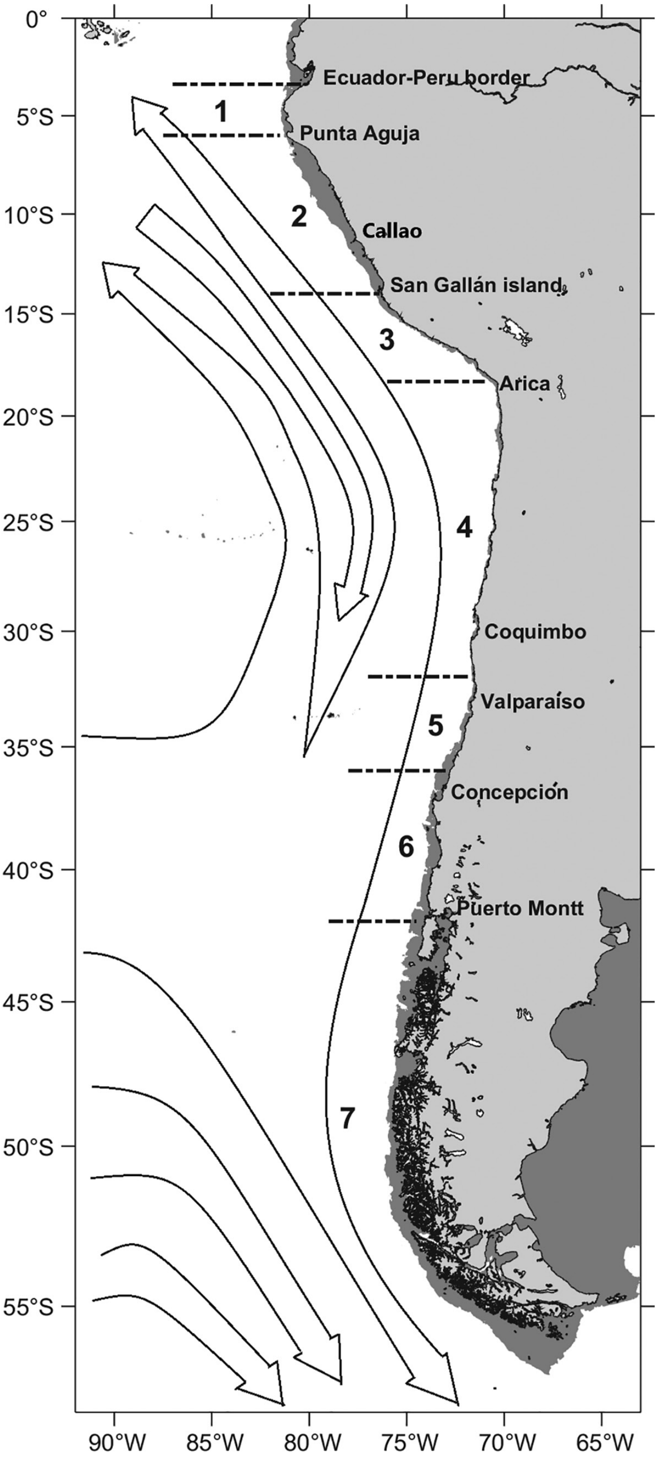


Figure 12 Outline map of western South America showing the approximate positions of the major coastal currents in the Humboldt system: the continental shelf is shaded. The numbers (1–7) refer to distinct latitudinal regions that are discussed in the text.

The width of the Peruvian continental shelf is variable and is in direct relation to the geodynamics of the shelf break: it can be divided into three latitudinal areas (Figure 12). In the north (area 1 in Figure 12), from the Ecuador–Peru border (3°23′S) to Punta Aguja (6°S), the continental shelf is relatively narrow and the shelf break is parallel to the coastline. The shelf-width varies between 6 and 60 km offshore until Máncora (4°05′S), and almost disappears between Cabo Blanco (4°15′S) and Punta Pariñas (4°40′S) before widening again (25–35 km) to Sechura Bay (5°45′S). In the central region (area 2 in Figure 12), between Punta Aguja and San Gallán Island (14°S), the shelf is relatively wide between Pimentel (6°50′S) and Chimbote (9°03′S) (100–130 km offshore), and then, it narrows towards the south between Huarmey (10°S) and Callao (12°S) (55–75 km offshore). In the south (area 3 in Figure 12), between San Gallán and the Peruvian–Chilean border (18°20′S), the shelf break is particularly narrow and can be found between 10 and 25 km offshore (Schweigger 1964, Teves & Evangelista 1974, Morales et al. 2020).

The Chilean coast can be divided into four latitudinal regions. North of ~32°S (area 4 in Figure 12) the shelf is extremely narrow (<10 km offshore) and receives little freshwater influence; between 32 and 36°S (area 5 in Figure 12), there is a widening shelf with low and scattered river inflow; and from 36 to 42°S (area 6 in Figure 12), the shelf is wider (~70 km offshore) and is seasonally influenced by freshwater inflow, and the southern region (>42°S; area 7 in Figure 12), which has a wider topographically complex, fjord-indented coastline and experiences strong river runoff (Figueroa 2002, Riascos et al. 2009). Offshore, the continental shelf, the deep canyons associated with river basins and the Atacama Trench off the Peruvian–Chilean coast play an important role in biogeochemical cycles, which may be highly sensitive to climatic change (Thiel et al. 2007, Aguilera et al. 2019).

Three key features distinguish the physical and chemical conditions of the Humboldt Current system among EBC systems. First, it extends closer to the equatorial line than any other major EBC system. Second, there is an intense and extremely shallow oxygen minimum zone (OMZ) – a thick layer of water whose upper limit is located at a few tens of metres below the surface, and where oxygen concentrations are so low that, except for bacteria, few species can adapt or temporarily survive (Chavez et al. 2008, Bertrand et al. 2018). Third, the Humboldt Current system is the region where the effects of El Niño and La Niña phases of El Niño-Southern Oscillation (ENSO) are most notable (Chavez et al. 2008). These last two features are expected to change in a warming climate. Model projections and observational data suggest a deoxygenation trend and an intensification of coastal upwelling-favourable winds in poleward portions in EBCs under future climate scenarios (e.g. Levin 2018). In turn, climate projections show that extreme El Niño and La Niña episodes are likely to occur more frequently with unabated greenhouse gas emissions (Cai et al. 2015, Wang et al. 2019). Evidence is emerging that changes in ENSO behaviour have occurred, with El Niño episodes differing substantially in their spatial pattern, intensity and impact. Canonical Eastern Pacific episodes display strongest surface thermal anomalies in the far eastern equatorial Pacific, whereas peak ocean warming occurs further west during Central Pacific episodes sometimes referred to as "El Niño Modoki". The latter type has become more common in recent decades relative to past centuries, a trend that is projected by some studies to continue with ongoing greenhouse warming (Freund et al. 2019). Furthermore, climatic regimes and marine ecosystem functioning in the Humboldt Current system are being modified by a wider array of ocean and land-based human activities, including pollution, resource harvesting, increased nutrient input, habitat destruction and ocean sprawling (Gutiérrez et al. 2016, Halpern et al. 2008, Riascos et al. 2019).

The South Pacific High represents the main forcing for equatorward upwelling-favourable winds in the Humboldt Current system, which display considerable spatial and temporal variability. The following is a brief description of this variability, which has been analysed in detail by Thiel et al. (2007). North of ~35°S winds remain upwelling-favourable throughout the year up to ~5°S, where the seasonal north–south migration of the Inter-Tropical Convergence Zone brings winds and precipitation, thus favouring the stratification. Three provinces of maximum alongshore wind stress can be identified in this zone (Thiel et al. 2007, Gutiérrez et al. 2016). The most productive province is located off Peru, where strong offshore Ekman transport creates a coastal productive belt that ranges between 100 and 200 km with an average annual primary production rate of 1.2 $kg{\cdot}C{\cdot}m^{-2}{\cdot}yr^{-1}$. In Peru, this high primary productivity supports a fishery at least 20 times greater in landings than other similar upwelling boundary current ecosystems worldwide (Bakun & Weeks 2008). Off central Chile (centred at ~30°S), the mean annual primary production rate is over 1 $kg{\cdot}C{\cdot}m^{-2}{\cdot}yr^{-1}$, with a strong seasonal fluctuation. The northern Chilean coast is a narrow (<50 km) productive province, with annual primary production rate of 0.66 $kg{\cdot}C{\cdot}m^{-2}{\cdot}yr^{-1}$ and low seasonality. South of ~35°S, seasonality in the influence of the South Pacific High promotes an alternation between summer upwelling maximums and winter conditions characterized by poleward, downwelling-favourable winds driven by storms associated with the polar front (Shaffer et al. 1999, Rutllant et al. 2004). Moreover, coastal stratification imposed by freshwater runoff becomes important even during summer upwelling conditions (Atkinson et al. 2002).

Off Peru, primary production during winter is negatively correlated with upwelling favourable winds intensity, which seems explained by the light limitation imposed by deeper wind mixing, while in summer, the decreased upwelling strength allows periods of thermal stratification that foster phytoplankton blooms (Gutiérrez et al. 2016). Periods of decreased upwelling strength – associated with warmer SST – off Peru are concomitant with decreases in the larger size fraction of phytoplankton (i.e. chain-forming diatoms) at seasonal and interannual scales (Ochoa et al. 2010). Off northern Chile, the highest primary production is associated with microphytoplankton mostly restricted to a narrow inshore zone, whereas pico- and nanophytoplankton predominate offshore, with little seasonal fluctuations. Off central Chile, primary production is associated with upwelling-favourable winds, which predominate during the spring and summer months. Phytoplankton assemblages proliferating off the Chilean coasts are mostly dominated by no more than 10 species of chain-forming diatoms (Thiel et al. 2007).

In terms of biomass, the zooplankton community in the Humboldt Current system is dominated by large copepods and euphausiids (Thiel et al. 2007, Ayón et al. 2008, Aronés et al. 2019). Off Peru, the continental shelf is dominated by *Acartia tonsa* and *Centropages brachiatus*, but species composition and biomass vary on short time scales due to advection and interspecific interactions. Upwelling intensity drives seasonal variability of zooplankton biomass and composition, while ENSO represent a major driving force for community changes at interannual scales (Ayón et al. 2008). Off the Chilean coast, the zooplankton community is dominated by two species endemic to the Humboldt Current system (*Calanus chilensis* and *Euphausia mucronata*), several cosmopolitan species and a typical tropical species (*Eucalanus inermis*) (Marín et al. 1994, Hidalgo & Escribano 2001). The OMZ interacts with zooplankton that typically aggregate near upwelling centres (Escribano & Hidalgo 2000); epipelagic species concentrate in surface waters without exhibiting DVMs, but some euphausiids may temporarily enter this zone, and some copepods may even inhabit this zone (Antezana 2002, Escribano 1998, Hidalgo et al. 2005)

Industrial fisheries in the northern Humboldt Current system developed in the mid-twentieth century, and there is some indication that the recent time period represents a period of exceptional productivity in relation to that of the last thousand years (Chavez et al. 2008, Gutiérrez et al. 2009, Salvatteci et al. 2018). The main landed species are the Peruvian anchovy, the Chilean jack mackerel (*Trachurus murphyi*), the jumbo flying squid (*Dosidicus gigas*), the common sardine (*Strangomera bentincki*), the Pacific chub mackerel (*Scomber japonicus*) and the Pacific sardine (*Sardinops sagax*) (Gutiérrez et al. 2016). At present, the Peruvian anchovy represent the main pelagic fish resource in the Humboldt Current system (84% and 34% of fish landings composition off Peru and Chile, respectively) in comparison with the Pacific sardine (26% of fish landings in Chile) for the period 2009–2013 (Gutiérrez et al. 2016). A regime shift has long been proposed between an anchovy-dominated state and a sardine-dominated state in the Humboldt Current system, related to long-term ENSO-related variations in oceanographic conditions and mediated by the availability of prey items (Alheit & Niquen 2004, Espinoza & Bertrand 2008, Ayón et al. 2008). A reconstruction of the ENSO in the Holocene (10,000 years) showed that ENSO variance was close to the modern level in the early Holocene and severely damped ~4000–5000 years ago. The modern ENSO regime was established ~3000–4500 years ago, being sensitive to changes in climate boundary conditions during the whole Holocene (Carré et al. 2014). Recent studies based on fish scale remains suggest that shifts are related to upwelling-dependent habitat changes driven by regional and large-scale forcing (Salvatteci et al. 2018). However, climate change may shift the system out of its current productive state; global models predict a moderate decline in catch potential between 2050 and the end of the century (Cheung et al. 2018).

Owing to competitive trophic interactions between jellyfish and forage pelagic fish and projected physical changes under expected greenhouse-associated warming in the Humboldt Current system, Bakun et al. (2010) predicted that overexploitation of small pelagic fishes would define the balance between a fish-dominated state and a much less desirable jellyfish state. As some of the most important fish resources in the system are either collapsed, overexploited, fully exploited or unmanaged (Gutiérrez et al. 2016), we are left with the message that there is much to learn yet about jellyfish in the Humboldt Current system.

Macromedusae

Species composition

The last census of cnidarians carried out around the coasts of Latin America (Oliveira et al. 2016) shows that the most important macromedusae recorded in the Humboldt Current system are the scyphozoans *Chrysaora plocamia*, *Pelagia noctiluca* (Family Pelagiidae), *Phacellophora camtschatica* (Family Phacellophoridae), *Aurelia* sp. (Family Ulmaridae), *Stomolophus meleagris* (Family Stomolophidae) and an unidentified Lobonematidae, as well as the large Hydromedusae *Aequorea coerulescens*, *Aequorea forskalea*, *Aequorea globosa* and *Aequorea macrodactyla* (Family Aequoreidae). In addition, some deep-water species have been recorded including *Atolla chuni*, *Atolla wyvillei* (Family Atollidae) and *Periphylla periphylla* (Family Periphyllidae).

In the Humboldt Current system, the most common and abundant species, particularly during spring and summer, is *Chrysaora plocamia* (Supplementary Figure 4). This species is abundant between Punta Falsa (6°S) in northern Peru to Antofagasta (23°40′S) in northern Chile, a distance exceeding 2400 km (Mianzan et al. 2014, Quiñones et al. 2018). It is less commonly found southwards along the Patagonian shelf to the southern tip of Chile (55°S). On the Atlantic Ocean coast, this species is also present in northern Patagonia (Mianzan et al. 2014).

Unpublished reports and by-catch information from IMARPE indicate that *Pelagia noctiluca* is mainly distributed in the offshore waters off Peru, although it may occur at the Peruvian coast in low numbers and even occasionally in the coastal waters of northern Chile. *Phacellophora camtschatica* has been recorded only along the northern coast of Peru between Paita (5°S) and Punta Guañape (8°27′S) and mainly in oceanic waters (IMARPE, unpublished data). In Chile, this species has been collected from near-surface, neritic waters between 18 and 43°S (Fagetti 1973, Kramp 1952, 1968). Moon jellyfish *Aurelia* sp. have been recorded off Sechura Bay in Peru (5°19′S, 81°16′W: L. Caccha personal communication), and in southern Chile from 53°S to ~55°S in the Patagonian interior waters (Häussermann et al. 2009, Pagès & Orejas 1999, Palma et al. 2014). The rhizostome jellyfishes *Stomolophus meleagris* and *Versuriga* sp. have been reported from stranding events in northern Peru (between ~3 and 9°S), but neither has been documented as occurring off Chile.

Several species of the large hydrozoan genus *Aequorea* have been recorded in the Humboldt Current system. These species occur in relatively low numbers in coastal and offshore waters. Medusae of *Aequorea coerulescens* have been registered from 3°30′ to 43°S (Fagetti 1973, Kramp 1966, 1968, Palma et al. 2011), *Aequorea forskalea* occurs from 37 to 52°S (Kramp 1957), *Aequorea globosa* is found south of Concepción Bay (Chile) at 38°8′S (Fagetti 1973, Kramp 1966) and from

41°30′S to 43°38′S along the Chiloé Interior Sea (Palma et al. 2011), and *Aequorea macrodactyla* has been reported from 18°30′S to 55°50′S (Fagetti 1973, Kramp 1965, 1968, Pagès & Orejas 1999).

Distribution

Space There is limited information from incidental catches from the scientific cruises carried out by IMARPE to survey fisheries resources. These surveys indicate that *Pelagia noctiluca* is more abundant in waters offshore of the shelf break between Punta Sal (4°S) to Islay (17°S), and big blooms have been registered between 7 and 12°S, where they are associated with the presence of Subtropical Superficial Water (SSW). This species has been noted in neritic waters and although it usually occurs in low numbers, a big bloom was observed during autumn 2016 some 10 km offshore of Puerto Morin (~8°30′S), which was coincident with a Modoki – El Niño event with sea surface anomalies of 2.2–2.7°C above the historic record (NOAA 2020) and with a strong eastward intrusion of SSW.

Most of the information about the distribution of macromedusae in the region applies to *Chrysaora plocamia*. Throughout its range in the Humboldt Current system, *Chrysaora plocamia* is patchily distributed (Oliveira et al. 2016, Palma et al. 2014), although abundances are much higher off Peru than off southern Chile (Mianzan et al. 2014). It is difficult to disentangle the effect of time on distribution as distribution (and abundance) varies considerably between climatic periods (e.g. El Niño vs. La Niña scenarios), which reflects the species' response to changes in the environment (Quiñones et al. 2018).

During El Niño years, both the spatial distribution and abundance of *Chrysaora plocamia* are expected to increase (Quiñones et al. 2015). Such years are accompanied by very weak winds, which produce little mixing and lead to a highly stratified water column with a deep thermocline. Cold, nutrient-rich bottom waters do not outcrop at the surface and phytoplankton communities are dominated by small and motile cells that in turn favour small zooplankton: a seemingly perfect environment for *Chrysaora plocamia* (Figure 13A). Massive blooms of this species have been observed in pelagic waters of the northern Humboldt Current system between 6 and 18°S and within 75 km of the coast (extending to 280 km offshore) during the early stages of strong El Niño years such as 1982/1983 and 1986/1987 (Quiñones et al. 2018) (Figure 14). When El Niño SST anomalies become stronger, there is a southward migration to between 14 and 18°S, and it is assumed that this southward migration could reach to Antofagasta (~23°S).

During neutral (or slightly warm) years, *Chrysaora plocamia* occurs at high abundances only in neritic waters (Figure 13B). Such was observed in 2014, when *Chrysaora plocamia* was restricted to the nearshore zone within 35 km from the coast and mainly between 6 and 14°S. Neutral years are characterized by a local relaxation of upwelling, which leads to reduced mixing and waters with a low concentration of nutrients; phytoplankton communities are dominated by flagellates and dinoflagellates. Although the effects of these altered environmental conditions on the growth and survival of *Chrysaora plocamia* are unknown (Figure 13B) (Quiñones 2018), they are clearly not favourable to large extensive populations.

During La Niña years, *Chrysaora plocamia* appears to be absent in pelagic coastal and offshore waters (Figure 13C), but persists below the thermocline in the subsurface waters of semi-enclosed areas. Such was observed in 2007 and 2013. The environment is characterized by strong coastal winds, leading to high levels of turbulence and a well-mixed water column rich in nutrients that leads to abundant large phytoplankton but few micro-gelatinous organisms and small zooplankton, which limits the growth and survival of *Chrysaora plocamia* and relegates them to subsurface shallow and semi-protected areas like Independencia Bay (14°14′S).

Space-time Medusae of *Chrysaora plocamia* are present in the water column of the Humboldt Current system for between 9 and 10 months of the year, from mid-winter until late autumn or early winter. Off southern Chile not a single individual was captured during winter surveys of 2006 (Palma et al. 2011) or 2007 (Bravo et al. 2011). Off southern Argentina (42–46°S), post-ephyra and

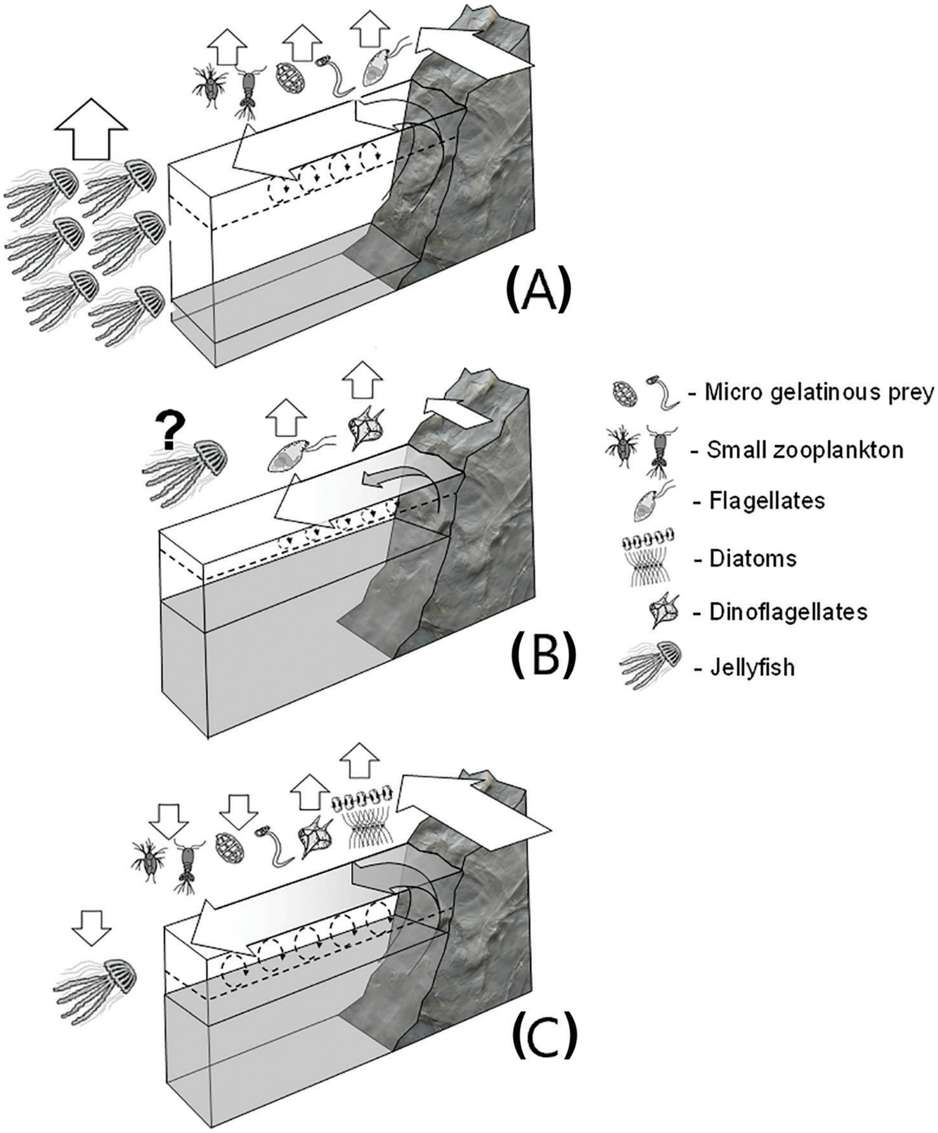


Figure 13 Diagram of the variability in the productivity of the northern Humboldt Current system at inter- and intra-annual level. The thermocline is represented by the separation between the light and the shaded layer; the shaded layer represents cold, nutrient-rich waters below the thermocline. The coastal wind strength is represented by the width and size of the white arrow parallel to the coast. The mix layer in the water column is represented by the cut line and eddies. The Ekman degree of transport is represented by the white line perpendicular to the coast. (A) Typical "El Niño" year with high productivity of *Chrysaora plocamia*, (B) neutral period with uncertain productivity of *Chrysaora plocamia*, (C) typical cold year or "La Niña" with low production of *Chrysaora plocamia* (adapted from Ochoa et al. 2010).

juveniles have been observed in spring (Mianzan 1989), sexually mature individuals were found between summer and autumn, and a few senescent, damaged and decomposing individuals have been noted in late autumn (Mianzan et al. 2014, Schiariti et al. 2018).

Data suggest that moving southwards through the Humboldt Current EBC system, *Chrysaora plocamia* becomes more temporally restricted in appearance. Sighting surveys conducted in

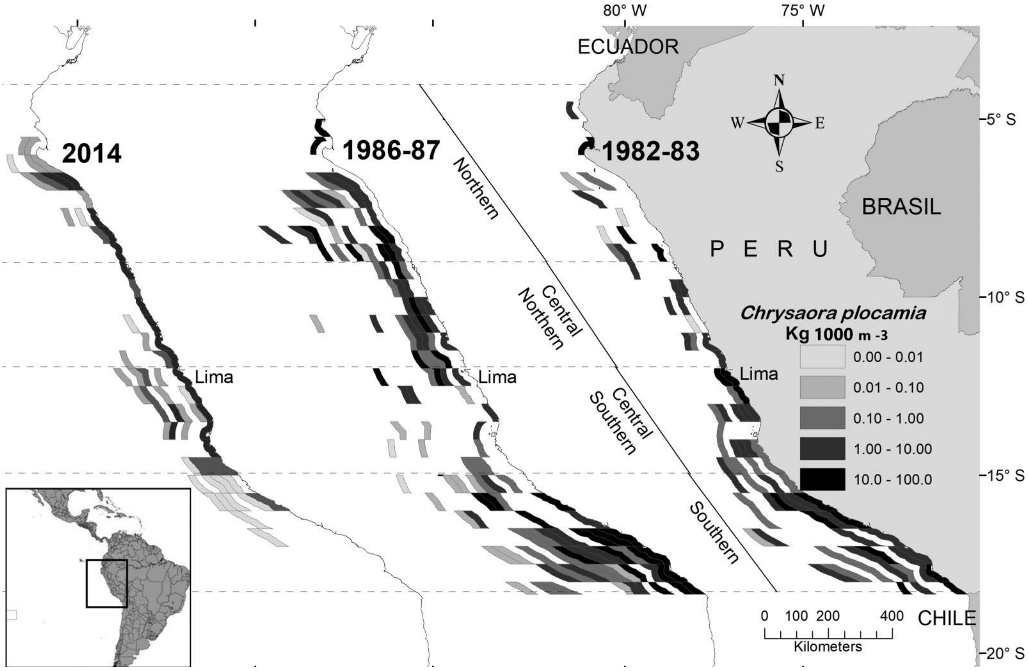


Figure 14 Spatial biomass distribution of *Chrysaora plocamia* by iso-paralitoral areas during El Niño years (1982–1983, 1986–1987) and during a neutral year (2014). Abundance is expressed in kg 1000 m^{-3}.

Independencia Bay (14°14′S) suggest that *Chrysaora plocamia* is most abundant and animals are most conspicuous (largest) during summer and autumn (Table 5A, Figure 15), and this agrees with the results of by-catch surveys in the artisanal purse seine fishery in the same area (Table 5B). Off Mejillones Bay (~23°S) in northern Chile (Figure 16), *Chrysaora plocamia* is mainly found between November and January (summer), while in central Chile, sightings of *Chrysaora plocamia* are restricted to summer; off southern Chile its appearance is transient, with densities of up to 93 individuals 1000 m^{-3} during spring (Palma et al. 2011). Mass die-offs of *Chrysaora plocamia* have been observed in Peru during early winter on two occasions: in Bahia Independencia (14°20′S) in 2012 and in Puerto Eten (06°30′S) in 2018 (Quiñones unpublished data). During these events, dead and dying specimens accumulated at the seafloor and this suggests that the majority of the population dies after sexual reproduction, mainly during autumn or early winter (Decker et al. 2014). It is important to note that adult *Chrysaora plocamia* have been recorded in the middle of winter, but only on two occasions (2012 and 2018), implying that overwintering in Peru is an unusual occurrence.

As noted above, the abundance of *Chrysaora plocamia* is strongly influenced by the state of the climate. The results of an IMARPE study conducted over a 42-year period from 1972 to 2014

Table 5A Seasonal changes in the number of sightings of *Chrysaora plocamia* the water column in Independencia Bay, during 2004–2007

Season	Number of stations with jellyfish	Total number of sighted jellyfish	Jellyfish area (km^2)
Spring	48	474	3.82
Summer	127	1045	22.43
Autumn	73	610	10.29
Winter	3	7	0.07

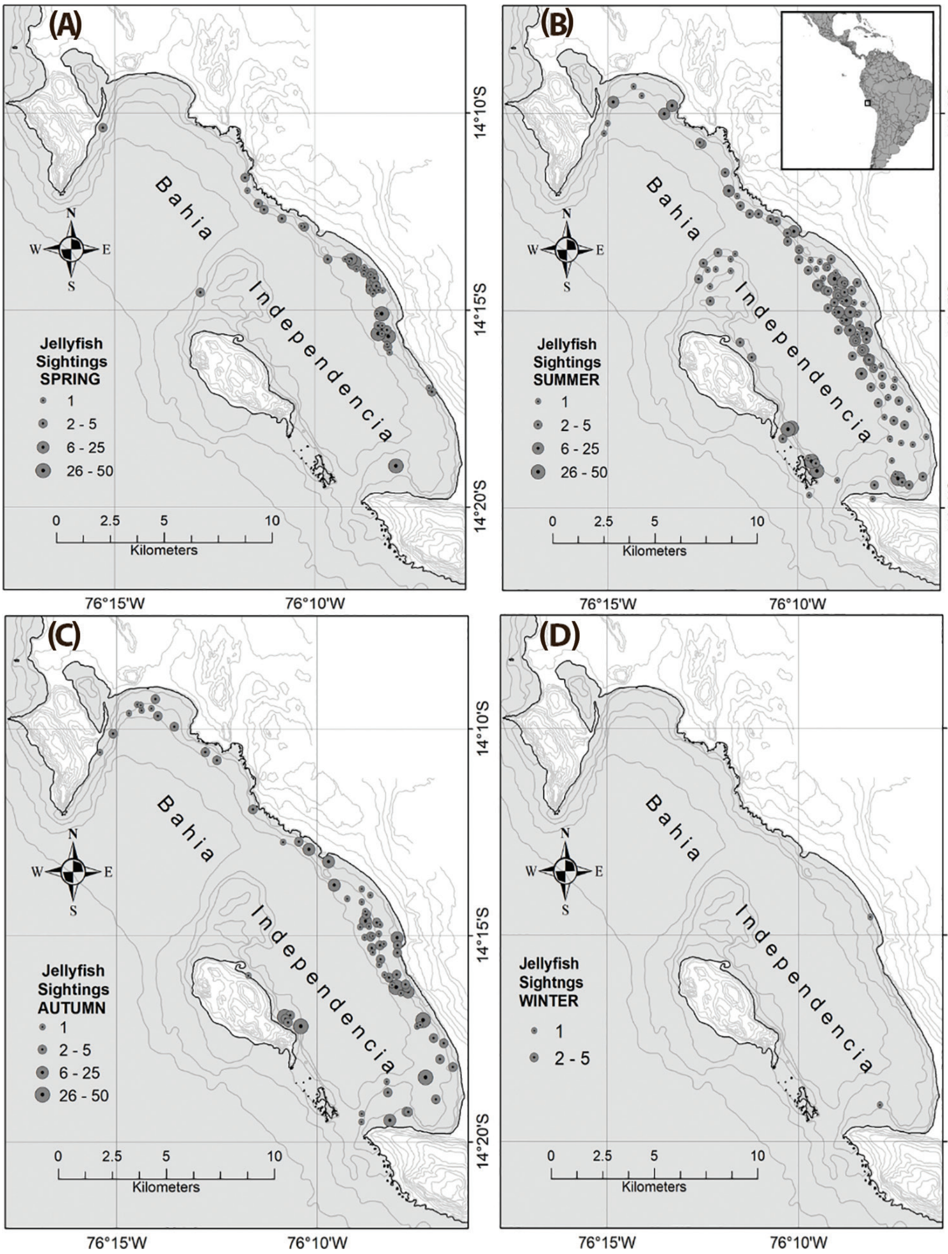


Figure 15 Seasonal changes in the abundance of *Chrysaora plocamia* in Independencia Bay, central Peru (pooled data for 2004–2007). Open circles represent scuba diving sightings in the water column, and size of the circle means abundance per sighting (Quiñones unpublished).

indicate that between 1972 and 1989, abundances were highly variable, ranging from (averages of) zero to 12 kg 1000 m^{-3}. A dramatic decrease was noted early in the second period (1989), and jellyfish were extremely rare or absent for the next 20 years. However, a small increase is recorded at the end of the time series (2009–2014: see Figure 2 in Quiñones et al. 2015). The pattern of two distinct periods coincides with warm–cold interdecadal fluctuations known as the El Viejo and La Vieja regimes (Chavez et al. 2003), respectively. Both regimes are visualized in the Regimen Indicator

Table 5B Jellyfish (*Chrysaora plocamia*) by-catch (kg jellyfish 1000 m^{-3} of filtered seawater) in the artisanal purse seine fishery of Pisco (Oct 2016–Sep 2017)

Season	Mean captures	Standard error	Total numbers of hauls
Spring	0.00498	0.0028	798
Summer	0.05378	0.0129	643
Autumn	0.00291	0.0014	950
Winter	0.00021	0.0001	991

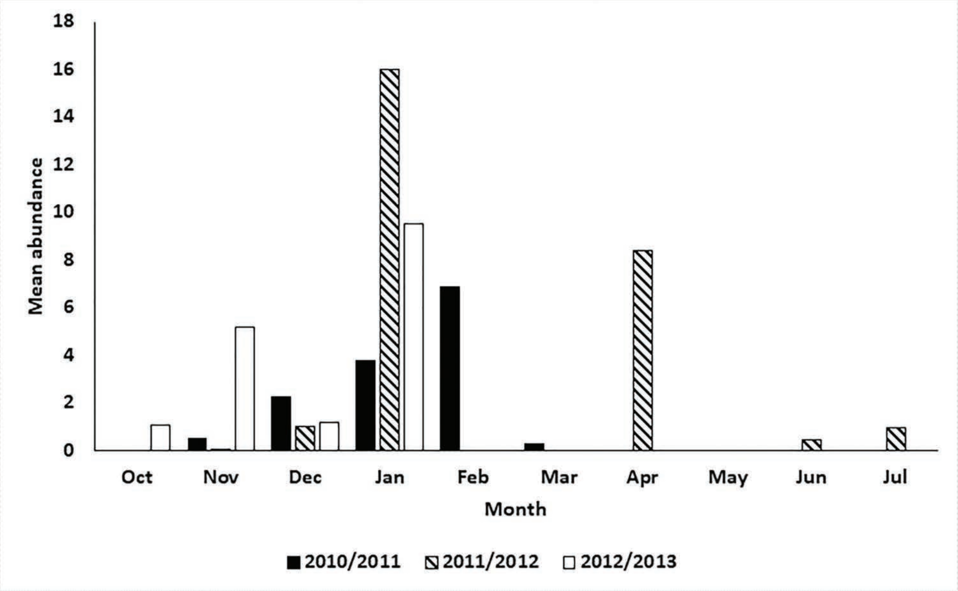


Figure 16 Monthly changes in the abundance (individuals per sighting) of *Chrysaora plocamia* in Mejillones bay between 2010 and 2013. Estimations are based on between 45 and 55 sightings performed by scuba divers in surface waters (max 15 m water depth) (Riascos unpublished).

Series (RIS3) (Kamikowski 2012), which shows a positive regime between the early and mid-1970s to the early 1990s, and then a negative regime between the 1990s and 2000s. This same pattern is evidenced in anchovy catches and fishing effort, with reduced landings noted during the El Viejo warm regime (positive RIS3 values) and increased landings during the La Vieja regime (negative RIS3 values; Quiñones et al. 2015).

In the northern Humboldt Current system, medusae tend to be small during spring, and then grow and mature through the following seasons to attain maximum size in autumn (Figure 17). It is assumed that a single seasonal cohort is produced around mid-winter, although additional cohorts may be generated during spring. No small individuals have ever been seen during summer or autumn, implying that strobilation only occurs during late winter and spring (Quiñones unpublished data). Considering that Figure 17 represents seasonal changes in body sizes over several years' worth of measurements, it must be assumed that most of the adult population consistently dies by the end of autumn. Off Mejillones Bay in northern Chile, by contrast, there is a suggestion that some large, sexually mature medusae may appear during October–November (Figure 18), and these likely represent overwintering adults from the previous year (Ceh et al. 2015). Thereafter,

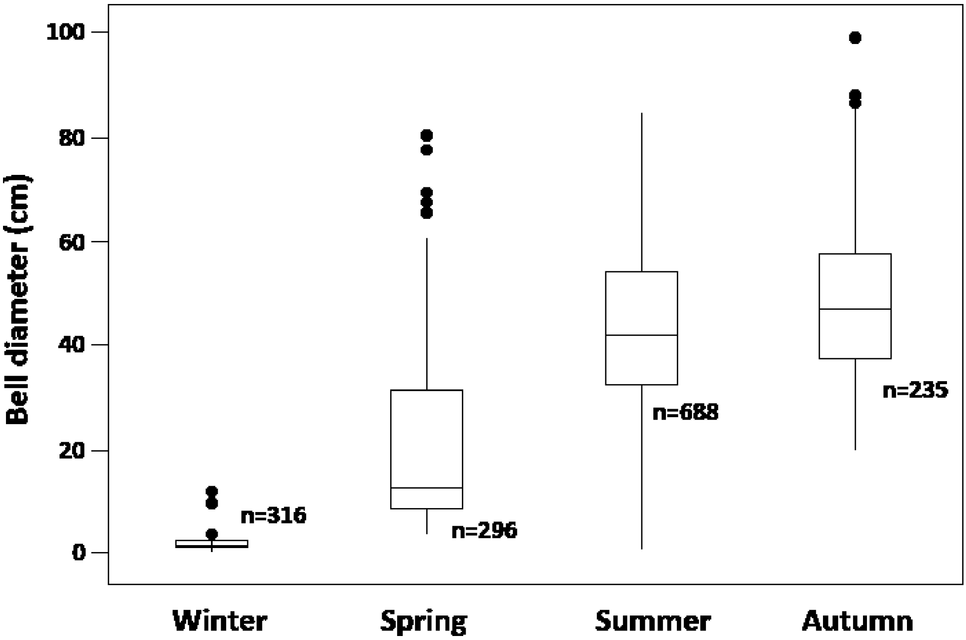


Figure 17 Boxplot of seasonal changes in bell diameter of *Chrysaora plocamia* off central Peru, from years 2007–2009 to 2012–2018 (No jellyfish were reported in 2016/2017). Lines within boxes represent the median, boxes represent the upper and lower quartiles and error bars represent the highest and lowest observed values. Small open circles represent outliers (Quiñones unpublished).

there is consistent decrease in body size, reflecting the protracted mortality of large medusae and possibly the recruitment of juvenile medusa by the end of summer (Ceh et al. 2015).

Biomass, growth and mortality

Biomass The length–mass relationship for *Chrysaora plocamia* was studied by Cáceres (2012) from individuals collected in two periods (2010/2011 and 2011/2012). These data are shown in Supplementary Table 1A. Although there are no region-wide estimates of jellyfish biomass, the biomass of *Chrysaora plocamia* was determined off the coast of Peru (from Punta Sal at ~4°S to the border with Chile, ~18°S) during a pelagic survey by IMARPE in summer 2009. The main objective of the cruise was to estimate the biomass of the Peruvian anchoveta, using multi-frequency hydroacoustics (SIMRAD EK60 echo sounder), which were supplemented with pelagic trawls and a Remotely Operated Vehicle. Echoview was employed to process the acoustic data collected and distribution was interpreted by kriging interpolation: biomass was determined from isoparalittoral stratification using areas of 10×30 nm (Simmonds & MacLennan 2005). The measurements of TS were carried out *in situ* when catches were comprised exclusively of *Chrysaora plocamia*. At a frequency of 120 kHz, target strength values between -84.9 and −66.15 dB were obtained (average −75.9 dB) for animals with a bell diameter of between 30 and 78 cm, and at a frequency of 38 kHz, the target strength values ranged between −84.8 and −63.0 dB (average −73.81 dB).

The distribution of *Chrysaora plocamia* was purely coastal and extended up to 12 nm offshore between Paita (5°S) and Punta Caballas (15°S). In the interior of Bahia Independencia (14°20′S), slightly smaller individuals with lower target strength values were recorded. At the 120 kHz frequency, biomass was estimated at 448,351 t with a confidence limit of 25.11%, while at the 38 kHz frequency, it was estimated at 382,153 t with a limit of 17.82%. Almost the entire abundance was found between 0 and 10 nm from the coast. Latitudinally, the largest biomass was located in the

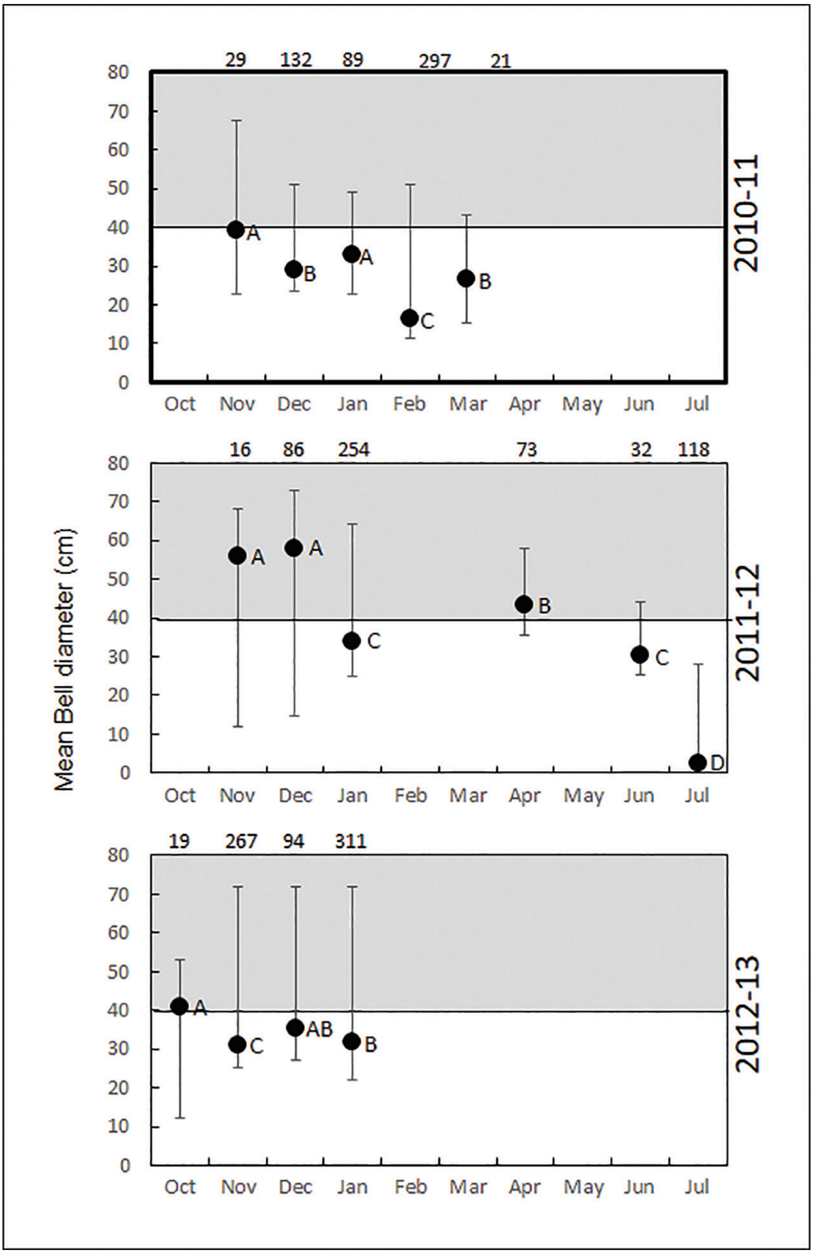


Figure 18 Monthly changes in mean body size of *Chrysaora plocamia* medusae during three years. Error bars show the maximum and minimum size. The black horizontal line represents the body size above which all animals were expected to be sexually mature. Different capital letters indicate significant differences between months (post hoc comparisons, Tukey-Kramer HSD). Numbers above panels represent the number of animals sampled (after Ceh et al. 2015).

area between Salaverry (8°S) and Callao (12°S). In general, the estimated biomass is an average of 410,000 t (biomass estimate of anchoveta ~8.2 million t) with the highest densities compared to Chancay and between Chimbote–Huarmey. The total extension area of *Chrysaora plocamia* during summer 2009 was 5410 km^2 (Castillo & Quiñones unpublished data).

Growth, mortality and longevity Estimates of growth rate for *Chrysaora plocamia* in Peru are lacking, although juvenile medusae grow rapidly from winter until summer, when most of the population consists of adult, sexually mature medusae (bell diameter: 40 cm; Ceh et al. 2015: Figure 18). Broadly similar results have been noted off Peru: the smallest individuals were noted in winter (mean 1.5 cm, $n = 316$), and these increased progressively through spring (mean 20.5 cm, $n = 296$) to reach a maximum in summer (mean 43.5 cm, $n = 688$) and autumn (mean 48.6 cm, $n = 235$) (Quiñones unpublished data).

Given the unusual dynamics of the *Chrysaora plocamia* population in Mejillones Bay, classical approaches to estimate the parameters of the von Bertalanffy growth function (i.e. modal progressions from length–frequency distributions) are not applicable. Therefore, Cáceres (2012) used the overall pooled length frequency distribution (Figure 19) for each year, which was subjected to

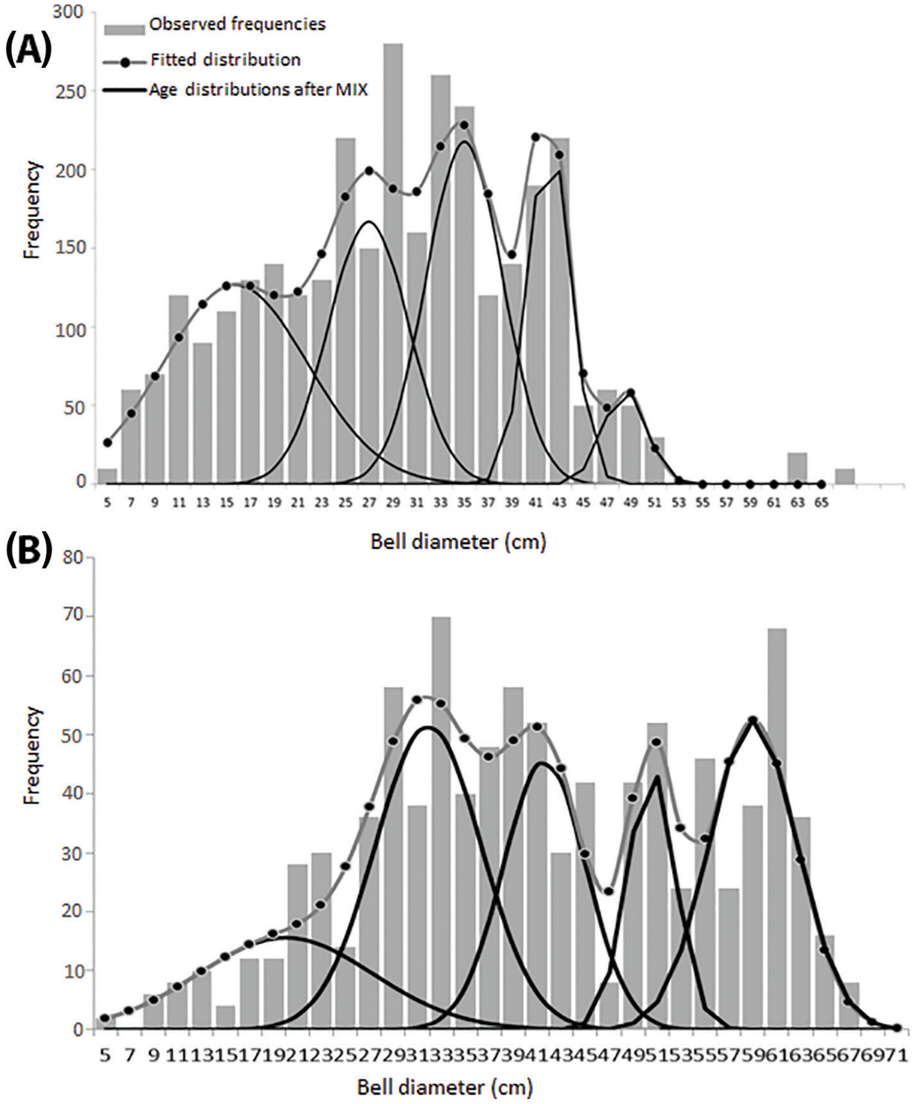


Figure 19 Pooled length–frequency distributions of *Chrysaora plocamia* for the season 2010/2011 (A) and 2011/2012 (B) with the fitting distribution from distribution mixture analysis and the resulting normal distributions of age groups (after Cáceres 2012).

distribution mixture analysis (Macdonald & Pitcher 1979) to decompose the mixture of age/length distributions into their separate components. These analyses indicated a slow growth ($K = 0.96$ yr^{-1}; $L_\infty = 80$ cm) for the year 2010–2011 and a faster growth ($K = 1.28$ yr^{-1}; $L_\infty = 80$ cm) for the year 2011–2012. For the same periods, total mortality (Z) was estimated by Cáceres (2012) using the single negative exponential model and a length-converted catch curve method (Pauly 1983) from pooled length frequency data. These estimations (Figure 20) indicated a much higher mortality for the first season (2010/2011), which was attributed to the higher abundance of *Chrysaora plocamia* during this season. Results on growth and mortality may also reflect interannual differences in climatic regimes in the area; the season 2010/2011 was characterized by strong, cold La Niña conditions in eastern Pacific in comparison with the season 2011/2012. Locally, these conditions may translate in increased upwelling strength and thus colder temperatures and increased food availability that may explain the combination of lower growth and higher abundance observed during this season.

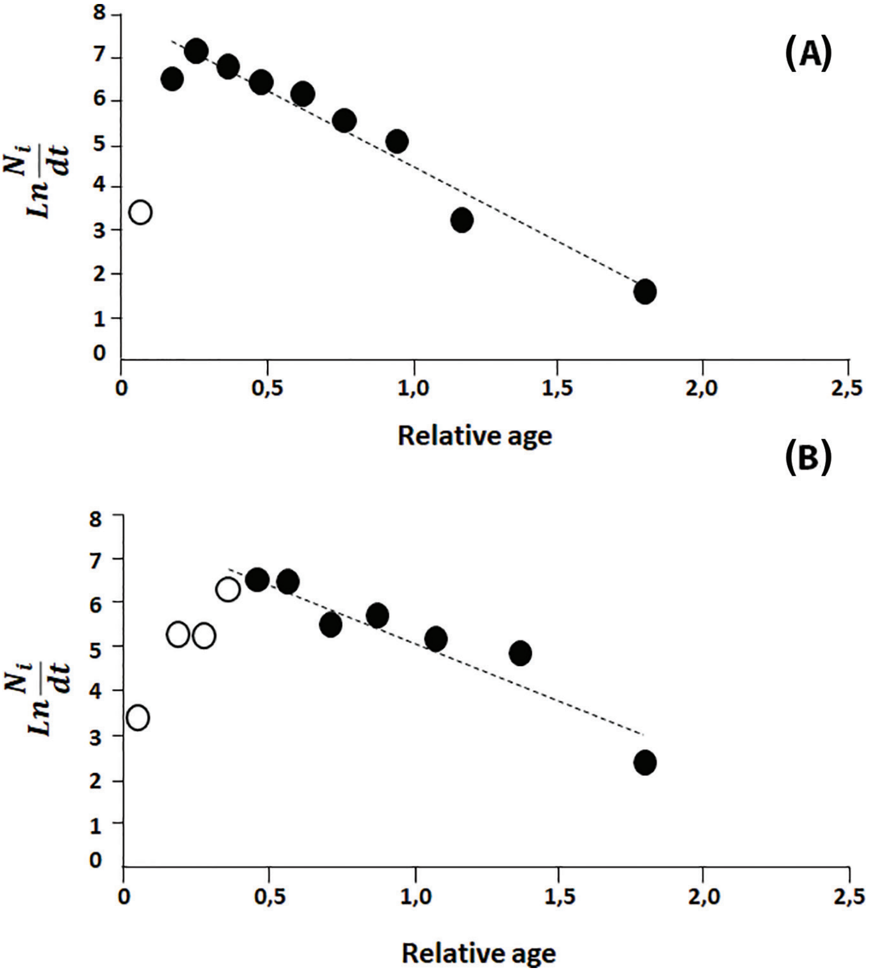


Figure 20 Estimations of total mortality for *Chrysaora plocamia* from length-converted catch curves for the season 2010/2011 (A) and 2011/2012 (B), based on pooled length–frequency data and the von Bertalanffy growth parameters. N_i is number in size class i, dt is the time required to grow through this size class. Filled data points used for regression, open data points excluded from regression. (A) $y = -3.498x + 7.969$, $r^2 = 0.945$, $Z = 3.498$; (B) $y = -1.993x + 7.516$, $r^2 = 0.887$, $Z = 1.993$.

Reproduction

Sexual Although a description of the full life cycle of *Chrysaora plocamia* is still pending (but see Morandini et al. 2013), it displays the typical metagenetic life cycle of most scyphozoans. *Chrysaora plocamia* is dioecious and presents no evident sexual dimorphism. Morandini et al. (2013) reported that mature medusae of *Chrysaora plocamia* may be caught in Ilo, southern Peru (17°S) during early November. Ceh et al. (2015) showed that sexually mature medusa (bell diameter ≥40 cm) occurs through the year when medusae are present in northern Chile, suggesting asynchronous reproduction.

Brood planulae are found within the long and spiralled oral arms and gastric cavity of fertilized females, and laboratory studies show that larvae will settle on available glass and plastic substrates from four to five days and metamorphose into whitish polyps. The settlement of planulae is influenced by temperature, suggesting that thermal anomalies observed during El Niño and La Niña affect the performance of settlement (Riascos et al. 2013a). Interestingly, it also appears that settlement is influenced by substrate colour, which may enhance polyp survival (Ceh & Riascos 2017).

Asexual No polyps of any Discomedusae have been observed *in situ* in the Humboldt region. Hitherto unpublished observations by Morandini and Schiariti at the University of São Paulo (São Paulo, Brazil) and INIDEP (Mar del Plata, Argentina) indicate that polyps reproduce asexually mostly by means of podocysts. Lateral budding has been also observed but only occasionally. Strobilation is polydiscal with the formation of a variable number of ephyrae (from 5 to 20) apparently depending on the size of the polyp. Although no specific studies have been performed, strobilation is regularly observed in cultures kept in darkness under constant conditions of temperature (20°C) and food supply (fed with newly hatched *Artemia* nauplii once weekly).

Riascos et al. (2013a) performed laboratory experiments to test for the effects of temperature on the performance of scyphistomae (polyps), observing that anomalous temperature regimes associated with El Niño-La Niña cycle, had a negative effect on somatic growth and survivorship of polyps of *Chrysaora plocamia*. This suggested that these fundamental processes perform better within the species-specific or even population-specific thermal tolerance limits related to their respective “normal” seasonal range of temperature.

The ephyrae (1–2 mm diameter) of *Chrysaora plocamia* have been described by Morandini et al. (2013) as translucent and have a purplish coloration; nematocyst warts can be found on the exumbrella at the base of each lappet. Fed a diet of scallops (*Nodipecten* – well let’s face it who wouldn’t!), the development of ephyrae/juvenile medusae is relatively fast and the first eight tentacles develop in just in two weeks at temperatures between 20 and 22°C; secondary tentacles appear after three to four weeks, and medusae reach a diameter of 5 cm in 45 days (Morandini et al. 2013). Detailed studies of ephyrae in plankton samples have not been undertaken in the region, although as noted previously they are assumed to be released during winter.

Interactions with other species and human activities

Diet

The dietary preferences and trophic roles of macromedusae in the Humboldt Current system is limited to the most abundant and conspicuous species of this system: *Chrysaora plocamia*. Using traditional gut content analysis, Riascos et al. (2014) counted and classified prey items found in the gastric cavities of 68 *Chrysaora plocamia* medusae (Bell diameter: 7–47 cm) collected from Mejillones (23°S, northern Chile) during summer (November 2010) and spring (March 2011). Their findings indicate that holoplanktonic crustaceans and fish eggs and larvae are the major components of the diet (from 52% to ~96%). Aller (2018) analysed the gut content of 35 adults (bell diameter: 23–65.5 cm) of *Chrysaora plocamia* from south-central Peru (Bahía Independencia, 14°S) during a warm El Niño episode and found that prey items comprised mostly zoea larvae (81%) and fish eggs

(6%, Mugilidae). It is important to highlight that these differences could be related to different environmental conditions, because while the Chilean study coincided with periods when SST anomalies were negative (–1.3°C), the Peruvian one was associated with positive anomalies (+1.9°C). In addition, these results could be related to a spatial component in prey availability. Despite the small scale of the studies conducted, the results provided by Aller (2018) show that *Chrysaora plocamia* are capable of feeding on a wide prey spectrum depending on environmental or biological factors.

Our knowledge of the dietary patterns of *Chrysaora plocamia* could be biased due to the fact that medusae have been collected only in surface waters during daytime. There is evidence to suggest that *Chrysaora plocamia* may be able to exploit both pelagic and benthic resources, reflecting unrecognized life-history traits (see Riascos et al. 2015). A diverse assemblage of benthic and benthic-emergent prey items has been noted in the gut of *Chrysaora plocamia* medusae, which could reflect the overwintering of adult medusa near the seafloor (Ceh et al. 2015). Alternatively, given that animals were sampled from a relatively shallow area (~50 m), it has been suggested that the vertical movements of predator and/or prey as well as the suspension of prey by bottom currents may contribute to the observed results (Ceh et al. 2015).

Parasitism

The hyperiid amphipod *Hyperia curticephala* has been described associating with medusae of *Chrysaora plocamia* in the Paita Bay (northern Peru) and Mejillones Bay (northern Chile) (Oliva et al. 2010, Riascos et al. 2015). Riascos et al. (2015) reported a high number of amphipods per host (median = 388; range 112–993). Associations between hyperiid amphipods and medusae are complex and vary greatly in timing, in the degree of host dependence (shelter and/or food) and the extent of maternal care (Gasca & Haddock 2004). The presence of small portions of mesoglea in the gut contents of all amphipods dissected by Oliva et al. (2010) suggests that *Hyperia curticephala* uses *Chrysaora plocamia* not only as substrate in the pelagic realm, but also as a food source (Oliva et al. 2010). Interestingly, this hyperiid was also observed parasitising medusae of the hydrozoan *Aequorea* sp. during the months when *Chrysaora plocamia* was scarce (April).

Another parasitic association has been documented by Riascos et al. (2013b) involving *Chrysaora plocamia* medusae and the sea anemone *Peachia chilensis*. These authors studied temporal patterns of parasite intensity biomass and the distribution pattern of parasites among hosts and found that the percentage of medusae harbouring larval actinians was high, fluctuating from 100% in November to 67% in March. They also observed that the host size is correlated with the intensity of infestation only in certain months suggesting that when parasite loads are high, space or other resource within the host may impose limits for further increases in parasite load. Riascos et al. (2013b) concluded that the parasite-induced host mortality and reduction of fecundity, represented by parasitic castration, are restricted to a few hosts and are therefore under the expected levels that characterise the dynamic equilibrium of host–parasite systems (Riascos et al. 2013b).

Predation

There is little empirical evidence of jellyfish predation in the Humboldt Current system. That said, *Chrysaora plocamia* forms part of the diet of some sea turtle species (Hays et al. 2009) and three of the five turtle species reported in Peruvian waters feed specifically (leatherback turtle, *Dermochelys coriacea*), or at least opportunistically (green turtle, *Chelonia mydas agassizii*, and olive ridley, *Lepidochelys olivacea*), on medusae (Goya et al. 2011, Quiñones et al. 2010). The biomass of medusae appears to be sufficient to support *Chelonia mydas agassizii* in the region (Quiñones et al. 2010).

Although the centrolophid fish *Seriolella violacea* has been shown to eat large quantities of jellyfish (including salps, pyrosomes and ctenophores; Mianzan et al. 2014), it is clear that the amphipods that parasitize *Chrysaora plocamia* are an important food source for the fish too (Riascos et al. 2012). Riascos et al. (2012) observed that juvenile *Seriolella violacea* prey exclusively on the hyperiids and not on their jellyfish host, suggesting that the relationship between fish and jellyfish is a facultative mutualism: juvenile fish obtain food and probably also protection from the medusa, whereas the medusa benefits from parasite removal: *Chrysaora plocamia* is a passive host, and *Seriolella violacea* is an active opportunist. However, this relationship changes to a predator–prey one with increasing fish size because larger fish eat both jellyfish and hyperiids (Riascos et al. 2012). It is interesting to note that when *Hyperia curticephala* parasitises the hydrozoan *Aequorea* sp., the number of hyperiids in the stomach contents of fish was negligible. This suggests that the timing of the association between fish and jellyfish may depend on the opportunities for preying on large quantities of densely aggregated hyperiids, as suggested by Mansueti (1963) for most fish–jellyfish associations.

Humans must also be considered as predators of jellyfish in the Humboldt Current system, because Mianzan et al. (2014) have reported Peruvian artisanal fishermen using the gonads of *Chrysaora plocamia* as bait to catch *Seriolella violacea*. Senescent or dead *Chrysaora plocamia* resting on the seabed have been observed being eaten by a variety of crabs (*Hepatus chilensis*, *Platymera gaudichaudii* and *Canary Currenter plebejus*) in both Independencia Bay and Puerto Eten (~7°S).

Jellyfish are involved in different biological associations other than trophic interactions (e.g. Ohtsuka et al. 2009), and numerous invertebrate taxa utilize *Chrysaora plocamia* as a substrate within the structureless water column. The large bell and conspicuous oral arms may also provide shelter and food for schools of juvenile starry butterfish (*Stromateus stellatus*) (Elliot et al. 1999).

Fisheries and human activities

Off the coast of Iquique (~20°S) in northern Chile, massive strandings of *Chrysaora plocamia* have occurred in the last two decades, and these have had far-reaching impacts on the local economy (Mianzan et al. 2014). The stings caused by jellyfish to bathers have caused the closure of some beaches, with the consequent effects on tourist activity during peak summer periods (January–February) (Mianzan et al. 2014; Riascos unpublished data).

Significant salmon farming operations are located around Chiloe Island in Patagonia, and when large numbers of *Chrysaora plocamia* occur in coastal waters there, the effects to the industry are severe. Such was witnessed between February and June 2002, when a bloom of jellyfish clogged and destroyed the nets of the culture cages, and pieces of jellyfish tissue penetrated the cages to contact and damage fish gills, causing starvation and mortality (Mianzan et al. 2014, Palma et al. 2007).

However, it is with commercial and artisanal fisheries that jellyfish impacts are the greatest. The high productivity of the northern Humboldt Current system supports one of the largest mono-specific fisheries in the world (Chavez et al. 1999, 2008, Pennington et al. 2006), making one of the largest contributions to the world fishery (Bakun et al. 2010). A fleet of >1200 industrial purse seiners operate along the coast at an industrial level (Fréon et al. 2008) and annually capture more than five million t of the Peruvian anchovy *Engraulis ringens* (FAO 2016). As noted previously, the environment of the northern Humboldt Current system is characterized by interannual and interdecadal fluctuations, with *Chrysaora plocamia* being a conspicuous member of the coastal fauna during the summer (Quiñones 2008, Quiñones et al. 2010, 2015). When the distribution of *Chrysaora plocamia* overlaps with that of anchovies (Ganoza et al. 2000, Bertrand et al. 2004), the jellyfish by-catch generates economic losses mainly to artisanal and industrial purse seine fisheries. These incidental catches are particularly problematic during pre-ENSO warm phases when *Chrysaora plocamia* is abundant, since fishermen have many problems finding waters without jellyfish in which to operate.

At broadscales, jellyfish by-catch increases sharply during El Niño periods and other warm events mainly within a warm El Viejo regime (Quiñones et al. 2010, 2015) when a simple fishing operation or set can capture over 100 t of *Chrysaora plocamia*. Economic losses to commercial operations will therefore be much greater in years of high jellyfish abundance, when the volume of jellyfish can be increased by up to 400% (Quiñones et al. 2018).

More locally, the oceanographic dynamics of the Peru–Chile elbow produce insolation warming in the zone between southern (17°S) and northern Chile (20°15′S), whereby very little cloud cover leads to surface warming mainly in spring and summer (Takahashi 2005). These processes are not necessarily linked to El Niño, but rather to Rossby tangential waves (Kiladis 1998), which originate in the central Pacific and propagate to impact the Peru–Chile elbow area. This localized warming, and the ingress of subtropical waters with elevated iodine concentrations, could trigger asexual reproduction of *Chrysaora plocamia* [polyps], which in turn can produce large blooms that can then interact with fishing. When abundant, medusae of this species interact (mainly) with the purse–seine fisheries and have a negative economic impact on the anchovy fishery. For instance, in southern Peru, 4% of the total industrial catch was discounted in the processing plants as a result of being mixed with *Chrysaora plocamia*. When jellyfish by-catch exceeded 40%, the whole catch was discarded, including anchovies. This occurred 13 times in the port of Ilo (17°38′S) with a total discard of ~387 t. When the deduction of USD160 per ton landed (jellyfish and anchovies discarded = 1268 t) was applied, the total estimate exceeded USD200,000 over 35 days with an average loss per boat of USD5 466 (Quiñones et al. 2013). Extrapolating these results, the economic loss for the entire jellyfish season (November–May) (Quiñones 2008) is ~USD1.2 million, with a national annual loss of ~USD7.1 million (Quiñones 2018). This would be a fairly moderate figure if we compare it with other ecosystems in which annual loss values between 10 and 40 million USD have been calculated (Kim et al. 2012, Palmieri et al. 2014). However, these losses are substantial in a country with economic limitations. In Northern Chile, between Arica (18°30′S) and Antofagasta (23°40′S), medusae of *Chrysaora plocamia* can become abundant during summer, and the species is constantly recorded as by-catch in the industrial purse seine pelagic fishery, according to reports of some governmental organisations.

Jellyfish not only interact with industrial fisheries in the Humboldt Current system, but also impact artisanal fisheries, which in Peru are extensive and numerous: there being more than 100 landing points, more than 9500 boats with a total population of 37,000 fishermen (Alfaro-Shigueto et al. 2011). Total landings approximate 500,000 t annually (Alfaro-Shigueto et al. 2010), which are much higher than the industrial landings of many countries (FAO 2016). In one pilot evaluation, carried out only in the port of Pisco (~14°S), a loss of USD27,500 was determined for the entire season of *Chrysaora plocamia*, so theoretically losses of the order of USD2.7 million could occur along the entire Peruvian coast (Quiñones 2018). It should be noted that this estimate was derived during a neutral phase of the Oceanic Child Index (ONI) (see NOAA 2020), when the seasonal abundances of *Chrysaora plocamia* are intermediate (Quiñones 2018). It is expected that economic losses for fishermen would increase significantly during WEs. It should be emphasized that the above cited case studies encompass a relatively short time period, both were pilot studies in artisanal and industrial fisheries; therefore, to estimate the impact that could occur on a larger scale, more studies would be needed and different scenarios should be considered.

Macromedusae in ecosystem models

The pelagic foodweb of the Humboldt Current system, being one of the most productive marine ecosystems in the world, has been modelled extensively using different approaches (e.g. Walsh 1981, Jarre & Pauly 1993, Carr 2001, Neira & Arancibia 2004, Taylor et al. 2008). However, only a few ecosystem modelling studies for this system have included gelatinous zooplankton (e.g. Moloney et al. 2005, Tam et al. 2008, Neira et al. 2014), and just one study have incorporated a macromedusae (*Chrysaora plocamia*) as a functional group (Chiaverano et al. 2018).

Our knowledge of the ecological role of macromedusae in the Humboldt Current system is limited to the large jellyfish *Chrysaora plocamia* in the northern section of the Northern Humboldt

Current System. Using empirical data of biomass (Quiñones et al. 2015) and diet composition (Aller 2017) of *Chrysaora plocamia* from Peruvian waters, Chiaverano et al. (2018) adopted a steady-state trophic model for the northern Humboldt Current system, previously developed by Tam et al. (2008), to quantify the efficiency of macromedusae and forage fish (anchovies and sardines). Their modelled foodweb of the northern Humboldt Current system indicated that forage fish represent the most efficient, direct energy pathway from primary and secondary producers (i.e. phyto- and zooplankton) to top-level consumers, while macromedusae act as an energy-loss pathway, by diverting energy from plankton producers away from higher trophic-level consumers and towards several low and mid-trophic-level consumers, such as planktivorous fish (mostly butterfishes) (Figure 21). Hence, during macromedusae blooms in this system, the total system ecosystem production being transferred upwards in the foodweb is expected to be reduced compared to non-bloom scenarios,

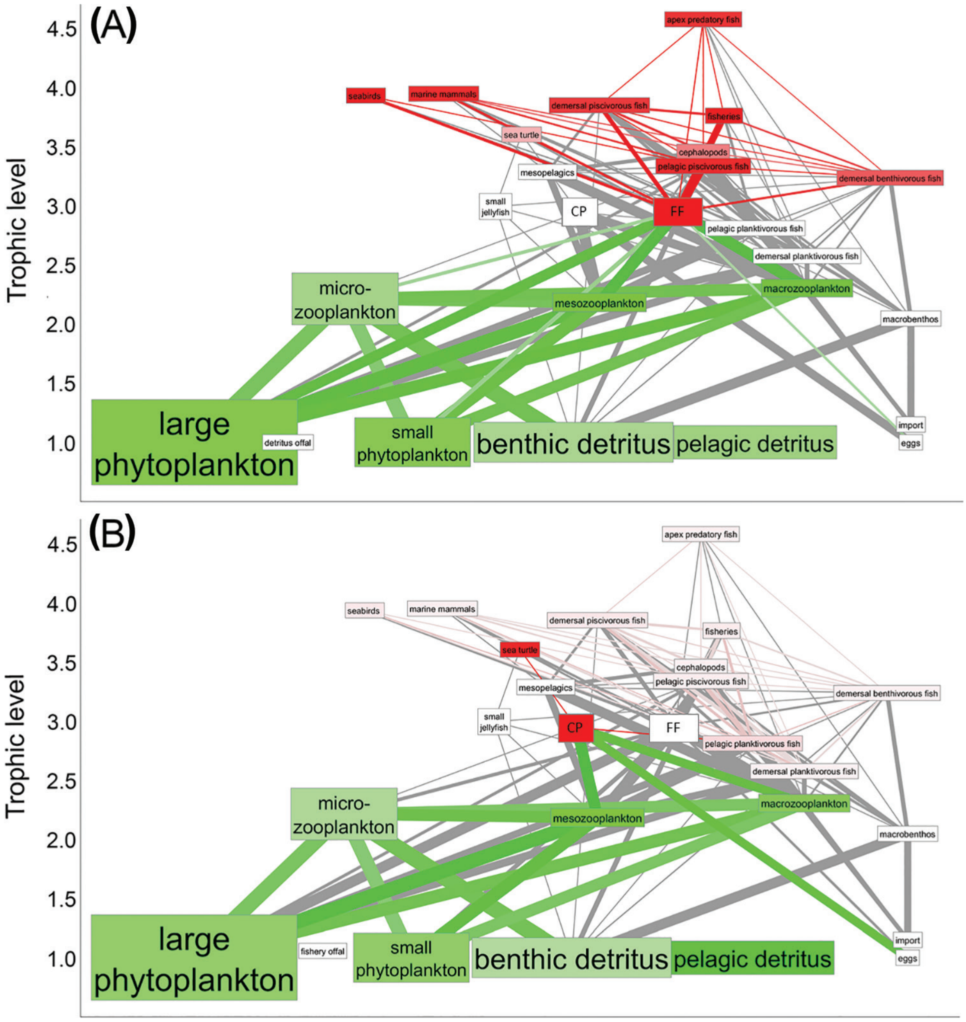


Figure 21 Modelled food web diagrams, highlighting energy flow patterns to (green) and from (red) forage fish (FF, A) and *Chrysaora plocamia* medusae (CP, B) in the Northern Humboldt Current system. Box size is proportional to functional group biomass. Colour intensity and width of lines are scaled to the amount of energy flow between forage fish and large jellyfish and the rest of the functional groups (modified from Chiaverano et al. 2018).

when forage fish dominate. These patterns are in congruency with those observed in the Northern California Current system (Ruzicka et al. 2012), supporting the role of forage fish and macromedusae as energy conduits and production-loss pathways, respectively, in marine ecosystems (Robinson et al. 2014). Interestingly, macromedusae represent a direct energy pathway to sea turtles (mainly leatherbacks) in the northern Humboldt Current system (Figure 21), highlighting the potentially important ecological role of macromedusae in the conservation of endangered, gelatinivorous marine reptiles (Paredes 2015, Quiñones et al. 2015), not only in this area, but in pelagic ecosystems worldwide.

In the northern Humboldt Current system, forage fish, macromedusae and forage fish fisheries appear to be interlinked. Through the use of modelled structural scenarios, Chiaverano at al. (2018) shows that an increase in macromedusae consumption translates into a decline not only in forage fish production, but also in the productivity of almost all mid-trophic- and upper-level consumers, with the exception of sea turtles (Figure 22A). On the contrary, a decline in macromedusae productivity occurs as a result of an increased forage fish consumption (Figure 22B). Forage fish and *Chrysaora plocamia* medusae are known to exhibit diet overlap (Espinoza & Bertrand 2008, Espinoza et al. 2009, Riascos et al. 2014, Ceh et al. 2015, Aller 2017); thereby, during macromedusae blooms, a reduced prey availability to forage fish can have strong subsequent effects throughout the entire ecosystem, considering how important forage fish are at transferring energy through the foodweb.

Interestingly, structural scenarios indicate that fisheries production can also be negatively affected by an increase in macromedusae consumption in this system (Chiaverano et al. 2018) (Figure 21A). This observed effect is likely the product of the negative effect of macromedusae on forage fish productivity, presumably via resource competition (see above). In Peru, forage fish (anchovies and sardines) make up >95% of the country's annual fishery landings, with the Peruvian anchoveta (*Engraulis ringens*) accounting for 99% of total forage fish landings (FAO 2011). For instance, a 37% increase in macromedusae consumption leads a 13% decrease in fisheries production in Peru. Considering that the Peruvian anchoveta fishery is one of the largest fisheries in the world, with an average annual landing of 6.5 million t (FAO 2011 cf FAO 2016), a 13% decrease in productivity of this fishery translate to a decrease in ~845,000 t of fish. During large bloom events in the northern Humboldt Current system, *Chrysaora plocamia* can reach up to a biomass 2.9–6.4 times greater (Quiñones et al. 2015, 2018) than the scenario tested by Chiaverano et al. (2018); thereby, such events are expected to have a much higher negative impact on forage fish production, and consequently, on forage fish fisheries. Future modelling efforts will aim at assessing the effects of such large blooms on fisheries productivity.

Interactions among macromedusae, forage fish and fisheries can potentially have large effects on productivity of upper trophic levels, since a decrease in production of a key functional group like forage fishes can lead to a significant reduction in productivity of seabirds (Cury et al. 2011) and economically important pelagic fish (Pikitch et al. 2014, Smith et al. 2011). We recommend macromedusae to be explicitly included in future ecosystem modelling efforts in ecosystem-based approaches to fishery management of coastal ecosystems worldwide (Brodeur et al. 2016).

The California Current Ecosystem

Description

The West Wind Drift or Subarctic Current flows across the North Pacific and then bifurcates off North America to form the Alaska Current that flows to the north, and the California Current that flows to the south. The California Current extends from southern British Columbia to Baja California, approximately 50–~22°N. The California Current, as it streams equatorward, mixes with oceanic waters and with those from the south, and these water masses are also subsequently

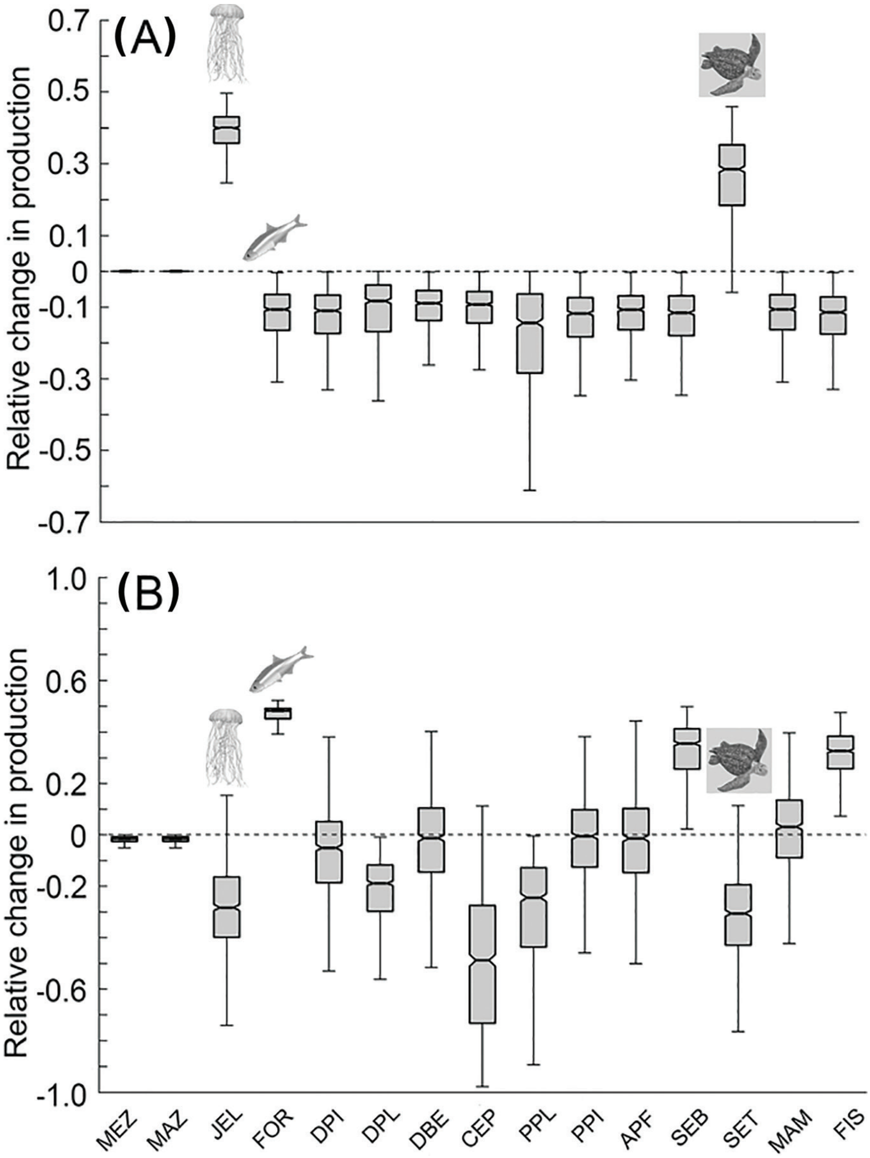


Figure 22 Ecosystem-wide responses to a modelled increased in *Chrysaora plocamia* medusae consumption (37%, A) and a forage fish consumption (50%, B). JEL: *Chrysaora plocamia*, FOF: forage fish, DPI: demersal piscivorous fish, DPL: demersal planktivorous fish, DBE: demersal benthivorous fish, CEP: cephalopods, PPL: pelagic planktivorous fish, PPI: pelagic piscivorous fish, APE: apex predatory fish, SEB: seabirds, TUR: sea turtles, MAM: marine mammals, FIS: fisheries. Box: 25%–75% quartile, whiskers: min–max. Notice different scale in *y*-axis (modified from Chiaverano et al. 2018).

modified by coastal processes such as runoff and upwelling in this EBC. Within the California Current, Checkley and Barth (2009) delineated three geographical regions based on a combination of biogeographic boundaries and wind stress which include (1) the northern region (40–48°N) where wind stress varies from poleward to equatorward, (2) the central region (34–40°N) with the strongest wind stress, mainly equatorward, and (3) the southern region (22–34°N) where wind stress is predominantly to the south (Figure 23).

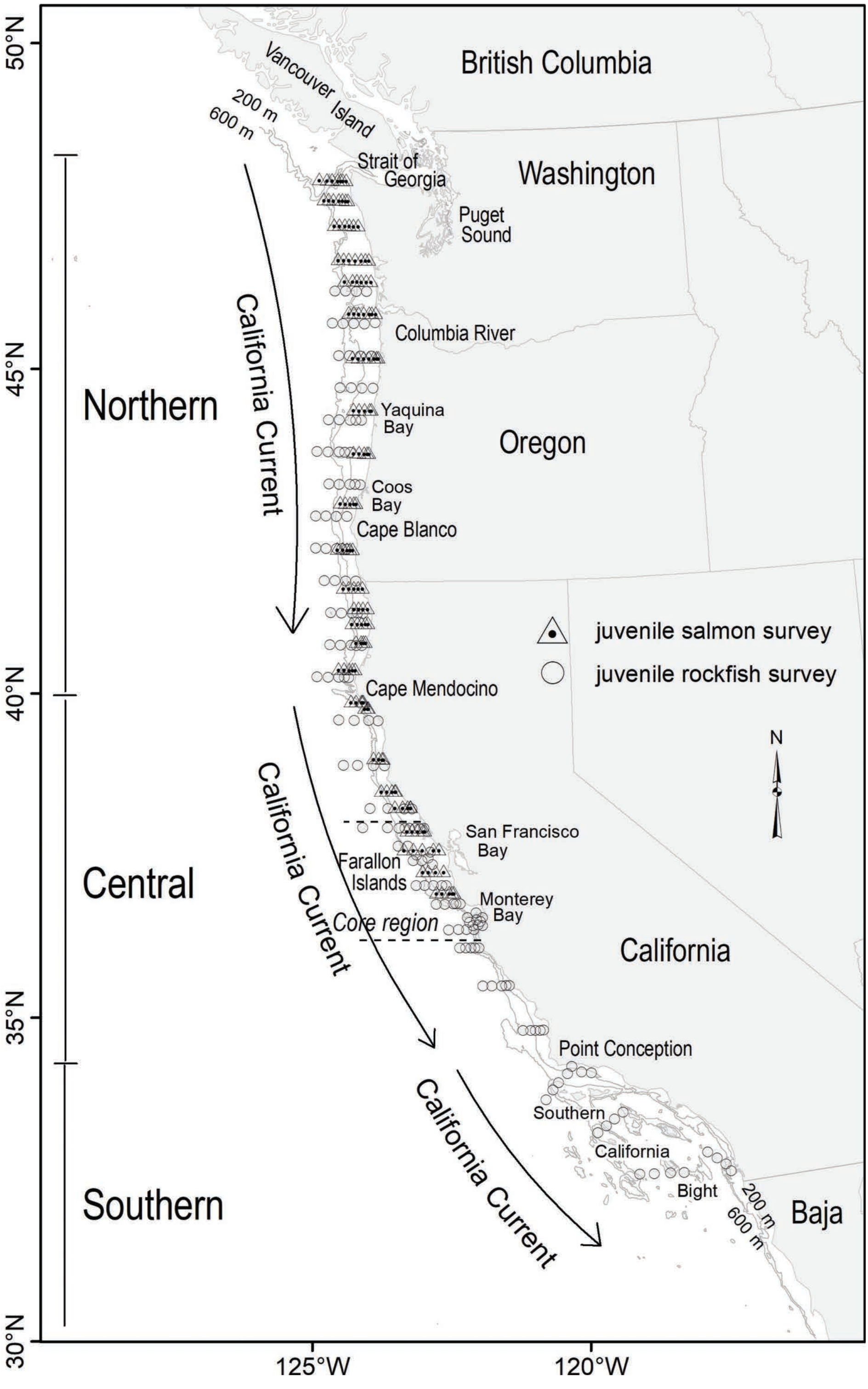


Figure 23 Main geographic features of the California Current showing stations sampled during the main research surveys along with geographic divisions used here.

These transitional regions in the California Current are highly dynamic and ocean conditions fluctuate widely over time and space. The regions have distinct seasonal as well as interannual and interdecadal fluctuations. In the northern California Current region, coastal upwelling is episodic off Oregon during summer, but more persistent off northern California. During the upwelling season, a coastal jet forms and dynamic frontal zones sometimes extend far out to sea. In winter off the Pacific Northwest coast, the California Current either moves offshore or is replaced by the poleward flow of the Davidson Current. The California Undercurrent is a subsurface poleward current generally confined to the continental slope and most intense during the summer (Hickey 1998). During El Niño events, the equatorward flow of the California Current is anomalously weak, and southern water intrusions move into region. Thus, interannual variations in the northern California Current result from both regional- and global-scale processes (Landry et al. 1989, Hickey 1998, Checkley & Barth 2009). Interdecadal fluctuations with periods of 15–25 years have also been documented in the North Pacific and in the coastal transition region (Hare & Mantua 2000). These were based on variations in sea surface temperatures and abrupt changes in the survival or species composition of pelagic animals, such as those which occurred in 1977 and 1989.

The oceanography of the central California Current varies considerably compared to that of the northern California Current (e.g. ocean waters offshore of Oregon and Washington coastlines) in several ways, some of which have relevance to pelagic jellyfish abundance and distribution. In the northern California Current, strongly seasonal upwelling winds during spring and summer and a relatively smooth coastline lead to the development of a strong coastal jet over the continental shelf, with variable but typically strong seasonal upwelling supporting high productivity. As that coastal jet develops around Cape Blanco, Cape Mendocino and other features towards the south, the jet as well as the offshore flow in the California Current begins to exhibit higher eddy kinetic energy, leading to a more complex mesoscale regime of jets, eddies and meanders due to coastal geomorphology and complex bathymetry (McClatchie 2014).

Strong upwelling centres are located adjacent to headlands; important regions of enhanced primary productivity occur downstream of these sites, many of which are characterized by substantial mesoscale (and finer scale) eddy activity and complex circulation patterns (Strub et al. 1991, Steger et al. 2000). Moreover, upwelling centres near headlands influence the production and spatial distribution of phytoplankton in relation to the continental shelf in both onshore–offshore and latitudinal dimensions. For example, within the central California Current, Largier et al. (2006) showed that upwelling centres are characterized by high-nutrient low-chlorophyll waters, with high chlorophyll waters located downstream from the upwelling centre. Furthermore, upwelling "shadows" exist along the coast in the lee of coastal headlands and capes; here, alongshore flow is reversed, and the retained water contains high concentration of chlorophyll and zooplankton (Graham et al. 1992, Graham & Largier 1997, Steger et al. 2000, Largier et al. 2006). These habitats are among the most important habitats for large pelagic Scyphomedusae in this region. In the Gulf of the Farallones, the upwelling shadow includes one of the widest areas of the continental shelf between Cape Blanco, Oregon (43°N) and Point Conception, California (34°30′N), such that there are approximately 50 km between shore and the shelf break in this region, relative to a coastal average closer to 20 km throughout most of the remaining coastline (Steger et al. 2000). Similarly, Monterey Bay is a widely recognized productive region for Scyphomedusae (among other organisms) due to its retentive circulation patterns and complex bathymetry (Graham & Largier 1997, Benson et al. 2007).

Most of the primary production in the California Current is generated by unicellular algae dominated by diatoms especially during upwelling, with dinoflagellates and cyanobacteria in more offshore and nutrient poor waters (Kudela et al. 2008). Grazers upon these phytoplankton are dominated by microzooplankton, copepods, euphausiids, pteropods and other small zooplankton, although in less productive waters, gelatinous forms such as appendicularians, salps and heteropods can become more important (Peterson et al. 2017). The next higher trophic level, microcarnivores, is dominated by micronekton such as larger crustaceans and squid, many larger gelatinous zooplankton including ctenophores, hydrozoans and scyphozoans, along with larval and juvenile fishes (Pearcy 1972, Brodeur et al. 2003). Similar to the other upwelling ecosystems, small pelagic fishes that consume primarily smaller planktonic prey including phytoplankton, copepods, pteropods, decapod larvae and juvenile euphausiids (van der Lingen et al. 2009, Brodeur et al. 2019a) can occur in high biomass (Zwolinski et al. 2012). The ability of small pelagic fishes such as sardines (*Sardinops sagax*) and anchovies (*Engraulis mordax*) to filter feed allows them to pass production on to higher trophic levels relatively efficiently. Finally, these small pelagic fishes and other micronekton become the main prey of a variety of larger pelagic and demersal fishes, seabirds and marine mammals leading to a highly productive marine ecosystem (Ware & Thompson 2005, Field et al. 2006).

Macromedusae

Species composition

One of the first studies to document gelatinous zooplankton from the northern California Current was the review of pelagic animals caught off Oregon from 1960 to 1968 by Pearcy (1972). He lists 33 Hydrozoa, 5 Scyphozoa, 2 Ctenophora, 1 Larvacea and 8 Thaliacea collected. "Coelenterates" had the second highest biomass after Copepoda of all the major zooplankton groups, including even the Euphausiacea, reflecting their importance in this region. Wrobel and Mills (1998) provide an overview of the gelatinous taxa found along the Pacific Coast of North America. Although many Scyphomedusae and Hydromedusae are known to occur in the California Current, we have restricted our coverage to the larger species that occur in relatively high abundances or are caught frequently in larger sampling gears. These include the scyphozoans *Chrysaora fuscescens* and *Chrysaora (Pelagia) colorata* (Family Pelagiidae), *Aurelia labiata* (Family Ulmaridae), *Cyanea capillata* (Family Cyaneidae), *Phacellophora camtschatica* (Family Phacellophoridae) and the large Hydrozoa *Aequorea* spp. (Family Aequoreidae). Representative photographs of these species are shown in Supplementary Figure 5.

In the California Current, early references of the moon jellyfish identified as *Aurelia aurita* are erroneous, and the species records should be regarded as *Aurelia labiata* (Mills & Larson 2007). Gershwin (2001) conducted an extensive morphological review of 17 populations of *Aurelia* from San Diego to Alaska and showed that all populations examined were attributable to *Aurelia labiata* and not *Aurelia aurita*. Mills & Rees (2007) have suggested that the smaller inshore specimens of *Aequorea* are likely to be the Northeast Pacific endemic species *Aequorea victoria*, but a second, larger oceanic species, possibly *Aequorea coerulescens*, may occur in coastal waters on a seasonal basis, and because of our inability to distinguish between the two species of *Aequorea*, we primarily refer to *Aequorea* as *Aequorea* spp. Finally, the main distribution of *Cyanea capillata* is somewhat north of the California Current, and although it is common in marginal seas at the same latitude such as the Salish Sea (Reum et al. 2009), it occurs relatively infrequently and in low abundance in the California Current and will only briefly be discussed in this review. Similarly, the subtropical species, *Chrysaora colorata*, is found only in the warmer regions of the California Current and is not very abundant, and thus much less studied, compared to the other species.

Distribution

Space Shenker (1984) analysed the Scyphomedusae from 263 fine-mesh purse seines made in the surface waters off Oregon and Washington from May through August of 1981. *Chrysaora fuscescens* was the numerically dominant species and occurred in >82% of the collections made, followed by *Aurelia labiata* (24.3%) and *Cyanea capillata/Phacellophora camtschatica* (22.4% combined). Densities of *Chrysaora fuscescens* were highest in a narrow band close to shore, especially during strong upwelling periods (Shenker 1984). *Aurelia labiata* were generally less abundant later in the summer and were found mostly between 10 and 15 km from shore. Pearcy et al. (1985) contrasted similar purse seine collections of gelatinous zooplankton from a strong upwelling year (1982) with that of an El Niño year (1983) and found that the frequency of occurrence of most of the large medusae with the exception of *Aurelia labiata* decreased the second year. Heitstuman (1994) conducted extensive surveys for medusae offshore by SCUBA diving and found few specimens during the 1993 El Niño, but they were more apparent during the more normal summer of 1994.

Extensive fine-mesh surface trawl collections ($n = 365$) from June and August of 2000 and 2002 from Central Oregon (45°N) to northern California (42°N) were characterized for their medusa composition by Suchman & Brodeur (2005). The dominant species caught were the scyphozoans *Chrysaora fuscescens*, *Aurelia labiata* and *Phacellophora camtschatica* and the hydrozoan *Aequorea* spp. The latter species showed the highest frequency of occurrence overall due to its broad cross-shelf distribution, but *Chrysaora fuscescens* and *Aurelia labiata* were substantially more important in terms of biomass especially inshore, whereas *Phacellophora camtschatica* was important only during the August cruise, mainly in the southern part of the sampling area. There were no day–night differences in catch based on some limited diel sampling (Suchman & Brodeur 2005). It was suggested that mesoscale physical features such as eddies and fronts may affect the distribution patterns of these weakly swimming organisms, leading to dense aggregations at convergent zones (Suchman & Brodeur 2005). There also seemed to be some larger-scale habitat partitioning among the dominant jellyfish species, with *Chrysaora fuscescens* being found closer to shore and at the more northerly stations, whereas *Aurelia labiata* were found more offshore and to the south of the sampling area.

Suchman et al. (2012) analysed interannual and seasonal variations in the abundance of large medusae from 1746 surface trawls off Oregon and Washington in the northern California Current over eight years (2000–2007). *Chrysaora fuscescens* and *Aequorea* spp. were caught in a similar proportion of the trawls (42% and 40%, respectively), but the abundance of the former, which peaked later in the summer, was an order of magnitude higher than the latter, which had a June peak in density. *Chrysaora fuscescens* tended to occur mainly at the innermost stations along each transect, while *Aequorea* spp. were more broadly distributed with their centre of abundance further offshore.

In the coastal waters of the central and southern California Current, relatively little focused research has been conducted on large medusae. One of the first accounts for this region have noted that blooms have been historically described as frequent events in this region over time, such as the account of Galigher (1925), who noted “the hordes of jellyfish which appear annually along our shores”. Graham (1994) conducted a rigorous evaluation of the distribution of swarms of *Chrysaora fuscescens* in Monterey Bay relative to persistent hydrological features (upwelling shadows) and the swimming behaviour that led to the characteristic swarms that are commonly encountered in coastal regions of the southern California Current. Some of the data from Graham (1994) were derived from an ongoing survey of juvenile rockfish and other micronekton in central California waters. Since 1983, the Rockfish Recruitment and Ecosystem Assessment Survey (RREAS), using a modified Cobb midwater trawl, has been conducted in the waters off central California during the spring (May–June) upwelling season to sample the abundance and distribution of juvenile rockfish and other young-of-the-year fishes and forage species (Lenarz et al. 1995, Ralston et al. 2013, Sakuma et al. 2016). The initial survey area was along the Central California coast (~36–38°N); however, the range of the survey was expanded to cover most or all California waters starting in 2004. Although not the target of the survey, jellyfish have been integral to the survey since its inception (Graham 1994). Data on the species composition and abundance of the three most frequently encountered large scyphozoans (*Chrysaora fuscescens*, *Aurelia labiata*, *Chrysaora colorata*) have been collected reliably since 1990 (occasionally before then), with the exception of the years 2002 through 2004, and have begun to yield insights regarding the distribution, year-to-year variability and ecosystem interactions of these species in this region. Data on the abundance of *Phacellophora camtschatica* have been collected since 2009.

Due to the large-scale biogeographic features and circulation patterns described earlier, the central California region also appears to be the region of greatest relative abundance of these scyphozoan species, as illustrated by mean catch rates over the broader southern California Current survey range using data available from 1990 through 2019 (Figure 24). The two more abundant species of scyphozoans, *Chrysaora fuscescens* and *Aurelia labiata*, have their greatest relative abundance in nearshore central California waters, particularly the Gulf of the Farallones and Monterey Bay, with *Chrysaora fuscescens* more frequently found in offshore waters to the north and south of this

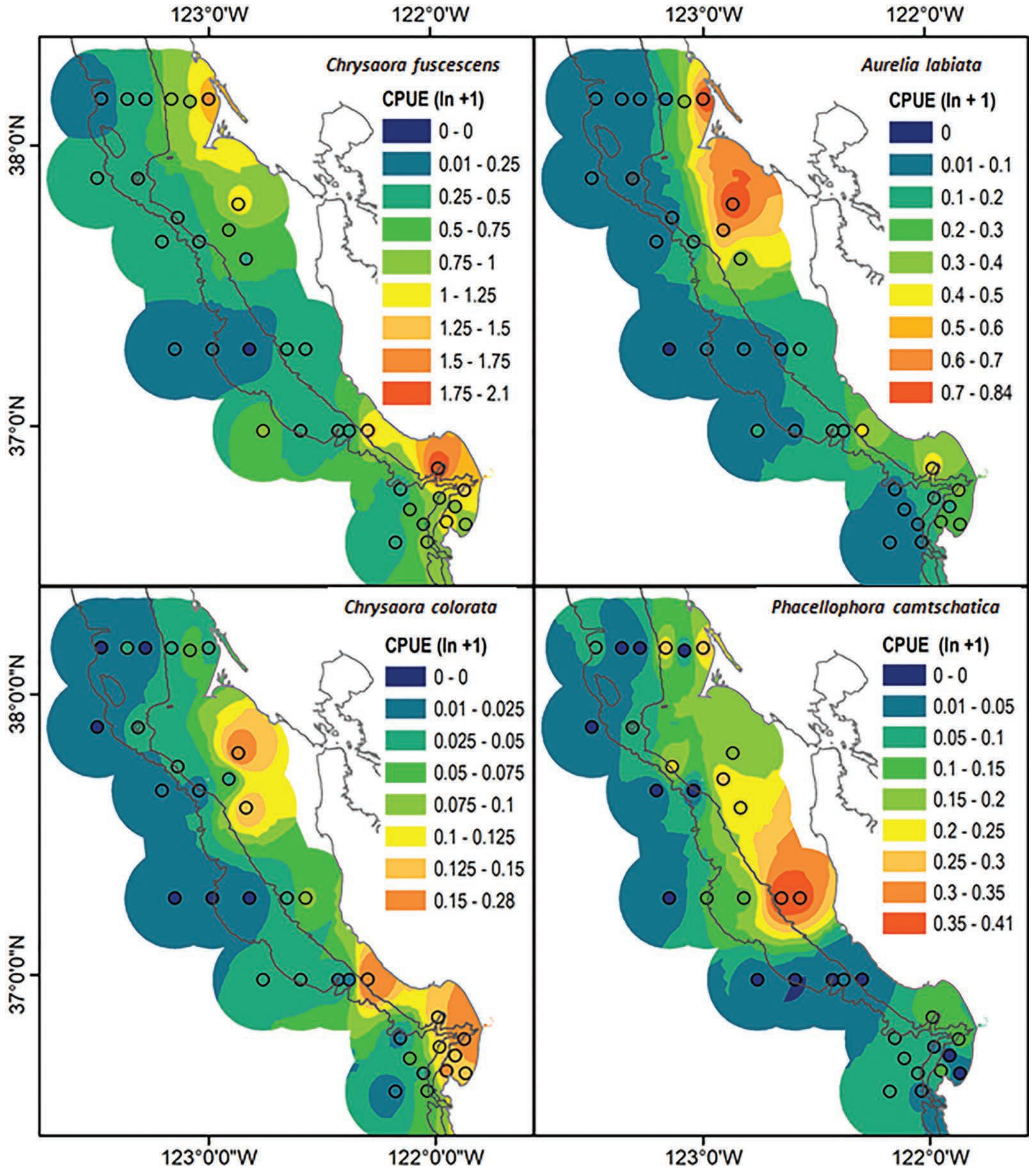


Figure 24 Average catch per unit effort (CPUE) of the four dominant Scyphomedusae using the core area climatology from 1990 to 2019 (note jellyfish were not recorded from 2002 to 2004). Circles represent the catch for stations ($n = 35$) that were sampled 13 or more times in the 27 years of sampling. Note that the range of catches are different for each species to indicate relative catch within species.

region. The next species, *Chrysaora colorata*, a solitary rather than swarming species, has a similar distribution but is considerably less abundant than the first two, although it is more abundant in nearshore waters (Figure 24). Finally, *Phacellophora camtschatica*, another non-aggregating species, has a centre of distribution situated between the peaks of the other species (Figure 24).

Since 2013, the RREAS has been expanded to include much of the northern California Current from southern Washington to the U.S.A – Mexico border (Figure 23), using similar methodology throughout (Miller et al. 2019). The annual distributions of the previous four species and *Aequorea* spp. show substantial broadscale overlap in many years (Figure 25). *Chrysaora fuscescens* showed centres of abundance at the northern end of the survey and in Monterey Bay, with lower abundances in between (Figure 25A). A similar distribution pattern was observed for *Aurelia labiata*, with the exception of slightly higher abundances off Cape Mendocino in the latter two years (Figure 25B). In contrast, *Phacellophora camtschatica* were caught in much lower abundances and were more broadly distributed along the coast both inshore and offshore (Figure 25C). The distribution of *Chrysaora colorata* was confined to south of Cape Mendocino in all but the warm year of 2017 and was close to shore in most years (Figure 25D). The large hydrozoan *Aequorea* spp. was generally most abundant in the northern part of the northern California Current (although they were not quantified off California prior to 2016) and were particularly abundant in 2015 during the first year of the marine heatwave (Figure 25E).

With respect to scyphozoan distribution patterns, Santora et al. (2012) evaluated 20 years of abundance data from the core area of these coastwide surveys to evaluate distribution and species association patterns of a suite of marine micronekton sampled in that survey (juvenile groundfish, forage fishes, krill, squid and jellyfish) off central California. They found that mesoscale variability of ocean conditions is the principal driver behind the spatial organization of the micronekton assemblages, with regions of species assemblages correlated to physical factors, latitudinal differences and the influence of localized upwelling and retention patterns. In other words, jellyfish distribution patterns, like those of other micronekton in this ecosystem, are largely defined by bathymetric and physical patterns, with centres of upwelling and relaxation leading to distinct micronekton assemblages (Graham 1994. Graham et al. 2001, Santora et al. 2012). For example, the retention areas north and south of Point Reyes typically included high numbers of the jellyfish (primarily *Chrysaora fuscescens*), resulting in strong loading with respect to spatial overlap patterns with the krill *Thysanoessa spinifera* and juvenile salmon (*Oncorhynchus* spp.).

A comparison of the large-scale macromedusae distribution in cool and warm ocean conditions was made from the early summer (June and July) surface trawl collections described by Suchman et al. (2012) but expanded to include a similar survey off southern Oregon and northern California (Harding et al. 2011). Distribution maps were made from the stations shown in Figure 23 for a seven-year period which included three cool years (2011–2013) and four warm years (2010, 2014–2016) for the dominant species (Figure 26). The dominant inshore species, *Chrysaora fuscescens*, showed three main centres of distribution (off Washington, southern Oregon and off central California) during both warm and cool years, and although their abundances were somewhat higher during the cool years, they were not significantly more abundant than the warm years (Figure 26). *Aurelia labiata* tended to be more abundant and widespread during warm years and tend to occur in more offshore waters than *Chrysaora fuscescens* (Figure 26). The largest macromedusae species, *Phacellophora camtschatica*, tended to be distributed the furthest offshore, and was significantly more abundant in warmer years especially south of Cape Mendocino (Figure 26). In contrast, *Cyanea capillata* was found almost entirely north of Cape Mendocino and showed no significant differences between cool and warm years. Finally, the Hydromedusa, *Aequorea* spp., was more broadly distributed and significantly more abundant in warmer years especially closer to shore (Figure 26).

Data from across Puget Sound, an adjacent inland sea which forms a major part of the Salish Sea together with the Strait of Georgia, show that large jellyfish are a major portion of pelagic biomass and that spatial heterogeneity exists in the relative abundance of jellyfish and small pelagic

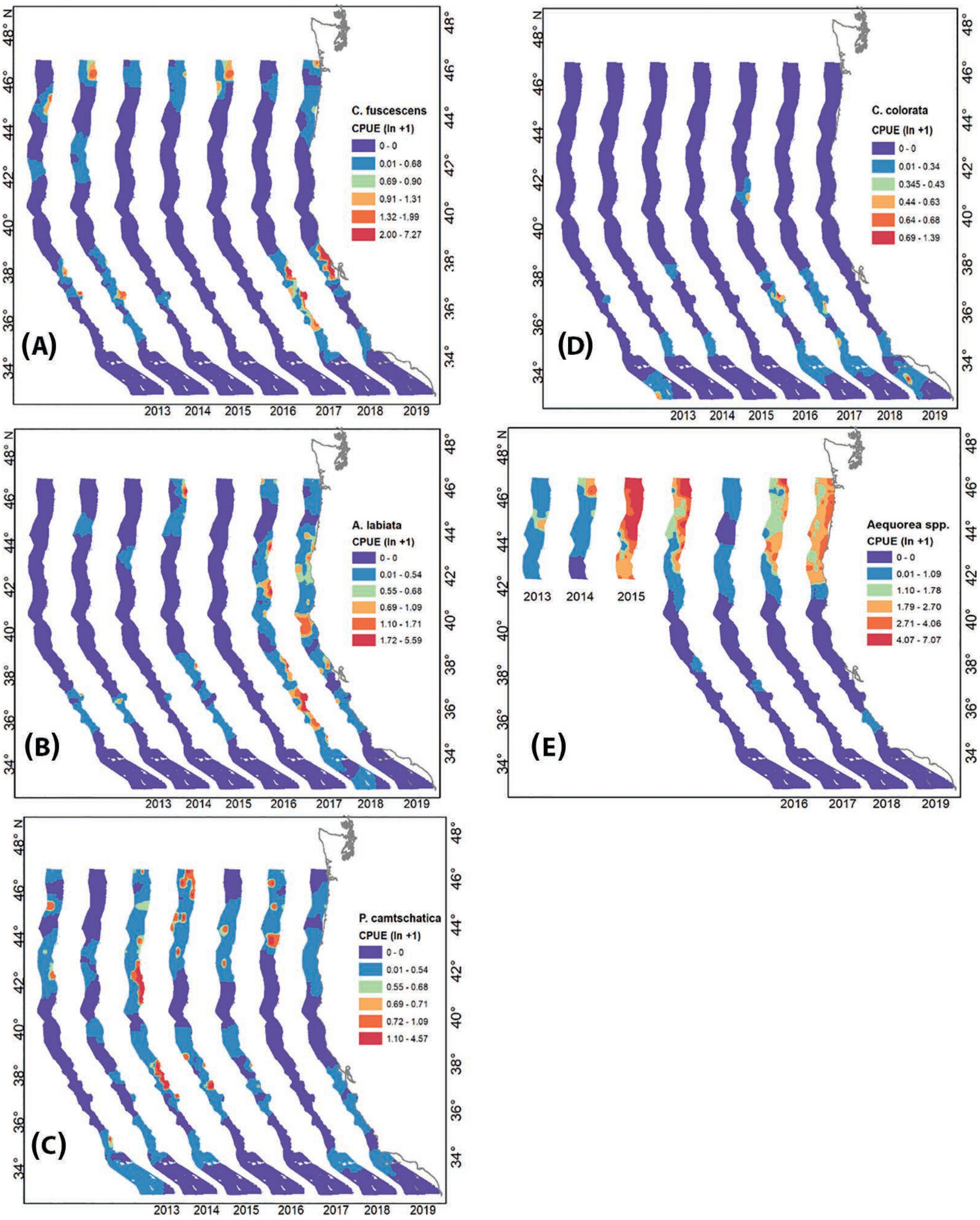


Figure 25 Relative abundance (log of the average numbers of individuals per haul) of (A) *Chrysaora fuscescens*, (B) *Aurelia labiata*, (C) *Phacellophora camschatica*, (D) *Chrysaora colorata* and (E) *Aequorea* spp. in the California Current in the May–June period, from 2013 to 2019. See Figure 23 for location of sampling stations. No data for *Aequorea* spp. were collected south of 42°N during the first three years. Classifications are based on the quantile distribution of positive catches (0; 0.01%–19%; 20%–39%; 40%–59%; 60%–79%; 80%–100%)

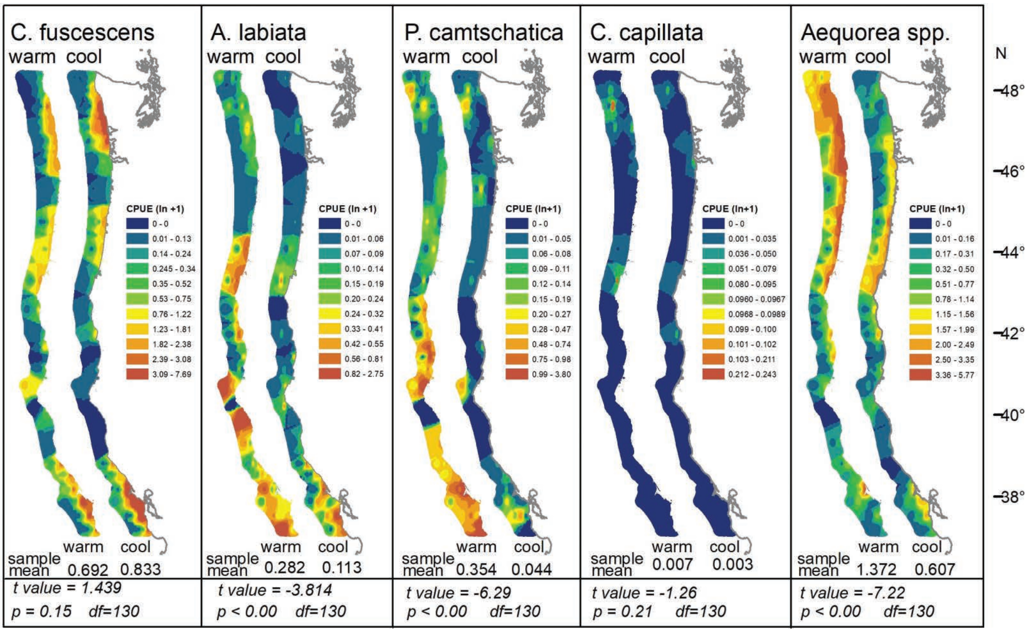


Figure 26 Large-scale distribution maps for the dominant macromedusae for cool (2011–2013) and warm years (2010, 2014–2016) in the California Current from daytime surface trawls for juvenile salmon (see Figure 23 for station locations). A total of 131 stations were included that had at least one sampling during both environmental regimes. Shown at bottom is the mean catch of a given species in the different conditions along with the results of a paired *t*-test comparing the catches from the two regimes.

fishes (Rice et al. 2012), and in the species composition of jellyfish assemblages (Reum et al. 2009). Based on trawl surveys in inlets inside Puget Sound in June and September 2007, Reum et al. (2009) determined that three species of Scyphomedusae (*Phacellophora camtschatica*, *Cyanea capillata* and *Aurelia labiata*) and one species of Hydromedusae (*Aequorea* spp.) were the most common species caught in these waters. The biomass of all species decreased seasonally between June and September and showed much variability among the four sampling areas. Rice et al. (2012) sampled a broader region of Puget Sound using pelagic trawls from May to August of 2003. Jellyfish from these surveys were not identified to species level but were combined as jellyfish biomass to compare with various fish species that were caught. However, these authors noted that the above species tended to dominate the catch along with the smaller hydrozoans and ctenophores. Jellyfish biomass was highest in the southern part of the sound, often exceeding 80% of the total biomass of the catch, but this decreased substantially to the north. Monthly changes were also observed and related to the changing physical environment in the area throughout the summer. In a recent study, Greene et al. (2015) analysed longer-term patterns of biomass of jellyfish using the above studies and comparing it to earlier work done in the 1970s and 1980s. They found that the proportion of hauls with large jellyfish catches have increased over this period in all three sub-basins examined, and these were related to increases in anthropogenic stressors, although negatively related to total forage fish biomass. These patterns suggest significant differences in the structure of pelagic foodwebs within Puget Sound that could have important management implications.

Substantially less is known about the vertical distributions of large medusae in the California Current, although recent efforts on tagging suggest that *Chrysaora fuscescens* performs stereotypical vertical excursions (Fannjiang et al. 2019). Based on a comparison of tows made in the upper 18 m to simultaneous tows made from 20 to 40 m during daytime in the California Current, Suchman et al.

(2012) found no significant difference in the density of either *Chrysaora fuscescens* or *Aequorea* spp. Brodeur et al. (2019) conducted tows at three depths during nighttime at two stations along the northern Oregon coast. Neither station showed a definitive pattern in the vertical distribution of *Aequorea* spp. with one station showing the highest abundance in the shallowest tow (upper 20 m) and another showing the highest at the deepest tow (around 50 m). However, both these studies were done without closing nets, so there is likely to be some contamination from the shallow layers in the deeper nets. Utilising a ROV, a total of 771 *Chrysaora fuscescens* were counted (from 24 dives) between the surface and the seabed, over bottom depths ranging from 20 to 40 m off central Oregon between June and September 2008. Approximately 77% of jellyfish were observed in the upper 20 m, although the mean depth of abundance varied among stations (Figure 27).

Space – time Densities of the two dominant larger medusa species in the northern California Current, *Chrysaora fuscescens* and *Aequorea* spp., have been monitored as part of a surface trawl survey in the northern California Current conducted every June and September from 1999 to 2012 (Suchman et al. 2012, Morgan et al. 2019). With few exceptions, *Chrysaora fuscescens* dominated the catch and was generally one to two orders of magnitude higher than that of *Aequorea* (Figure 28).

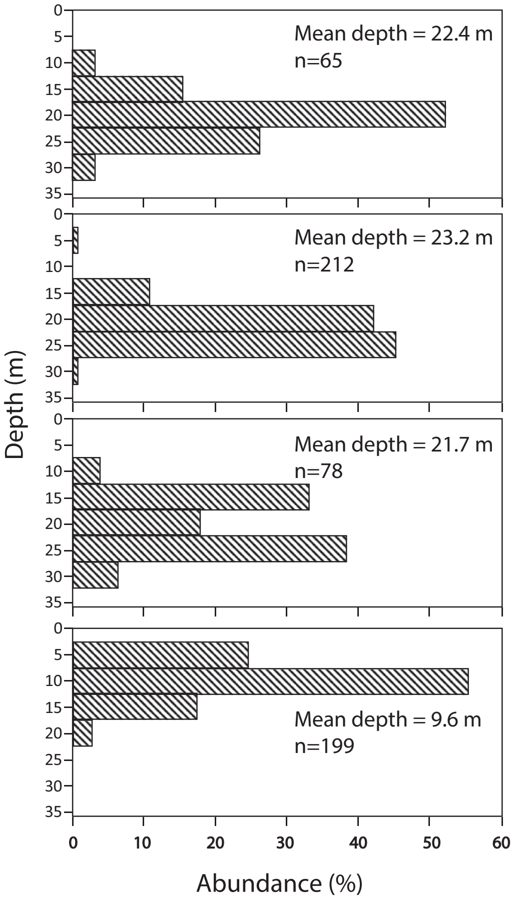


Figure 27 Daytime vertical distribution of *Chrysaora fuscescens* off Oregon (45.0°N, 124.3°W) based on four deployments of a ROV by the Oregon Department of Fisheries and Wildlife (ODFW) on September 16, 2008 (Data courtesy of D. Fox, ODFW). Shown in the upper right corner are the proportions of the total found at each 5 m depth interval with the mean depth (m) and number of individuals observed during each deployment.

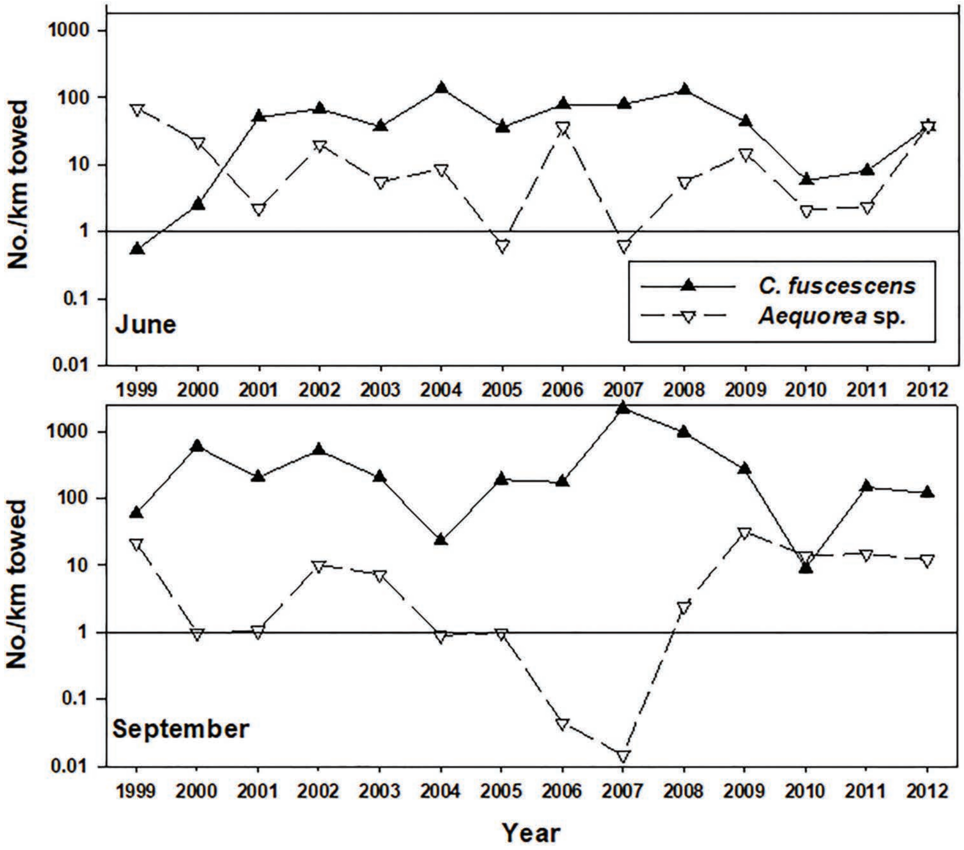


Figure 28 Catches of *Chrysaora fuscescens* and *Aequorea* spp. in annual surface trawl surveys off Washington and Oregon in June (upper panel) and September (lower panel) from 1999 to 2012.

Catches of both species returned to a more typical level in June 2012, following below-average catches for 2010 and 2011, possibly due to the lingering effects of the 2010 El Niño (Figure 28). In September 2012, catches of both species were similar to those seen in 2011, with densities of *Chrysaora fuscescens* being approximately an order of magnitude higher than those of *Aequorea*, similar to that seen in earlier years by Suchman et al. (2012). Morgan et al. (2019) analysed 20 years (1998–2017) of June surface trawl catch data and showed that the last few years were the most anomalous in jellyfish catches, with *Aequorea* spp. exhibiting densities two standard deviations (SD) above the long-term mean in 2015 and 2016, whereas *Chrysaora fuscescens* was one SD below the mean for these two years. The recent increase in *Aequorea* was attributed to relaxed upwelling and onshore transport associated with the large marine heatwave that occurred during those two summers (Di Lorenzo & Mantua 2016, Peterson et al. 2017).

Sorenson (2018) examined in detail the time series of the abundance of *Aequorea* to 18 years (1999–2017) and showed it was highly variable interannually, seasonally and across stations. The highest abundances were recorded in 2015 and 2016, reaching more than 16,000 km^{-2} at some locations. Using generalized additive models of *Aequorea* abundance and distribution related to environmental variables, Sorenson (2018) showed a close relationship of these with *in situ* environmental conditions, with a positive correlation to both SST and salinity. Larger-scale environmental drivers including the Pacific Decadal Oscillation (PDO), discharge from the Columbia River and upwelling strength also influenced *Aequorea* abundance.

Another long-term dataset involves the by-catch of gelatinous zooplankton (mostly large medusae) in triennial bottom trawl surveys conducted by the Alaska Fisheries Science Centre, NOAA from 1980 to 1992 (data provided by M. Wilkins, Alaska Fisheries Science Center, NOAA) that extend from northern Washington to Southern California. Catches were highly variable but showed low jellyfish abundance during the El Niño events of 1983 and 1998, similar to those seen in other studies covered here, but also in 1986.

With respect to temporal trends in abundance in the southern California Current, the mean log-transformed catch of *Chrysaora fuscescens* and *Aurelia labiata* for the core survey area between 1990 and 2019 (excluding the years 2002–2004, for which data were not collected) was examined. This index is useful as a relative abundance time series, although developing an absolute abundance index is difficult given the uncertainty regarding net selectivity and the real or likely depth stratification of jellyfish, which are probably present at greater densities in the upper 20 m of the water column relative to the typically 30–40 m depths targeted in this survey. Note that a key assumption made in the development of this index is that "problem hauls", in which the nets are either damaged or "blown out" due to an extremely high (but subsequently un-quantified) abundance of jellyfish, or in which hauls were aborted due to the high presence of jellyfish in the water (in such cases, an approximate species composition is estimated visually), have the estimated catch rate set to that of the highest observed abundance in good performance hauls. Despite these limitations, the two species show dramatic interannual variations in abundance (Figure 29). During some periods, the abundance of these two species appears to be inversely related, while in some years (especially 2018 when both species reached peak abundance), they coincide (Figure 29).

The temporal trends observed in these indices suggest both high interannual variability (consistent with high interannual variability observed in many of the time series of micronekton documented in this survey), and no clear indication of either a monotonic increase or decline in jellyfish abundance in this region over time. In general, years of greatest jellyfish abundance tended to be relatively cool, high transport years that also favour increased abundance of young-of-year groundfish, krill and market squid (*Doryteuthis opalescens*), while during warm, less productive years (such as the 1998 El Niño year and the unusually low productivity period between 2005 and 2006), jellyfish abundance declines considerably (unpublished data; J. Field). Off California, the temporal trends of midwater Hydromedusae have been related to major climate forcing such as El Niños (Raskoff 2001).

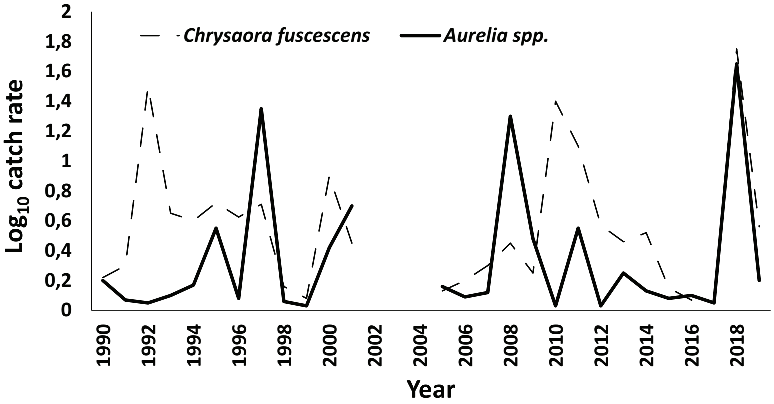


Figure 29 The mean of the log-transformed catch rate for the two most frequently occurring scyphozoan species encountered in the Southwest Fisheries Science Center midwater trawl survey conducted off Central California, 1990–2019 (no data available for 2002–2004).

Biomass, growth and mortality

Biomass The length–mass relationships for *Chrysaora fuscescens* and *Aurelia labiata* are shown in Supplementary Table 1A. With respect to absolute abundance, some work has been done to develop estimates of jellyfish abundance in the California Current region using acoustic backscatter from which estimates of abundance by area were developed for the Monterey Bay and Gulf of Farallones regions (Graham et al. 2010), with mean densities estimated to be on the order of a quarter of a million jellyfish within a square mile of ocean habitat. Ultimately, some combination of net sampling and acoustics could lead to greatly improved estimates of abundance, distribution and year-to-year variation in large Scyphomedusae in this region.

Growth, mortality and longevity Spatial variations in the mean and variation in size of the dominant macromedusae were evident in the coastwide rockfish surveys based on the regions shown in Figure 24. Both *Chrysaora fuscescens* and *Aurelia labiata* showed their largest sizes and greater variability in bell diameters off central California compared to the northern California Current (Figure 30). There was relatively little interannual variation in the bell diameter sizes for *Aequorea* spp. in the northern California Current, although the sizes during the warm year of 2017 was substantially lower than the other years (Figure 30).

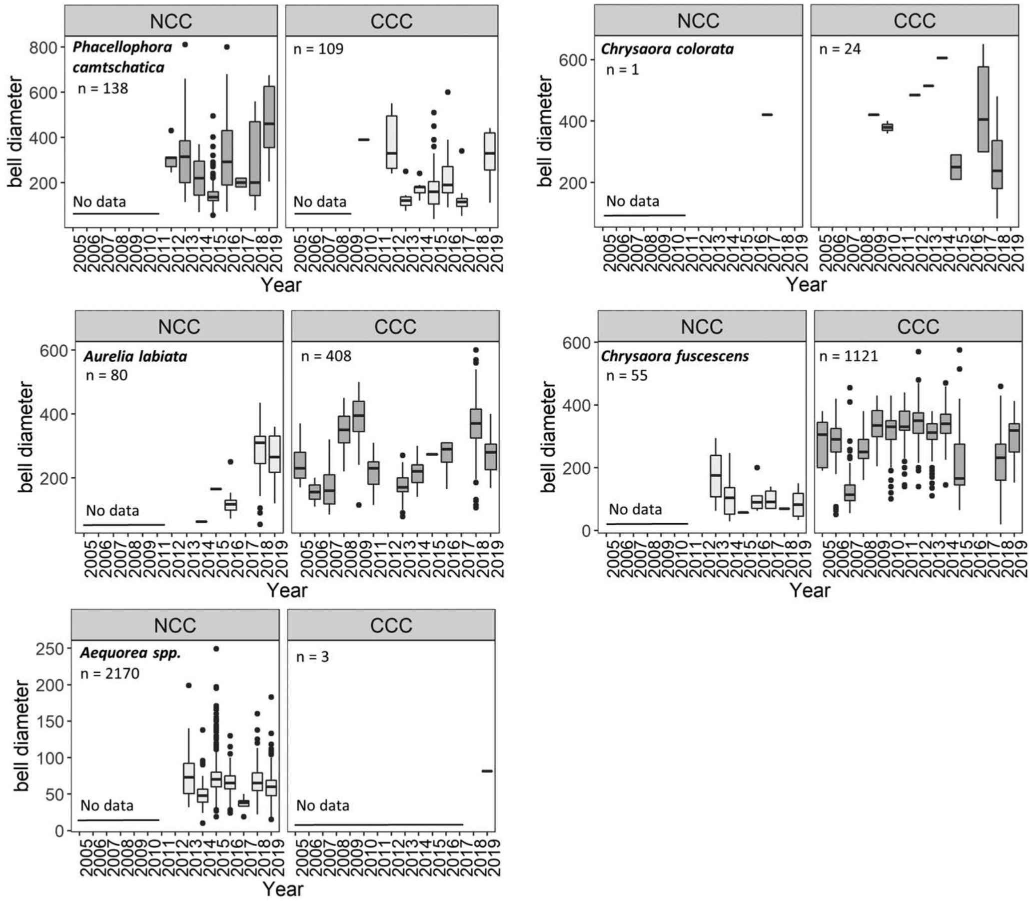
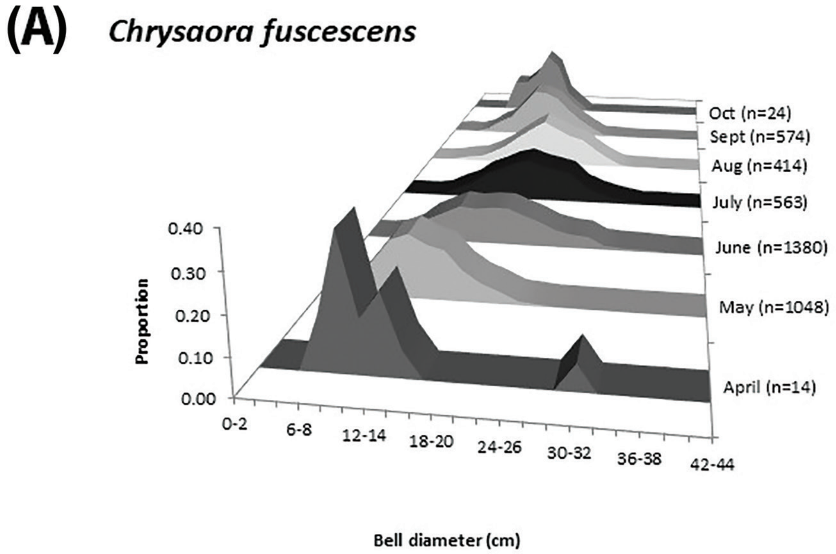


Figure 30 Spatial variation in bell diameters (mm) of the dominant species by year and geographical area. See Figure 23 for extent of the geographical regions (NCC northern California Current, CCC Central California Current). Total number of measurements (*n*) is given for each species.

The first study to examine seasonal growth patterns of Scyphomedusae in the California Current was that of Shenker (1984). Based on changes in umbrella diameter, *Chrysaora fuscescens* grew rapidly in the summer months from a mean size of 8.6 cm in May to 18.5 cm in August. Using monthly data collections described in Suchman et al. (2012) from April to October (Figure 31), it was noted that *Chrysaora fuscescens* increased in bell diameter from May through August, but



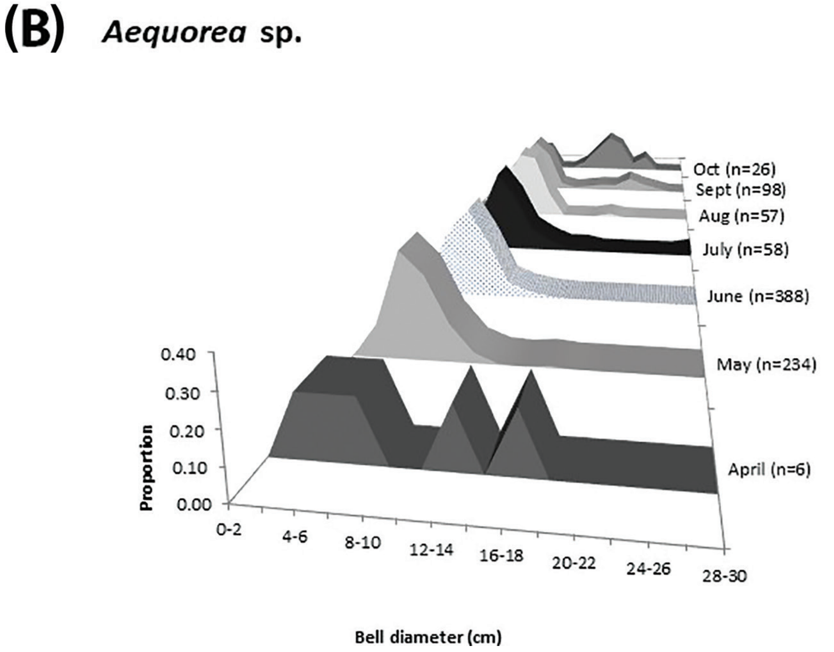


Figure 31 Bell diameter frequency for *Chrysaora fuscescens* (A) and *Aequorea* spp. (B) by month from surface trawl collections off Oregon and Washington from 2001 to 2009. All collections were made from off the Columbia River, Oregon to Grays Harbor, Washington. The sample size for each month is given in parentheses.

subsequently decreased in September and October. Whether this reflects natural senescence, shrinkage due to less food available or a preferential mortality of the larger individuals in the population is not known. Potentially because of different life histories, *Aequorea* spp. shows a more bimodal size distribution pattern with a moderate increase in the main smaller mode but with a second mode appearing in late summer and even persisting until April (Figure 31). This pattern is not likely to be caused by increased growth during this brief period, but instead these larger individuals likely correspond to the larger offshore species (*Aequorea coerulescens*) occurring in this region (Mills and Rees 2007) that may be advected into coastal waters when the seasonal upwelling subsides. There were two survey years when winter samples along with other seasonal data were taken: 2003 when May, June, September and November had surveys, and 2018 when March, May and June were sampled. While *Chrysaora fuscescens* showed significant declines in bell diameter by November 2003, compared to June and September (Kolmogorov–Smirnov; $p < 0.001$; Figure 32A), the *Aequorea* spp. almost doubled in size in November relative to the other months in the year (Figure 32B) possibly indicating that two species were present. In March 2018, *Chrysaora fuscescens* was of a similar size in March and May (Figure 32C), while *Aequorea* in March were again almost double the size of the May and June period, although with low sample size, showing large winter bell diameters (Figure 32D).

As a measure of growth, the change between the average bell diameters of *Chrysaora fuscescens* between May and June (2001–2019; 15 years of survey) and *Aequorea* (11 years of survey) was

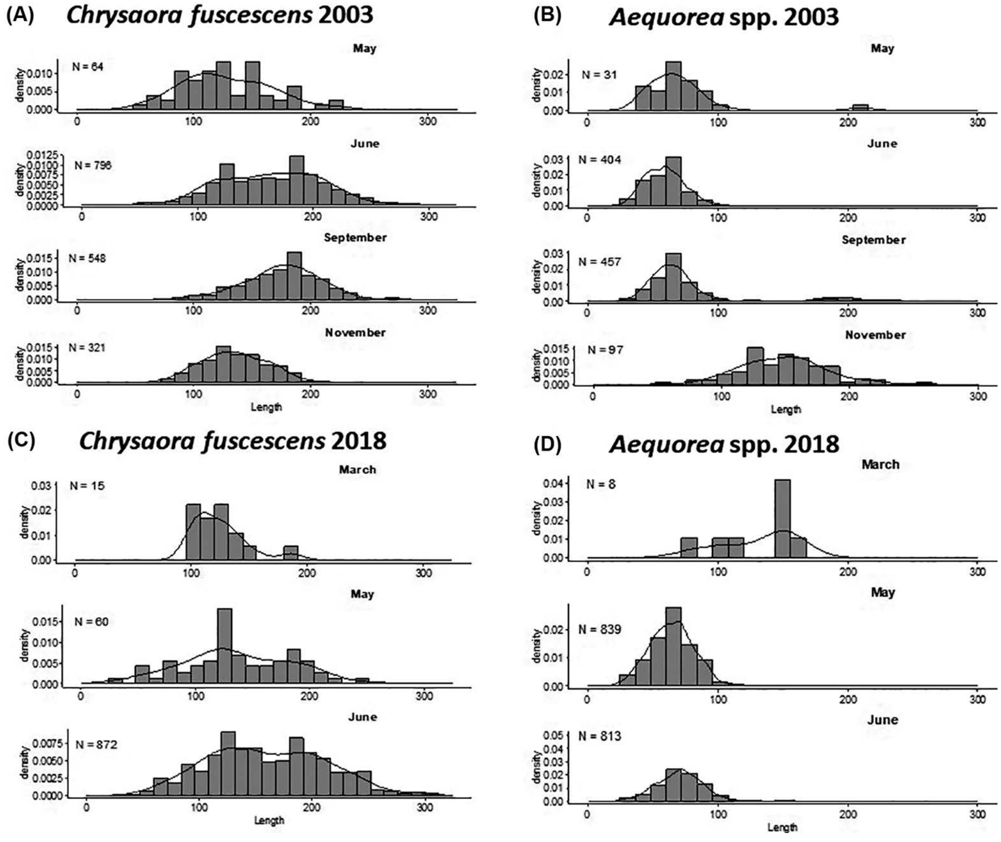


Figure 32 Bell diameter (mm) density plots of *Chrysaora fuscescens* (A and C), and *Aequorea* spp. (B and D) by month (May, June, September and November) in 2003, and March, May and June 2018. The number of measurements is shown in the upper left of each plot.

estimated and related to ocean conditions as measured by winter PDO (Figure 33). The growth of *Chrysaora fuscescens* and *Aequorea* between May and June was significantly higher during more negative, or colder, winter conditions (Figure 33). Using the same time series, years were divided into cold or warm regime based on the rank of the means from the ocean ecosystem indicator table provided by NOAA Fisheries ocean ecosystem indicator data.[4] In May, the size of *Chrysaora fuscescens* was significantly larger during warmer ocean condition (Kolmogorov–Smirnov; p <0.001; Figure 34A), suggesting faster spring growth, yet by June, *Chrysaora fuscescens* were significantly larger in cold ocean conditions (Kolmogorov–Smirnov; p <0.001; Figure 34A) suggesting faster summer growth of the population. For *Aequorea*, there were not significant size differences between May ocean conditions (Figure 34B), nor between May and June during warm ocean conditions, but there was a significant increase in size between May and June during cold ocean conditions (Kolmogorov–Smirnov; p <0.001; Figure 34B).

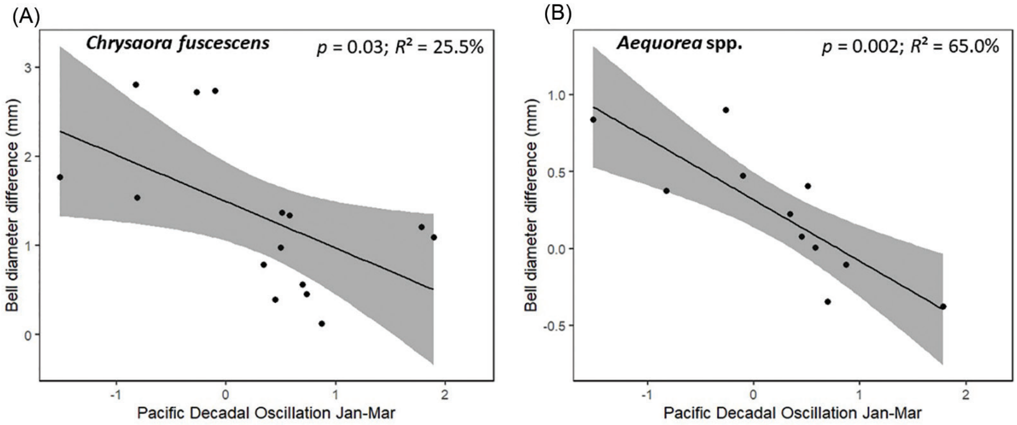


Figure 33 Relationships between the difference in average bell diameter (mm) between (A) *Chrysaora fuscescens* and (B) *Aquorea* spp. caught in May and June for each survey year to the January–March PDO. The relationships between the January–March PDO and the difference in average bell diameter (mm) of jellyfish caught in May and June each survey year for (A) *Chrysaora fuscescens* and (B) *Aquorea* spp.

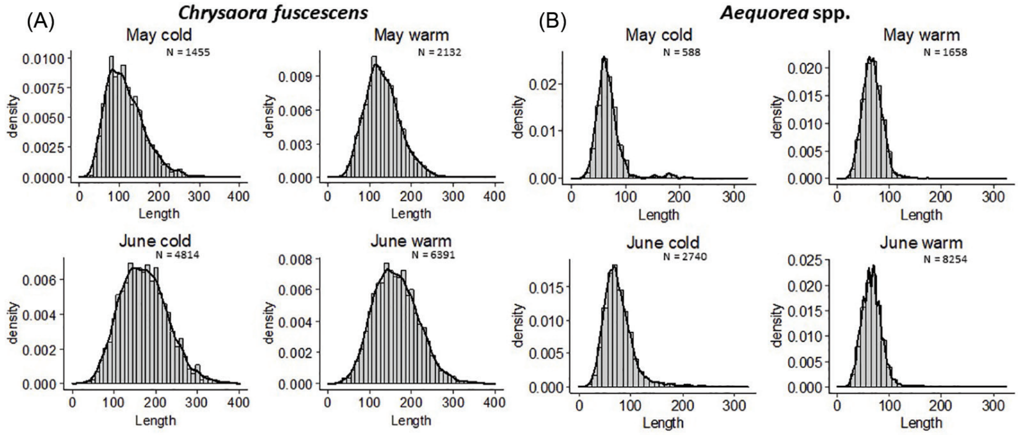


Figure 34 Bell diameter (mm) density plots of *Chrysaora fuscescens* (A) and *Aequorea* spp. (B) by month (May or June) relative to ocean conditions (cold or warm). The number of measurements N is shown in the upper right of each plot.

There are scant field data on the longevity of macromedusae in the NE Pacific Ocean. Albert (2005) studied a population of *Aurelia labiata* in an enclosed bay in British Columbia and found that medusae there generally lived for more than one year and that up to 40% of the adult medusae may be two years of age or older. The question of how long jellyfish can exist as medusae has been evaluated in the laboratory setting, as both *Chrysaora fuscescens* and *Aurelia labiata* have been maintained in aquaria for many years (Raskoff 2003), showing that they have the potential to at least overwinter in the ocean. Hydromedusae, on the other hand, live a relatively short time even in captivity (three to six months; Raskoff 2003), and individuals within a given cohort will tend to all die within a short period of each other.

Reproduction

Sexual The life histories of these (and other) species have been rigorously evaluated by a combination of field and aquarium studies (e.g. Raskoff 2003, Widmer 2005, 2006, 2008b). All Scyphomedusae and the one Hydromedusa included here are known to have separate sexes, with some having distinctive differences in gamete colour between the males and females. *Aurelia labiata* and *Cyanea capillata* are known to brood their planulae, with the males developing sperm follicles that are captured by the females and moved towards their gastric pouches that are lined with eggs (Arai 1997). Mature planulae are then released into the environment for transformation and settlement of the sessile phase. The remaining medusae are broadcast spawners and shed gametes into the water column, especially when in aggregations, and the drifting fertilized eggs then develop into planula larvae and settle to form scyphistomae (polyps) in the case of the Scyphomedusae, and gonozooids for reproduction in the case of the Hydromedusae. Cnidaria that are planula brooders may have less gene flow among populations (Hellberg 1996).

The seasonality of maturity and reproduction of jellyfish in the California Current is also a little-studied topic. The jellyfish *Aequorea* spp., *Chrysaora fuscescens* and *Aurelia labiata* have conspicuous gonads when sexually mature and ripe individuals have been consistently observed in the May, June and September surveys done in the northern California Current (E. Daly, unpublished data). In the California Current, mature *Chrysaora fuscescens* males and females were collected in January (Widmer 2008b), and also mature *Aurelia labiata* were collected February-May (Widmer 2005). At the most northern area of the northern California Current off the west coast of Canada, female *Aurelia labiata* have been shown to be carrying mature planula larvae in November, and as such, males were most likely mature in September or October (Albert 2005).

Asexual Very little is known about the benthic or early larval stages of medusae in the California Current. During an underwater survey of hard structures in Yaquina Bay, Oregon, Heitstuman (1994) found only a few occurrences of the polyps of *Aurelia labiata*, mostly on undersides of man-made structures (jetties and piers), and no *Chrysaora fuscescens* polyps were found despite extensive searching. Conley (2013) used molecular techniques to identify the scyphistomae of medusae in Coos Bay in Southern Oregon and the specimens that were sequenced were all identified as *Aurelia labiata*. The location of the benthic polyp stage for the larger medusae of the California Current continues to remain a mystery in the field. While *Aurelia labiata* polyps have been identified in several small bays of the Oregon coast and polyps may also be found on rocky reef areas further offshore, the adult medusae are generally oceanic.

Strobilation of *Aurelia labiata* polyps in Puget Sound occurred in January and February, when light, temperature and salinity were at the lowest recorded levels in the year (Purcell et al. 2009). In the California Current, strobilation of *Aurelia labiata* occurred in February–April (Galigher 1925, Widmer 2005). The timing and production of the sessile stage, as well as timing of strobilation, have been investigated in the laboratory for *Chrysaora fuscescens* in the California Current (Widmer 2008b). Mature adults were collected in January, and gametes were obtained; polyps were fully developed by 50 days post-spawning. By day 231, a single polyp had formed 51 polyps and 53 podocysts. The polyps began strobilation at 286 days post-spawning, and up to 60 ephyrae were produced per polyp (Widmer 2008b). Production of gametes by the Hydromedusa *Aequorea victoria* was measured at 300–8600 eggs day^{-1} medusa^{-1}, daily for seven days (Larson 1986). Changes in temperature, light levels, salinity and pH have all been shown to affect the return of the sessile stage to the pelagic medusa (Raskoff et al. 2003). The temperature range to maintain successful sessile states of California Current jellyfish of our study region ranged primarily between 10 and 15°C (Raskoff et al. 2003, Widmer 2005, Purcell et al. 2009, Treible & Condon 2019). The scyphozoan medusae of our study are all polydiscus – with many ephyrae being release per strobilation event (Purcell et al. 2009, Helm 2018), and the colony of *Aequorea victoria* hydroids produces many medusae (Larson 1986).

High survival and settlements of polyps, strong production of ephyrae and positive advection of medusae into coastal waters can create scenarios where high biomasses of jellyfish medusa can bloom (Moloney et al. 2010). Location of the ephyrae can potentially aid in the identification of where in the ocean the polyp phase is located, especially through the use of circulation models (Johnson et al. 2001, Barz et al. 2006). Key to this is the identification of ephyrae to species from plankton samples, which is not being done at present. Spawning of adult medusae in the laboratory and careful description of the ephyrae can allow us to use plankton samples to understand more fully the population dynamics of medusae in the California Current (Widmer 2006, 2008b).

Interactions with other species and human activities

Diet

There has been a limited number of gelatinous zooplankton diet studies from the California Current. Graham (1994) reported that preys of *Chrysaora fuscescens* in Monterey Bay included doliolids and siphonophores, which are often highly abundant in the same frontal region as jellyfish swarms. Suchman et al. (2008) analysed the diets of *Chrysaora fuscescens*, *Phacellophora camtschatica* and *Aurelia labiata* in relation to available plankton from specimens collected in August 2002. These authors found that euphausiid eggs, calanoid copepods, cladocerans and other gelatinous taxa were particularly important in their diets. Based on diet and laboratory measurements, these authors suggested that *Chrysaora fuscescens* had the potential to remove between 10% and 12% of the overall standing stocks of these preys per day and considered that jellyfish may be especially important predators on euphasiid eggs and copepods in nearshore waters (Suchman et al. 2008). More recent work on *Chrysaora fuscescens* conducted in June, July and September of 2014 shows that certain prey types are more vulnerable to predation by jellyfish (Zeman et al. 2016). Gut content analysis of the medusae showed positive prey selection for vulnerable, slow-moving taxa, (e.g. fish and invertebrate eggs and appendicularians). Predation on ichthyoplankton was particularly high in June when medusae are growing rapidly and when fish eggs, particularly those of northern anchovy *Engraulis mordax*, were abundant in the plankton. Copepods, though abundant in the plankton, were negatively selected relative to their availability (Zeman et al. 2016). Experiments in laboratory kreisels have shown that *Chrysaora fuscescens* have high clearance rates on *Artemia* prey and that these feeding rates are not affected by current speeds (Zeman 2015).

Several studies have used the stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) to examine trophic position and niche width of jellyfishes in this region. Miller et al. (2008) and Brodeur et al. (2008b) have used $\delta^{15}N$ to examine the relative trophic level of several common jellyfish species in the Northern California Current, comparing these to the dominant small pelagic forage species. They found that *Chrysaora fuscescens* and *Aurelia labiata* occupied about the same trophic level and were only slightly lower than such important forage fishes as Pacific herring (*Clupea pallasii*), Pacific saury (*Cololabis saira*), northern anchovy and Pacific sardines. Based on whole-body $\delta^{13}C$ values, *Chrysaora fuscescens* showed the most inshore distribution, while *Aequorea* spp., *Phacellophora camtschatica* and *Aurelia labiata* had similar isotope values indicative of more offshore distribution and feeding (Supplementary Table 4, Miller et al. 2008). A similar study conducted by Naman et al. (2016) in Puget Sound showed that although there were high overlaps in isotope ratios between the jellyfish species examined and forage fishes, jellyfish were often more enriched in ^{13}C and depleted in ^{15}N than fish, which may indicate a more marine-influenced diet. However, jellyfish were found to have narrower trophic niches than fishes, and these were less associated with physical and biological variables measured (Naman et al. 2016).

Parasitism

There are few direct observational studies of the associations of hyperiids with macromedusae in the California Current, although the most abundant hyperiids such as *Hyperia medusarum* and *Hyperoche medusarum* are often observed living within the bells of several medusan hosts in dip-netted specimens (Daly and Brodeur, personal observations). In Puget Sound, Towanda and Theusen (2006) found an increase in parasitism of *Hyperia medusarum* in the oral arms of *Phacellophora camtschatica* through the summer reaching 100% of the examined hosts by autumn with a maximum of 446 amphipods on a single medusae. Other crustaceans, such as larval crabs, are ectoparasitic on this same host species (maximum 336 larvae per individual), consuming parts of their host during development (Towanda & Theusen 2006).

Predation

When prevalent, gelatinous zooplankton may provide an alternate pathway for energy flow that can lead to production in higher trophic levels. Although Scyphomedusae can grow and feed at high rates, their bodies are composed mostly of water and thus are not typically a good food source for larger pelagic organisms. With the notable exception of the large ocean sunfish (*Mola mola*) that specialise in large medusae prey, most marine fishes do not consume large Scyphomedusae prey. Only a few fish species in the California Current are suspected to be selective feeders upon medusae, including prowfish (*Zaprora silenus*), and medusafish (*Icichthys lockingtoni*) and their relatives, which are often commensal with medusae as juveniles. Several species of rockfishes are known predators of a wide range of gelatinous plankton, particularly thaliaceans, but they also eat a broad range of cnidarians, ctenophores and other gelatinous macro-zooplankton (Adams 1987) particularly during low productivity years (Lee & Sampson 2009). Laidig et al. (1997) also noted that sablefish (*Anoplopoma fimbria*) caught in California waters preyed on both salps and gelatinous zooplankton, although neither constituted a substantial fraction of the total prey biomass. Brodeur et al. (2021) analysed the diets of many commercially important groundfishes in the northern California Current and found several species of rockfish were consumers of medusae, but they generally made up a small proportion of the diet.

Scyphozoans are also critically important prey for endangered Pacific leatherback sea turtles (*Dermochelys coriacea*), of which a significant fraction of the population migrates into the California Current during late summer and autumn to feed. Substantial fisheries management measures, including large area closures, have been implemented to protect sea turtles from fisheries impacts (particularly from the drift-gillnet fishery for swordfish and other highly migratory species). The spatial extent of the closures has been based on both survey data of turtle abundance and distribution, and telemetry data that indicate areas in which turtles engage heavily in foraging behaviour (Benson et al. 2007, 2011, Bailey et al. 2012). Individual turtles may eat 20%–30% of their body weight per day, and up to 1000 t per individual per lifetime, with the total Pacific-wide consumption by turtles estimated to be on the order of two million t per year (Jones et al. 2012). Consequently, a better understanding of the environmental drivers of scyphozoan abundance, population dynamics and distribution could help inform management measures taken to minimise fishing-related mortality on these critically endangered species.

There are likely to be few, non-parasitic invertebrate predators on the adult stages of living macromedusae, although some large medusae (e.g. *Phacellophora camtschatica*) are known to feed extensively on other adult medusae (medusivorous) in the California Current (Suchman et al. 2008). Although other jellyfish species are also known to be medusivorous, including *Chrysaora fuscescens*, *Aurelia labiata* and *Aequorea* spp., these are likely to eat mainly the younger stages of macromedusae, or other small gelatinous taxa such as ctenophores and salps (Suchman et al. 2008).

Associations with fish

As noted above, in the retention areas north and south of Point Reyes, there is a significant overlap in the distributions of *Chrysaora fuscescens*, the krill *Thysanoessa spinifera*, and those of juvenile salmon. This spatial overlap suggests that there may be potential competition between jellyfish and other animals that feed on zooplankton, such as forage fishes as suggested in the northern California Current (Brodeur et al. 2008b, 2014, Suchman et al. 2008). Brodeur et al. (2008b) examined the spatial overlap of the dominant jellyfish with important pelagic fish species in the Northern California Current. They found several fish species (particularly juvenile salmon and smelt) had relatively high overlap with *Chrysaora fuscescens* and to a lesser extent *Aurelia labiata* off southern Oregon (Brodeur et al. 2008b). Using a longer (13-year) time series of catches of *Chrysaora fuscescens* and catches of herring, anchovy and sardines, Brodeur et al. (2014) showed that the spatial patterns of the centroids of abundance and spatial overlap were highly variable during June and September. The three forage species showed inverse relations of abundance to the jellyfish abundance in both months. Finally, Ruzicka et al. (2016) showed that juvenile salmon had a high spatial overlap with *Chrysaora fuscescens* and they also showed inverse relationships of salmon survival to jellyfish biomass. These authors also noted that the feeding success of juvenile salmon in hauls with large numbers of jellyfish was lower than those caught in trawls with little or no jellyfish, implying that there was a negative impact of jellyfish on salmon possibly due to competition for food resources (Ruzicka et al. 2016).

Fisheries and human activities

The impacts of jellyfish blooms on humans are manifold, but the primary effects relate to those concerned with tourism (beach closures), power plant closures (clogging of intake systems), and both direct and indirect impacts on fisheries (Purcell et al. 2007, Graham et al. 2014). Unlike many systems at a similar latitude, the cool nearshore waters of the California Current are not conducive to the species of jellyfish that sting, much less kill, bathers, so they are generally not an issue for tourism here (Graham et al. 2014). Although blooms are known to clog intake systems of nuclear power plants in California, these have been attributed to salps and not medusae (Graham et al. 2014). However, large blooms of medusae can have major indirect effects on fish recruitment through consumption of early life stages (Purcell 1989, Zeman et al. 2016) and potential growth and survival of juvenile and adult fishes through shared use of food resources (Brodeur et al. 2008b). Due to the immensity and spatial variability of the California Current, these indirect effects are difficult to quantify and can only be approximated using models but are most likely to impact fish abundance and catch in years with major medusae blooms.

The direct economic impact of jellyfish upon commercial fisheries was studied by mail surveys sent to local fishers (Conley and Sutherland 2015) in the Northern California Current system off Oregon, where *Chrysaora fuscescens* is densely distributed (Suchman & Brodeur 2005, Brodeur et al. 2008b). Of the total respondents, 67% reported that jellyfish reduced their seasonal revenue, and the estimated economic impact of jellyfish on salmon and pink shrimp fishers was over USD650,000 during the peak jellyfish season in 2012. According to fishers' reports, the jellyfish impact is not solely upon net fisheries, but also upon hook and line fisheries. The spatial distribution patterns of the impacts on the salmon trolling fishing industry corresponded to the spatial distributions of *Chrysaora fuscescens* observed in large-scale research surveys (Conley & Sutherland 2015). Finally, as mentioned previously, extensive blooms of jellyfish can hamper surveys of fish populations by the scientific community, impacting and in some case preventing sampling in research surveys, leading to incomplete information on fish stocks, especially for pelagic species.

Macromedusae in ecosystem models

Although there is a substantial number of detailed food web models available for many of the LMEs of the world, very few of them have explicitly included gelatinous zooplankton, and if they did, they were often aggregated into a single group (Pauly et al. 2009), which did not capture the diversity of predator–prey interactions in this taxonomically diverse assemblage. One of the first modelling studies to examine the interactions of large scyphozoan jellyfish in a coastal ecosystem was an examination of the impact large blooms have on the Oregon upwelling ecosystem (Ruzicka et al. 2007). Using mass-balanced ECOPATH models parameterized for the pelagic ecosystem from numerous field studies, Ruzicka et al. (2007) compared the seasonal food consumption of large jellyfishes (primarily *Chrysaora fuscescens*) to that of forage fishes and other major components of the ecosystem. This study found that jellyfish can be the major consumers of zooplankton during the late summer months and can exert substantial top-down effects on several zooplankton groups. During time of peak abundance (summer), jellyfish pass on only 2% of their biomass to higher trophic levels, whereas forage fishes pass along 17% of their biomass to higher levels.

The previous consumer demand-driven ECOPATH model was re-expressed as a producer-driven end-to-end model (Steele & Ruzicka 2011) where the ecosystem-wide consequences of changes in energy flow through key nodes in the food web could be evaluated. As an example, increasing the energy flow to jellyfish without increasing the overall productivity of the model led to a substantial decline in the productivity of forage fish in this system (Figure 35).

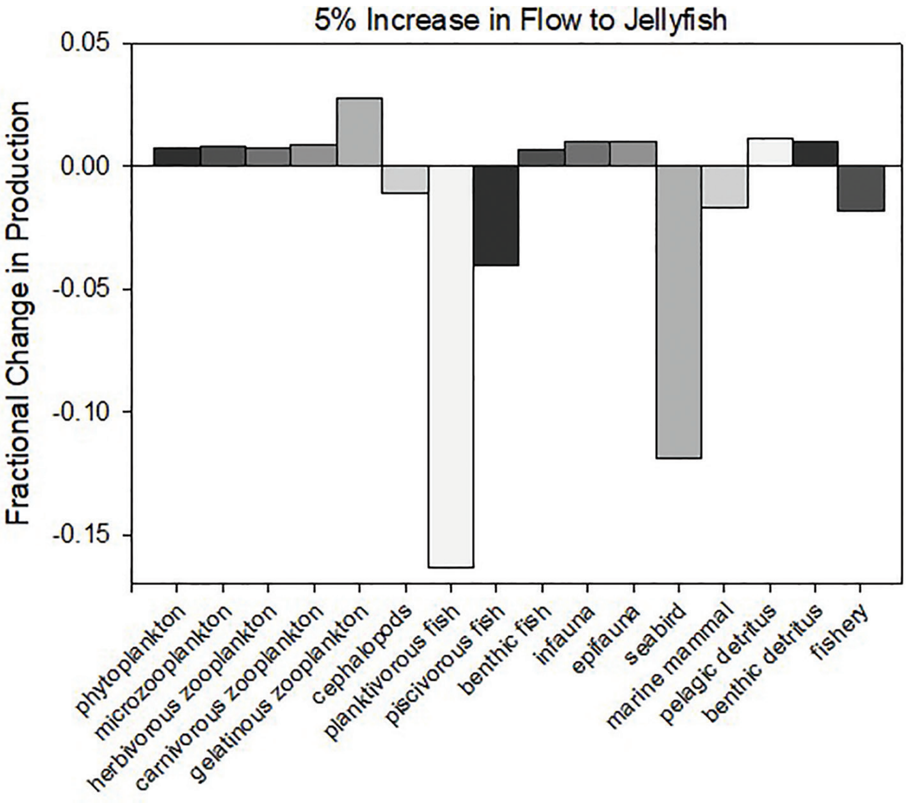


Figure 35 Output (fractional change in production of each trophic group) of a scenario from the re-expressed producer-driven end-to-end ECOPATH model where the amount of food going to jellyfish is increased by 5% compared to the base model, without any increase in the total productivity of the model (modified from Brodeur et al. 2011).

These end-to-end models have been extended to examine interannual variability in the relative roles that jellyfish, forage fish and euphausiids play in the Northern California Current driven by nutrient input rates (Ruzicka et al. 2012). These results indicate that jellyfish have a much greater footprint (the direct and indirect impact of a consumer on lower trophic levels) and smaller reach (the direct and indirect impact of a consumer on higher trophic levels) than forage fishes, and much less than euphausiids (Brodeur et al. 2011, Ruzicka et al. 2012). Jellyfish were thus a much less efficient energy transfer node in the foodweb than either other consumer groups. Additional work has compared the northern California Current to other North Pacific ecosystems including the Gulf of Alaska and eastern Bering Sea (Ruzicka et al. 2013, 2020, Robinson et al. 2014), and found that jellyfish are more important as consumers in the northern California Current than either of these other systems. Similarly, a lower trophic model that included a dominant scyphozoan jellyfish (*Chrysaora melanaster*) suggests the lower trophic Bering Sea ecosystem has little sensitivity to changes in jellyfish consumption (Gibson & Spitz 2011). However, the critical importance of *Chrysaora fuscescens* and other gelatinous prey to leatherback sea turtles, and potentially other select predators is a reminder that the role of jellyfish in food webs and to higher trophic-level groups should not be understated (Hetherington et al. 2019).

Canary Current ecosystem

Description

The Canary Current system is located along the NW coast of Africa from the Bissagos Islands in the South of Guinea-Bissau (around 11°N, 16°W) and Senegal to Morocco near the Strait of Gibraltar (around 36°N, 5°W), with a northern extension along Portugal and north-western Spain referred to as the Western Iberian Upwelling System. The whole system can be divided into two major domains associated with either the south-eastern boundary of the North Atlantic subtropical gyre (NASG) or the north-eastern North Atlantic tropical gyre (NATG) (Figure 36) (Pelegrí & Peña-Izquierdo 2015). The area is characterized by four waters masses: North Atlantic Central Water (NACW), North Atlantic Deep Water (NADW), Antarctic Intermediate Water (AAIW) and intermediate waters from the Mediterranean (MW) (Vélez-Belchí et al. 2015).

Three water masses are identifiable off Northwest Africa: South Atlantic Central Water (SACW), Eastern North Atlantic Central Water (ENACW) and Mediterranean Intermediate Water (MIW). In the upper water layer (0–500 m), the SACW and ENACW are dominant, with the well-oxygenated ENACW mixing with the salty sub-11°C MIW coming from the Strait of Gibraltar. A frontal zone is located off Cape Blanc at 21°N that separates the SACW and ENACW where mixing occurs. The ENACW has a salinity of ~36.7, whereas the SACW has a lower salinity maximum of 35.8 (Emery 2001), and off Mauritania the latter water has dissolved oxygen concentrations approaching 1 $\mathrm{mL \cdot L^{-1}}$ (Glessmer et al. 2009).

Seasonality in the rhythm of the Azores anticyclone, the Saharan depression and the Intertropical Convergence Zone (ITCZ) determines the balance of the trade winds in the region and therefore the mode of circulation along the West African coast (Wooster et al. 1976, Parrish et al. 1983): it influences the average length of the upwelling season. Upwelling along the coast of northern and central Morocco occurs in summer (Wooster et al. 1976, Roy 1991, Makaoui et al. 2005) when wind stress there is greatest (Barton et al. 1998, Pelegrí et al. 2005), while off Mauritania and Senegal it occurs in winter. The Saharan Morocco enjoys permanent upwelling in two well-defined zones: between Cape Boujdor and Dakhla and the between Cape Barbas and Cape Blanc (Hughes & Barton 1974, Parrish et al. 1983).

The Cape Blanc region (20°50′N) is the southern limit of summer upwelling (Barton et al. 1998). It is considered as a mixing zone of two bodies of water of different origins, ENACW and

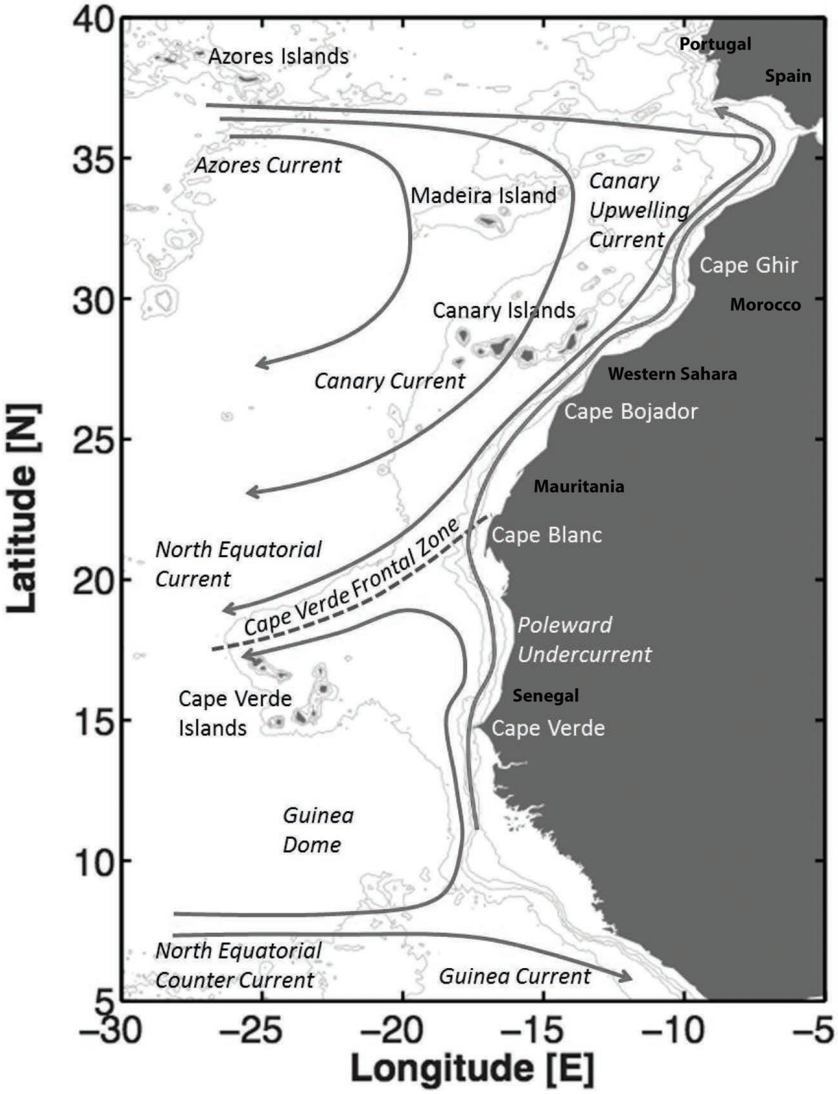


Figure 36 Map showing the key geographic features and oceanographic currents off NW Africa (Pelegrí & Peña-Izquierdo 2015).

SACW (Roy 1991). The shift of the SACW towards the north is observed up to a critical latitude of 23°N (Hagen 2001), which gives the zone between 21 and 23°N a particular-rich plankton (Binet 1991).

As would be expected, temperature at the surface and depths of 100 and 200 m shows winter and spring as the coldest seasons while summer and autumn are the warmest (Figure 37) (Benazzouz et al. 2014). According to Valdés & Déniz-González (2015), surface water temperatures in the region have increased by an average of 0.82°C per decade for the period 1982–2013.

The dynamics of plankton assemblages and populations following upwelling has been described in numerous works off NW Africa and, as in other EBC systems, the highest production is observed after the rise of deep water to the surface (Grall et al. 1982). In northern Morocco, where upwelling is seasonal, there is a significant lag between the development of phytoplankton and that of

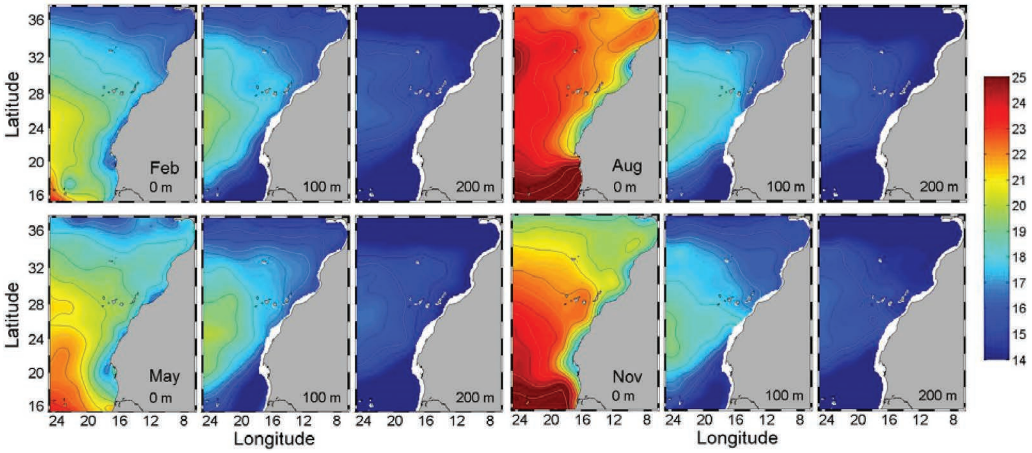


Figure 37 Seasonal changes in ocean temperature off NW Africa at sea surface, 100 and 200 m (Pelegrí & Benazzouz 2015).

zooplankton, which leads to a mismatch in productivity and a system imbalance (Furnestin 1957, 1976). Further south, where upwelling is permanent, the highest annual production rates are observed between Cape Barbas and Cape Blanc (Pelegrí & Peña-Izquierdo 2015). In this zone, phytoplankton blooms are observed on the fringes of the upwelling plume and zooplankton take maximum advantage of this downstream of the upwelling centre (Grall et al. 1974, Dupouy et al. 1986 in Binet 1991). Ecological transfer from phytoplankton to zooplankton is generally poor over the continental shelf owing to the temporal mismatch in response of primary and secondary producers (Binet 1991), although rapidly developing species, such as salps and cladocerans, can be abundant there (Le Borgne 1983).

North of 25°N, low concentrations of chlorophyll were observed offshore and high concentrations were noted near the coast (Auger et al. 2015) (Figure 38). In the south, however, high concentrations of chlorophyll extended well offshore (Figure 39). Based on the Intergovernmental Oceanographic Commission (IOC) Technical Series Report (Valdés & Déniz-Gónzález 2015), the chlorophyll concentration computed from SeaWIFS (1998–2003) shows a negative trend in the whole area, except for the area between Cape Blanc and northern Mauritania (Figure 39).

The Canary Current system is markedly heterogeneous, with a mosaic of mesoscale structures that reflect spatial and temporal variability often associated with the shape of the coast, bathymetry and local winds. Fronts, filaments and eddies play an important role in coupling physical and biological processes, exporting coastal water offshore (McGillicuddy et al. 1998) to increase primary production there. Surface eddies can modify circulation leading to a decrease in upwelling intensity McGillicuddy et al. 1998), whilst the relatively fine filamentary structures (Flament et al. 1985) that are often associated with capes (Marchesiello et al. 2003) can extend offshore over great distances to connect coastal upwelling with the open sea (Figure 39). These structures represent one of the permanent and dominant components of the dynamics of upwelling systems (Chavez et al. 1991), exporting nutrients (Jones et al. 1991), chlorophyll and zooplankton to the open sea, and their distinctive temperature and chlorophyll signals can be observed by satellite (Benazzouz et al. 2014). Two near-permanent filaments are located at Cape Ghir (30°38′N) and Cape Blanc (21°N), while other filaments may originate at Cape Juby (27°56′N), Cape Boujdor (26°12′N), or in between (Barton et al. 1998). Filaments are linked to upwelling and are therefore more frequent during summer in the north.

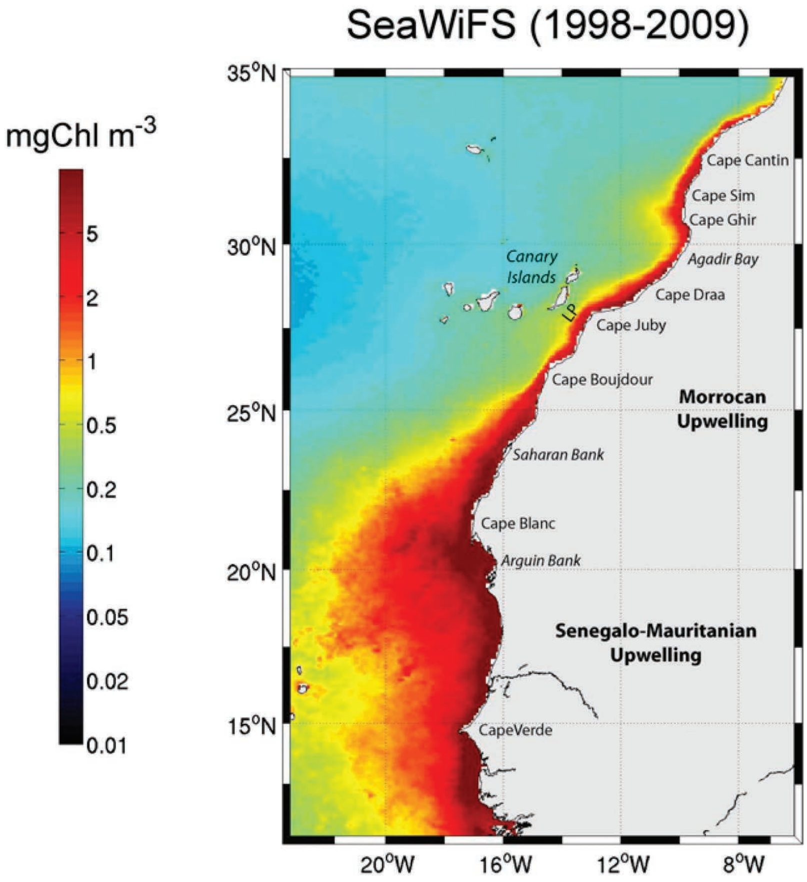


Figure 38 Surface distribution of chlorophyll a obtained from SeaWIFS, averaged over the period 1998–2009 (Auger et al. 2015).

Macromedusae

Species composition

Our knowledge of jellyfish in the Canary Current system is very limited by comparison with that from the other three systems, and mostly of a comparatively qualitative or anecdotal nature. Although jellyfish science in the region is in its infancy, it is already very clear that there are pronounced differences between the fauna of the Canary Current and the balance of the EBC systems.

According to data from the Institut National De Recherche Halieutique (INRH, Morocco) and the Consejo Superior De Investigaciones Científicas (CSIC, Spain) (Prieto & Idrissi 2020), and historic literature from the region, nine species of large jellyfish have been inventoried from the Canary Current system, the most common of which is the cystonect siphonophore *Physalia physalis*. Although this species is recovered throughout, it is more frequently observed in the northern zone, West of Africa. Of the scyphozoans, *Rhizostoma luteum* is now often observed along the Atlantic coast of the Iberian Peninsula (mainly in the Gulf of Cadiz), after having been rediscovered after 60 years without record (Prieto et al. 2013), and its distribution is known to include the Canary Current system (Kienberger & Prieto 2018). *Catostylus tagi*, although typically found further north, is known to occur occasionally in Canary Current system (Jarms & Morandini 2019). *Pelagia noctiluca* and *Chrysaora hysoscella* have both been recorded, with the former being significantly more

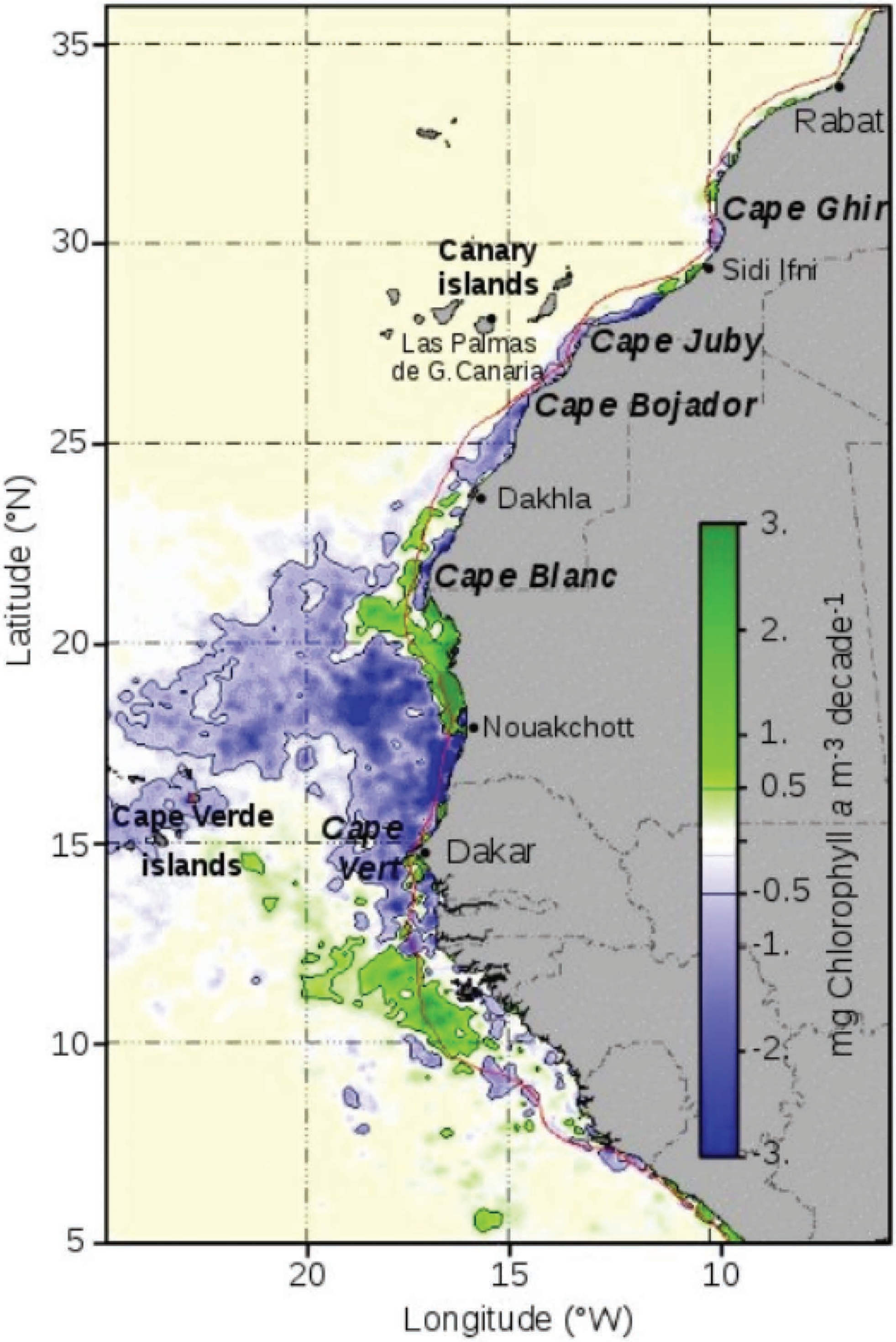


Figure 39 Trends in concentration of chlorophyll (1998–2003) off NW Africa over the period 1998–2003. Data SeaWIFS (Demarcq & Benazzouz 2015).

common than the latter. *Phacellophora camtschatica* is uncommon, as too are a species of *Aurelia* and a species of *Drymonema*. Finally, the cubozoan *Carybdea marsupialis* has a permanent population in the Gulf of Cadiz, and it has been spotted historically in the NW African coast of Morocco (Furnestin 1959). Although species of the hydrozoan *Aequorea* have been noted in the region, they are uncommon. Photographs of the commonly collected species are shown in Supplementary Figure 6.

Distribution

Information on the distribution of macromedusae in space and time is limited, primarily because jellyfish are neither routinely encountered nor measured during regular fishery surveys. Using pooled catch data from a variety of research cruises aboard the Amir Moullay Abdelah, Charif El Idrissi and the RV Dr. Fridtjof Nansen over the period 1998–2017, it would appear that jellyfish are most frequently caught between latitudes 22 and 23°N (Figure 40). Distribution changes seasonally and jellyfish are encountered across the sampling area to 32°N during autumn, but are more restricted (22–26°N) during spring and summer (Figure 40).

The INRH has set up a national programme to monitor gelatinous taxa, through a combination of field surveys and questionnaires. Surveys target commonly frequented beaches and areas most affected by stranding; questionnaires target fishermen, surfers, civil authorities and the local community members. The INRH also has a monitoring network along the Moroccan coastline in order

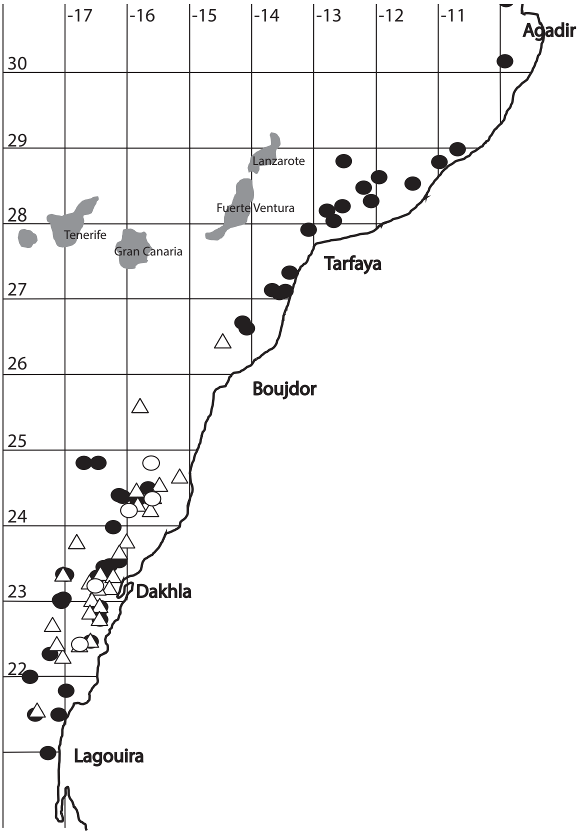


Figure 40 Seasonal distribution of jellyfish catches off the coast of Morocco, 1990–2016: spring (open circles), summer (open triangles), autumn (solid circles) (from Idrissi et al. 2018a).

to follow the development of these species and the evolution of invasions. In addition, land-based observation campaigns have been conducted jointly with the Maritime Fishing Delegations of the districts concerned, local artisanal fishermen's cooperatives and other stakeholders in the marine environment (Mdiq, Casa, El Jadida). The objective of this monitoring programme is to communicate public health alerts and to raise scientific awareness among fishers and other community members, while additionally allowing the collection of baseline biodiversity information.

Stranding data collected along the Atlantic coast of Morocco indicate that the dominant species are *Physalia physalis*, *Pelagia noctiluca* and *Rhizostoma luteum* (Figure 41). *Physalia physalis* appears on shores from February to June, with a maximum in April, while *Pelagia noctiluca* is stranded from June to November, being most frequent during August and September. In the case of *Rhizostoma luteum*, strandings occur in two periods: during March to May and then between September and December. Owing to the tourist value of beaches in the Canary Islands, a network of observers has been established who monitor popular resorts. The extensive data obtained from this monitoring programme confirm that the dominant and recurrent species are *Physalia physalis* and *Pelagia noctiluca* (Prieto & Idrissi 2020). As observed along the coast of Morocco, *Physalia physalis* is present from January to June, with a maximum in March, while *Pelagia noctiluca* is present year-round, with a maximum in November. The numbers of *Physalia physalis* and *Pelagia noctiluca* stranded in the Canary Islands are one and two orders of magnitude larger, respectively, than noted off Morocco (Figure 41).

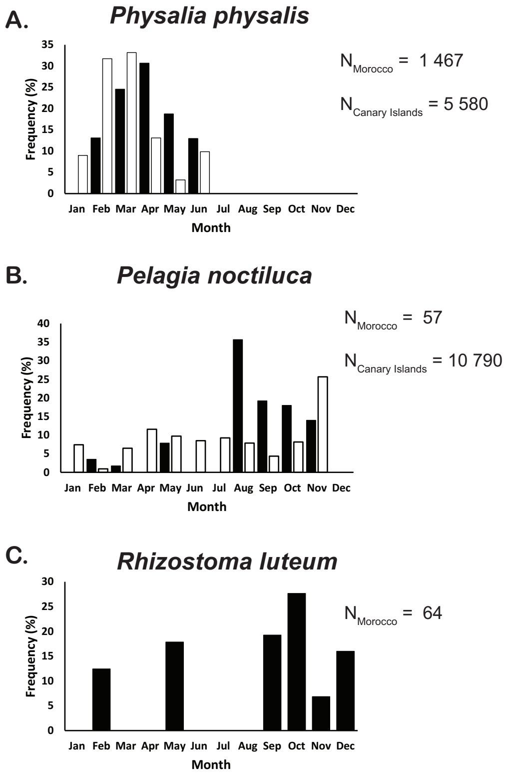


Figure 41 Seasonal changes in the relative abundance (% annual total, *N* shown) of commonly stranded jellyfish observed on the Atlantic coast of Morocco (solid bars) and on targeted beaches in the Canary Islands (open bars): 2009–2019 (Idrissi et al. 2018b, Prieto & Idrissi 2020).

It is very likely, in the case of *Physalia physalis*, that strandings would have followed periods of onshore winds (Shannon & Chapman 1983) and they often occur after strong west or west–north–west winds and very large swells; as has been observed off the Atlantic coast of the Iberian Peninsula (Prieto et al. 2015). Fishers at sea off Oualidia and El Jadida (southern Casablanca) have all confirmed the presence of what they refer to as "Affia" during late winter and spring and indicate that they are most abundant at depths of about 70 m.

Although specimens of medusae are now measured when collected, robust data are missing. Off Ain Diab, El Jadida and Laayoune, it would appear from unpublished data that *Physalia physalis* stranded early in the year have larger floats (mean 14.5 cm) than those stranded in late April and early May (mean 8.8 cm). Furthermore, the majority of individuals collected in winter are mature (70%), whilst only 41% were mature during late spring (INRH unpublished data).

From an analysis of all the data collected along the coastlines of both Morocco and the Canary Islands (Prieto & Idrissi 2020), it would appear that there is a considerable interannual variability in the number of stranded jellyfish (Figure 42), with total numbers reflecting the abundance of *Pelagia noctiluca* rather than *Physalia physalis*. The two dominant species do not appear to fluctuate in tandem, and evidence from further north (the Gulf of Cadiz) indicate that strandings of *Physalia physalis* there are related to very negative values of the North Atlantic Oscillation (NAO) (Prieto et al. 2015). The data are too scarce to demonstrate any clear relationship in the Canary Current system as yet, although the highest numbers of stranded colonies seem to be linked to positive (not negative) NAO indices (Figure 43). *Rhizostoma luteum*, which was absent from stranding records in the Canary Islands, also shows interannual variations in relative abundance but is generally uncommon.

Unfortunately, further information about jellyfish in the Canary Current system, for instance relating to their reproduction or their interactions with humans and fisheries, is entirely lacking, although as in the other EBC systems, jellyfish have been seen to be consumed by benthic scavengers (Supplementary Figure 7). Information on the fatty acid composition of *Rhizostoma luteum* is provided in Supplementary Table 5.

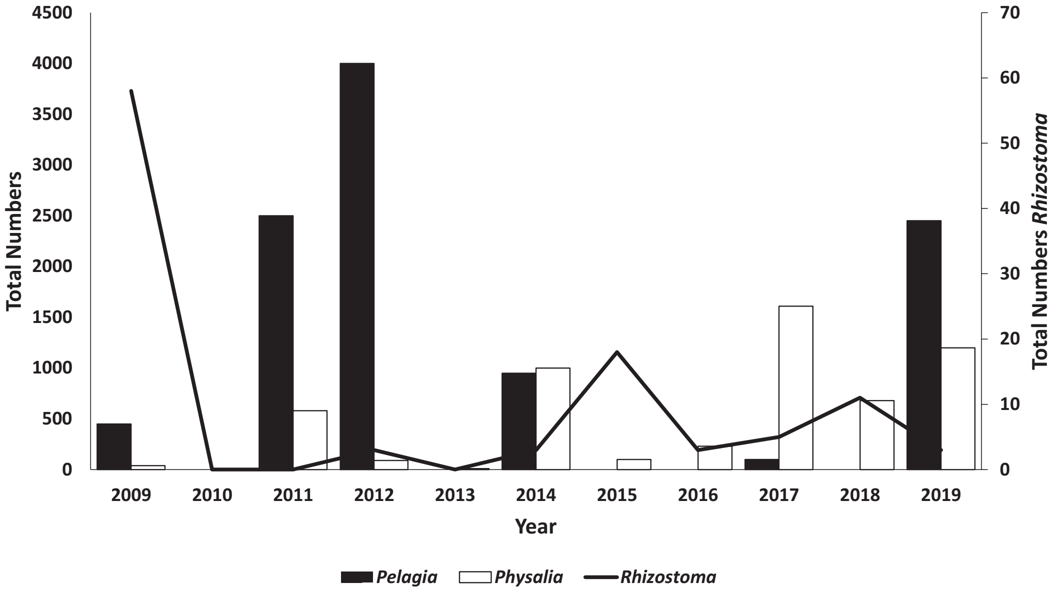


Figure 42 Interannual changes in the numbers of jellyfish stranded in the Canary Current system. Data for *Rhizostoma luteum* recorded only along the coast of Morocco. Data from Idrissi et al. (2018b) and Idrissi (2020).

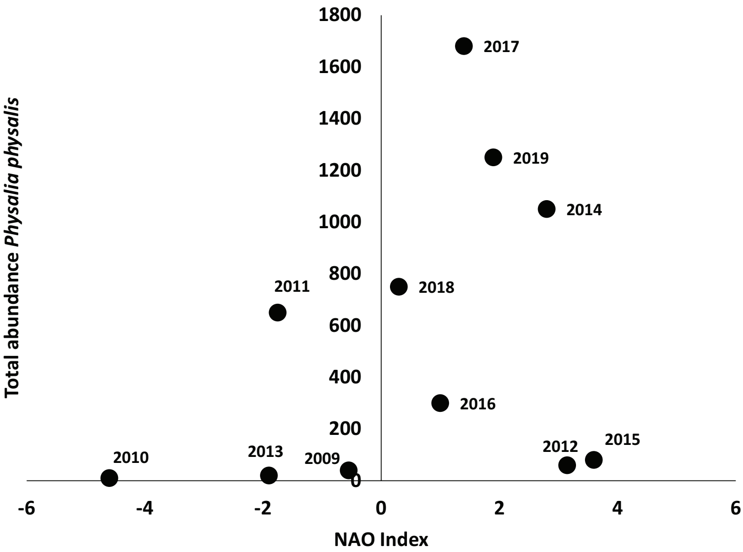


Figure 43 Scatterplot showing the relationship between the total number of stranded *Physalia physalis* recorded in the Canary Current system and the NAO index.

Synthesis

The species

Species of *Chrysaora* and *Aequorea* appear to dominate the macromedusae in three of the four EBC systems, the exception being the Canary Current, where robust data relating to abundance and distribution at the species level are lacking. Whilst our understanding of the phylogenetic relationships among species of *Aequorea* is poor, the same is not true of *Chrysaora* – although the pattern is far from clear. Bayha et al. (2017) have recently indicated that the genus *Chrysaora* is paraphyletic within the family Pelagiidae and argue that if the identity of *Mawia*, *Sanderia* and *Pelagia* is upheld, then it would be necessary to break up what is currently *Chrysaora* and erect an additional three genera to take account of the embedded structure (Bayha et al. 2017). Although these results are in contrast to those by Gershwin & Collins (2002), Morandini & Marques (2010) and Avian et al. (2016), they are based on a comprehensive suite of unambiguous molecular markers (Bayha et al. 2017).

Updated molecular trees are provided here as Figures 44–46, which incorporate the newly recognized *Chrysaora agulhensis* (Ras et al. 2020) and *Chrysaora pseudoocellata* (Mutlu et al. 2020). Sequence data for the COI and 18S gene regions were extracted from GenBank as these were available for the largest number of species. Detailed information around sequences used can be obtained from Supplementary Tables 6 and 7. Gene regions were aligned separately using the Geneious sequence aligner, under default settings, within Geneious v.11.1.4 (https://www.geneious.com). Datasets were then checked using GBLOCKS (Castresana, 2000) and regions with poor alignment were omitted from subsequent analyses. The Akaike and Bayesian information criteria were used in the programme jModeltTest v.2.1.2 (Darriba et al. 2012) to determine the best fit model of substitution for the COI (HKY+I+G), 18S (TrN+G) and a concatenated dataset (GTR+I+G). Datasets were analysed using both Bayesian Inference (BI) and maximum-likelihood (ML) frameworks, separately first and then as a concatenated dataset. Maximum-likelihood analyses were conducted using PhyML v.3.0 (Guindon et al. 2010), and node support was obtained using the substitution models determined previously by performing a 1000 bootstrap replicate analysis. Bayesian analyses were all performed using the BEAST v.2.3.2 software pipeline (Bouckaert et al. 2019), executed on the CIPRES high-performance computing portal v.3.1 (Miller et al. 2010). For the Bayesian analyses, three runs were executed and each run for 100 * 10^6 generations, sampling every 1000th generation. Runs were then checked for adequate chain mixing and convergence using the program Tracer v.1.6 (Rambaut et al. 2018) and 25% of trees discarded as "burnin" using the program LogCombiner v.2.6.3 (Bouckaert et al. 2019). Using TREEANNOTATOR v.2.6.3 (Bouckaert et al. 2019), the 50% maximum clade credibility tree was computed along with the mean branch lengths and posterior probabilities. We then attempted to calibrate a molecular clock onto the COI and concatenated trees using BEAST v.2.6.3 (Bouckaert et al. 2019). For the concatenated dataset, COI and 18S gene regions were analysed under different substitution models as determined earlier but with clock models linked. We also used a birth–death incomplete sampling prior for both datasets and ran the MCMC chain for 200 * 10^6 generations, sampling every 1000th tree. We again followed the steps listed earlier to summarize the trees. All trees were visualized in FIGTREE v.1.4 (Rambaut, 2014). Lastly, mean interclade and intraclade pairwise sequence divergence "P" values were computed using MEGAX v.10.1.8 (Kumar et al. 2018) for the COI gene region and are shown in Supplementary Tables 8 and 9. The above analyses were repeated for available sequences of COI (substitution model: GTR+I+G) for the genus *Rhizostoma (Rhizostoma pulmo*, *Rhizostoma octopus*, *Rhizostoma luteum)* (Supplementary Tables 10 and 11).

Our analyses of *Chrysaora* support previous findings (Gershwin & Collins 2002, Morandini & Marques 2010, Avian et al. 2016, Bayha et al. 2017, Gómez Daglio & Dawson 2017), which define a NE Pacific clade comprising the four species that can be encountered in the California Current as basal. The two most southerly species *Chrysaora achylos* and *Chrysaora colorata* show the lowest levels of pairwise sequence divergence (8.6% ± 1.2, Supplementary Table 8) in this clade, and a potential split between these taxa occurred only ~8.6 million years ago (mya) (Figure 44). The analyses of Bayha et al. (2017) and Gómez Daglio & Dawson (2017) have suggested *Chrysaora melanaster* as the most basal lineage within this NE Pacific clade. Our analyses support this, showing high bootstrap support (100) and posterior probabilities (1) (Figure 45) for the basal placement of *Chrysaora melanaster* in the concatenated analyses. Interpretation of subsequent relationships is clouded by the unresolved position of *Chrysaora chinensis*, an observation in agreement with Bayha et al. (2017). Within the COI tree (Figure 44), *Chrysaora chinensis* is basal to all remaining taxa (low bootstrap support (51%) and posterior probability (0.35)), which is in agreement with the analyses of Gómez Daglio & Dawson (2017). However, the high bootstrap support (100%) and posterior probabilities (1) within the concatenated analyses (Figure 45) suggest *Chrysaora chinensis* is more likely to be basal to the clade comprising *Chrysaora pacifica*, *Chrysaora africana* and *Chrysaora pseudoocellata*. Regardless, the existence of a pan-Pacific ancestor enjoying a distribution in warm waters is not unlikely.

Our analyses consistently place *Chrysaora pacifica* basally in the East Atlantic clade with *Chrysaora africana* and *Chrysaora pseudoocellata*, and a split between these lineages took place ~32–67 mya (Figures 43 and 44). The palaeoceanographic processes that might have accompanied divergence are unknown, but could reflect the formation of the Bay of Bengal (Hu et al. 2017) and subsequent eastward movement along the East African coast to the South-East Atlantic. The pattern observed is not unlike that noted for *Pelagia noctiluca* by Ale et al. (2019), who showed populations from the Indian Ocean to be basal to those collected off southern Africa which in turn were basal to those of the North Atlantic.

Chrysaora quinquecirrha and *Chrysaora lactea* appear to be ancestral to the remaining clade, splitting from populations in the (likely) equatorial Pacific some ~64 mya (Figures 43 and 44). Speculating, this loosely coincides with timing of an asteroid impact in Mexico, which created very different environments on either side of the impact site (Smit & Hertogen 1980). This in turn could have led to the further separation of populations now invading the North-East Atlantic: some spreading northward and diverging into *Chrysaora quinquecirrha*, others moving southwards to

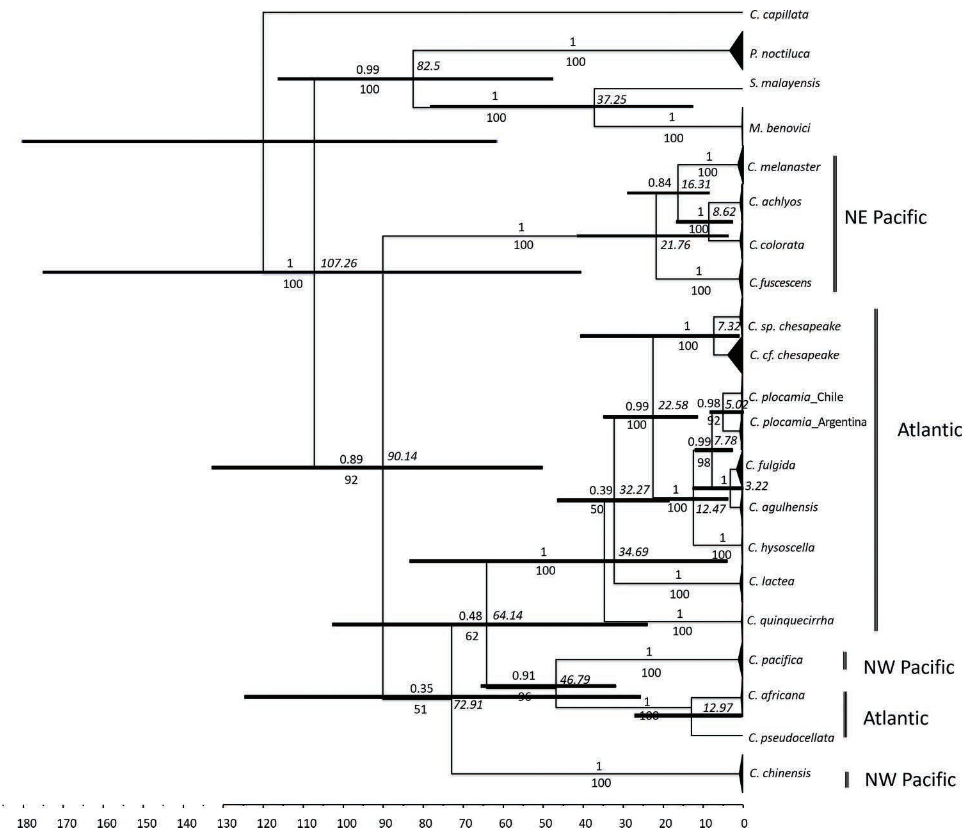


Figure 44 Rooted time calibrated phylogeny for all putative taxa within the genus *Chrysaora*, based on the COI gene region, extracted from GenBank. Sequences for *Mawia* and *Pelagia* have been included here as well for a total of 132 sequences. All analyses performed using BEAST v.2.3.2 (Bouckaert et al., 2019). Posterior probabilities are shown above branches while bootstrap support values are given below branches. Estimated divergence times are represented adjacent to nodes and node_height_95%HD applied to all internal nodes to display error rates. Scale is represented in mya. The tree has been shaded in order to illustrate well-supported lineages. Detailed information around the sequence data can be obtained from Supplementary Table 6.

eventually form *Chrysaora lactea*. Whilst the latter species does not appear at this stage to have undergone any further diversification, the taxa occurring within the North-West Atlantic appear to have been a source for those in the North-East (*Chrysaora hysoscella*) and then South Atlantic (*Chrysaora fulgida*, *Chrysaora agulhensis* and *Chrysaora plocamia*).

Our analyses consistently place *Chrysaora plocamia* from the South-West Atlantic and South-East Pacific in a close relationship with, but basal to, taxa from the South-East Atlantic (*Chrysaora fulgida* and *Chrysaora agulhensis*). Bayha et al. (2017) made similar observations, and our data indicate a potential divergence of *Chrysaora plocamia* around ~8 mya within the COI tree and an earlier split of ~16 mya within the concatenated tree. There are relatively low mean pairwise sequence divergences between *Chrysaora plocamia* and the South-East Atlantic species (~7%, Supplementary Table 8), and only slightly higher values (~9%, S3) are noted with *Chrysaora hysoscella* in the North-East Atlantic. Pairwise sequence divergences also revealed pairwise differences of 3.7% ± 0.6% between *Chrysaora plocamia* collected off the coast of Chile and those from Argentina. Dispersal is clearly a driver of diversification.

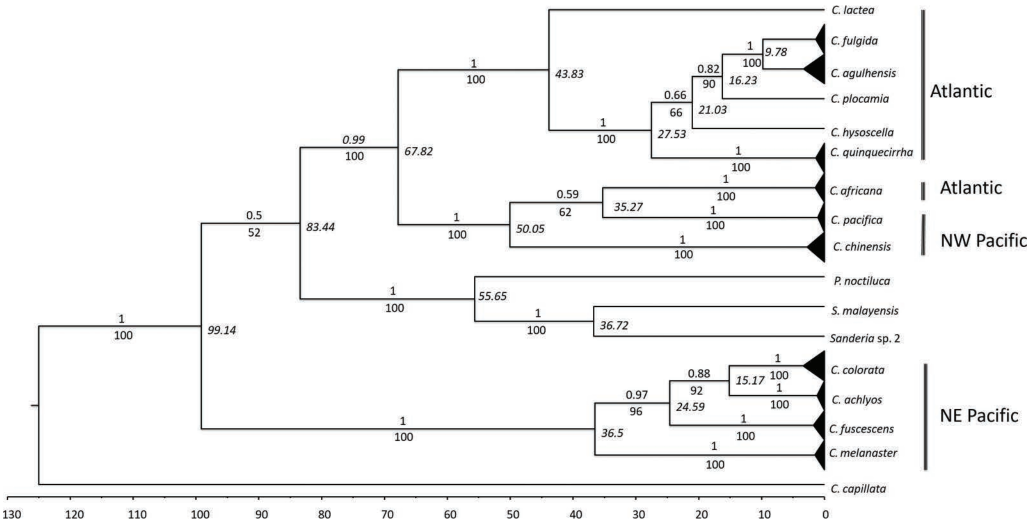


Figure 45 Rooted time calibrated phylogeny for all putative taxa within the genus *Chrysaora*, based on a concatenated dataset of COI and 18S gene regions, for a total of 50 individuals across various taxa within the *Chrysaora, Mawia* and *Pelagia*. Detailed information around the sequence data can be obtained from Supplementary Table 6. All analyses performed using BEAST v.2.3.2 (Bouckaert et al., 2019). Posterior probabilities are shown above branches, while bootstrap support values are given below branches. Estimated divergence times are represented adjacent to nodes. The tree has been shaded in order to illustrate well-supported lineages. Scale is represented in mya.

As previously noted, although species of *Chrysaora* dominate most EBC systems, this is not the case within the Canary Current system. Based on the close relationship between population in the South Atlantic, it is possible this system presents a recent break in gene flow between the northern and southern taxa. That does not mean to say that *Chrysaora* are not present in this system, because "during research vessel survey El Awam-IMROP, carried [out] in May 2014, a bloom of jellyfish, probably *Chrysaora fulgida*, which is probably a new species for the area, was observed in southern Mauritania's EEZ" (Inejih et al. 2014). Whilst we doubt that the named species was in fact *Chrysaora fulgida* (it was probably *Chrysaora hysoscella*, Supplementary Figure 6), the observation suggests that this species' rarity may be controlled by unknown environmental factors.

The genus *Rhizostoma*, which is widespread within the Mediterranean and North-East Atlantic, encompasses only three formally accepted taxa: *Rhizostoma pulmo*, *Rhizostoma octopus* and *Rhizostoma luteum* (Jarms & Morandini 2019). In both the Bayesian inference and maximum-likelihood analyses, *Rhizostoma luteum* is basal to the other two species, with the latter two showing a low mean pairwise divergence of only 5.4% ± 0.01 (Figure 46, Supplementary Tables 10 and 11). *Rhizostoma pulmo* and *Rhizostoma octopus* have been shown to have overlapping distributions, and the low pairwise divergence between the species suggests they may have diverged more recently. Within *Rhizostoma luteum*, our analyses revealed specimens from the South-East Atlantic have fewer nucleotide substitutions per site than those off North Africa and the western Mediterranean. As this species has also been recorded in the South-West Indian Ocean, it is not unlikely, given parallel patterns observed in *Pelagia* and *Chrysaora* (*pacifica, africana, pseudoocellata*) that colonization of the North-East Atlantic followed similar dispersal routes resulting in the patterns observed within their DNA.

As noted previously, the sardine *Sardinops sagax* (Bowen and Grant 1997) and species of the anchovy *Engraulis* (Grant et al. 2005, Silva et al. 2014) often dominate the biomass of small pelagic fishes in EBC systems, although they are not exclusively associated with them. Recent dispersal

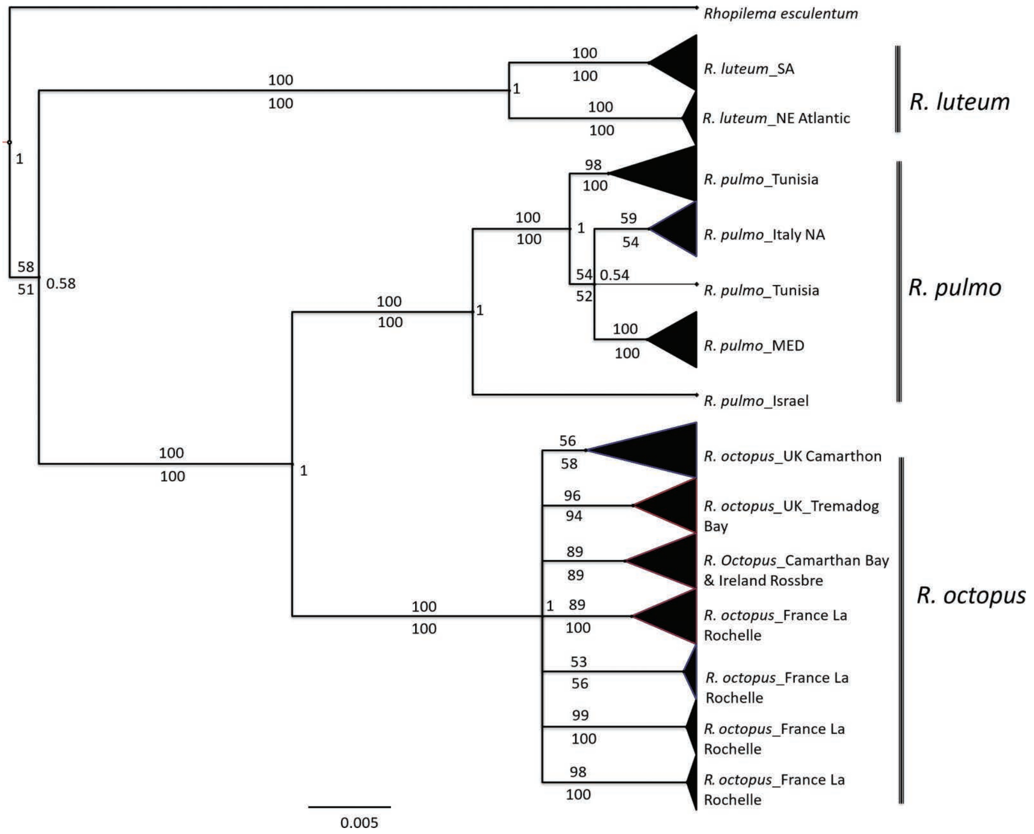


Figure 46 Maximum clade credibility BI tree, inferred using a dataset of 136 COI sequences for all putative taxa within the genus *Rhizostoma*, obtained from GenBank for various localities. Bayesian (BI) analyses performed using BEAST v.2.3.2 (Bouckaert et al., 2019); maximum-likelihood (ML) analyses performed in PhyML v.3.0 (Guindon et al., 2010). Bootstrap support values (BI) are shown above branches, while bootstrap support from the ML analysis are shown below branches. Posterior probabilities are displayed next to nodes. The tree has been shaded in order to illustrate well-supported lineages. Subtrees have been collapsed to improve readability, but detailed information around included sequence data can be obtained from Supplementary Table 7.

along the narrow, western margins of continental land masses, rather than vicariance, has been proposed to explain these distribution patterns (Bowen et al. 2016): the equator clearly having been a leaky barrier to antitopicality. The copepod *Calanoides nasutus* occurs in both the Canary and Benguela EBC systems (Viñas et al. 2015), where it may dominate mesozooplankton biomass (Peterson 1998). Although there are some differences in the genetic structure of populations of *Calanus nasutus* in the two Hemispheres, trans-equatorial dispersal is believed to maintain species integrity in the present (Höring et al. 2017). It has also been suggested that “founder dispersal may have played a major role in the generation of the current disjunct geographical distribution” among the four species of *Nyctiphanes*: three of which are also associated with EBC systems (D’Amato et al. 2008). Similar patterns have been described here for the *Chrysaora*.

The point of this wander off the beaten track is that some of the ecological characteristics of the different key species in the three EBCs that support populations of *Chrysaora* may have their roots in the different ancestries of the taxa involved. *Chrysaora fuscescens* in the California Current lacks richly folded oral arms and reaches a maximum size of only about 60 cm. By contrast, both *Chrysaora fulgida* and *Chrysaora plocamia* possess lush oral arms and may approach 1 m in diameter.

We should be careful not to over-generalize, as Abboud et al. (2018) have shown there can be significant genetic structuring within jellyfish populations of LMEs. These authors noted that this was especially pronounced within the California Current system[6] and in the genera *Aequorea* and *Chrysaora*: with some populations less than 1000 km distant from each other being quite distinct (Abboud et al. 2018).

Although the important marine resources within EBC systems may fail to display genetic substructure (e.g. Healey et al. 2020), it should be remembered that they are motile with different age groups using different parts of the wider system (e.g. Strømme et al. 2016). Fréon et al. (2009) implied that the major EBCs are neither latitudinally nor longitudinally homogeneous and as we have summarized above, different areas of each system have distinctly different environments, especially for organisms that are meroplanktonic, and whose benthic life-history stage is so closely tied to the benthos in shallow water. The data reviewed above suggest, perhaps not surprisingly, that there are regional differences in the ecology of populations within each system. In the Benguela Current system, for example, there is evidence of seasonality in the timing of reproduction by adult *Chrysaora fulgida* off Lüderitz, but not at Walvis Bay; there are differences too in the timing of strobilation (as evidenced by the presence of ephyrae in the water column) between Lüderitz and Walvis Bay. In the Humboldt system, *Chrysaora plocamia* shows a pronounced seasonality in appearance off Peru, which is at odds with that argued to be shown by populations off Chile. These differences may reflect localized adaptations to the local environment, but if there are barriers to mixing, then there is no reason to suppose that these differences may not become genetically fixed.

Following the methods employed by Abboud et al. (2018), our data for the Benguela Current ecosystem indicate significant geographic structure within populations of *Chrysaora fulgida*. This is most obvious at the southern boundary to the system, where *Chrysaora agulhensis* has recently been shown to have evolved from a common ancestor with *Chrysaora fulgida* only ~3 mya. The Agulhas Bank along the south coast of South Africa is environmentally distinct from that along the west coast, being influenced by the subtropical Agulhas Current, and local adaptations to the environment there have led to fixed genetic differences with respect to populations of *Chrysaora fulgida* in the Benguela *sensu stricto*. Interestingly, similarly large genetic differences appear to exist at the northern border of the Benguela, which influenced the subtropical Angola Current, with populations of *Chrysaora fulgida* north of Walvis Bay being ~1.2% ± 0.3% different (pairwise sequence divergence) from those to the south (Ras et al. unpublished data). Unsurprisingly too is the fact that populations of *Chrysaora plocamia* off the coast of Argentina are 3.7% different from those off Chile. As Abboud et al. (2018) note "analyses relying on fixed areas, such as LMEs, or a fixed geographic scale … are pragmatic but will often be mismatched to the actual scales and natural boundaries of jellyfish population structure. As a result, such analyses will often be mismatched to the actual scales, drivers, and consequences of jellyfish blooms" (Abboud et al. 2018, pp. 212).

The ecological role that jellyfish play in EBC systems: a synthesis

Large medusae are likely to play a critical, although poorly understood role in upwelling systems around the world. During bloom conditions, they are known to consume prodigious quantities of zooplankton that would otherwise be available for mid-trophic-level consumers that are utilized by larger fishes, seabirds and marine mammals and in some cases directly by humans (Robinson et al. 2014), thus indirectly affecting foodweb structure and fisheries production. A more direct negative effect on fish results from predation of medusae on early life stages of fish species (Purcell & Arai 2001), although assessing the impacts on fish populations has generally been attempted on a local scale (Möller 1984, Fancett & Jenkins 1988, Purcell 1989, Purcell & Grover 1990). Estimates of total numbers of a given larvae consumed in an ecosystem expressed as a percentage of total have been made in some larger shelf ecosystems (e.g. Brodeur et al. 2002, Tilves et al. 2016), but similar direct estimates have not been attempted in upwelling ecosystems. Fortunately, many larger medusae attain their peak biomass and likely consumption rates relatively late in the summer; hence, they are unlikely to overlap with the egg and larval stages of most fish species which spawn more often in non-upwelling seasons (see Suchman et al. 2008, Zeman et al. 2016). This may not be the case however in the Benguela system when peak biomass occurs when some fish species are known to spawn (Flynn et al. 2012). Therefore, predation impact on early life stages of fish by immature stages of medusae may be a significant source of mortality, but this interaction has not been examined in detail for any of the systems examined here.

Competition for limited prey resources is likely to have a more pronounced effect on many fish species, but it also much more difficult to quantify. Opdal et al. (2019) used time series data and energy consumption relationships to examine the relationship between jellyfish, forage fishes and available zooplankton in several ecosystems including the California Current and Benguela Current, and found little support for the hypothesis that jellyfish were trophically replacing forage fishes. In a more direct approach, several attempts have been made to examine the diet overlap and potential competition between large medusae and pelagic fishes (Purcell & Sturdevant 2001, Brodeur et al. 2008b). This has been stimulated by the observation of an inverse relationship between time series of abundances of macromedusae and small pelagic fishes (Brodeur et al. 2002, 2008b, 2014, Robinson et al. 2014). The spatial and trophic overlap of two large medusae, *Chrysaora fuscescens* and *Aurelia labiata*, and several pelagic fishes in the upwelling region of the Northern California Current was examined during late summer by Brodeur et al. (2008b). Diet overlap (based on stomach analyses and stable isotope ratios) was substantial for several key forage species, including Pacific sardine, Pacific herring, Pacific saury and northern anchovy due to a similar utilization of small copepods and euphausiid larvae. Combined with a measure of geospatial overlap, these species were considered by Brodeur et al. (2008b) to have the greatest potential to compete with both jellyfish species.

Although the interactions between jellyfish and other predators often appear to be negative, there are some benefits to fish from having large numbers of gelatinous zooplankton present. One is the notable importance of jellyfish as a food source for many upper trophic-level organisms, which is receiving new scrutiny with the use of alternative biochemical and genetic methods of examining predator–prey interactions (van der Bank et al. 2011, Cardona et al. 2012, Lamb et al. 2017, Hays et al. 2018, Marques et al. 2019). Anomalous increases in gelatinous zooplankton in upwelling systems could enhance production of species adapted to feeding on them (Utne-Palm et al. 2010) or lead to trophic shifts to gelatinous prey in normally crustacean feeding fishes (Brodeur et al. 2019). Another well-documented interaction between jellyfish and some fish species is the association of early life stages of fish with cnidarians (Purcell & Arai 2001). Griffin et al. (2019) reviewed the literature on this and found that jellyfish provide habitat for larval and juvenile fishes, many of which are commercially important, using their hosts for protection from predators as well as opportunistically feeding upon their hosts captured prey, which may lead to reduced fish mortality and increased recruitment. Although it is likely that a number of fish may be commensal with macromedusae in the systems examined here, this has not been the subject of extensive study up to this point.

Jellyfish, fisheries and climate: a synthesis

Using data available at the time, Bakun (1990) first highlighted the idea that an increase in global temperature would result in intensified upwelling, effectively as a result of the stronger atmospheric pressure gradients that are anticipated to develop between land and sea. While he suggested this would be accompanied by increased phytoplankton production, he emphasized the lack of certainty about the fate of this production, indicating it could be diverted to mesopelagic rather than epipelagic species and that it could result in increased organic sedimentation and an elevated chance of hypoxia (Bakun 1990). The Bakun Hypothesis, as it subsequently became known, has been elaborated upon by a number of authors in the intervening years (e.g. Snyder et al. 2003, García-Reyes et al. 2015, Sydeman et al. 2014, Wang et al. 2015), and although there have been some modifications to the detail, it has been widely accepted.

In their most recent contribution to the subject, Bakun et al. (2015) summarized the scenario thus: "anticipated changes include the poleward migration of the Oceanic High and source waters. Continental thermal lows are anticipated to deepen, which will intensify upwelling-favo[u]rable (equatorward) winds. Changes in the water column include greater stratification, greater rates of upwelling, and greater offshore transport as well as the offshore migration of the upwelling front" (Bakun et al. 2015; pp. 88). Although the exact implications of these anticipated changes are still unclear, Bakun et al. (2015) suggested they could include changes in the composition and production of autotrophs (hence too, heterotrophs), spatial and temporal mismatches between production and consumption, and changes in species distributions; the latter in part reflecting elevated anoxia and acidification, as well as changes in the distribution of prey. These, and other authors, have stressed that EBC systems are naturally variable, and as such may be resilient to some of these changes (Bakun et al. 2015, García-Reyes et al. 2015) in the absence of over-exploitation or additional major anthropogenic impacts (Bakun et al. 2015; our emphasis). Bakun et al. (2015) also noted that "shifts toward an increasing dominance by zooplanktivores", such as jellyfish, could lead to unpredictable and/or undesirable (from a human perspective) ecosystem states as "more versatile components … might successfully exploit opportune ecological loopholes that develop" (Bakun et al. 2015; pp. 91). The latter statement could be interpreted in the context of predator-free space, and in the case of jellyfish, it could effectively lead to the former: jellyfish enjoying such space in the absence of pelagic fishes that could then lead them to become dominant zooplanktivores (see e.g. Bakun 2006, Richardson et al. 2009).

Following Mills (2001), a number of (perhaps now dated) papers were published in the first decade of the twenty-first century that attempted to synthesize what we knew about jellyfish populations globally at the time (e.g. Purcell et al. 2007, Richardson et al. 2009). One of the key take-home messages from these two papers, in particular, was that jellyfish have a suite of adaptations that could enable them to take advantage of marine environments that have been modified in the Anthropocene: (some species have) a remarkable tolerance to low concentrations of dissolved oxygen as medusae and polyps; many species can feed across a very wide range of prey, including protistans, efficiently (Acuña et al. 2011); warming seas can promote individual and population growth (of some, but not all, species) (Boero et al. 2016), and the proliferation of hard substrata associated with coastal development, energy and aquaculture increases the opportunities for the settlement of polyps (Duarte et al. 2012).

With the exception of the latter, which is generic across all coastal systems, Bakun et al.'s (2015) scenarios talk directly to some of the adaptations of (some) jellyfish. Increased levels of hypoxia may benefit some jellyfish as they do not appear to be affected by low oxygen conditions as fishes are, with notable exceptions (Salvanes et al. 2015). Indeed, low oxygen has been shown to enhance jellyfish predation on fish larvae compared to fish predation on the same larvae (Shoji et al. 2005). An increase in temperature will place stress on both predation and competition between forage fishes and jellyfish in EBC systems by increasing the feeding and growth rates of some medusae and changing the structure of the plankton assemblages. A change in the characteristics (temperature, salinity, oxygen) of nearshore bottom water may stimulate/inhibit ephyra production, although subsequent offshore losses may weaken coastal populations. However, much of this is speculation and we must be cautious about making generalizations (Pitt et al. 2018). After all, while a warming sea may favour budding by scyphopolyps, it may decrease opportunities for strobilation and the actual recruitment of jellyfish (Lynam et al. 2004).

Although changes in global temperature will have an impact on climate-scale systems such as El Niño Southern Oscillation (ENSO), exactly how they will be affected is unclear (Bakun et al.

2015). In the Humboldt Current system, the spatial distribution and abundance of *Chrysaora plocamia* are both expected to increase during El Niño years and decrease during La Niña years (Quiñones et al. 2015). By contrast, populations of most cold-water species are expected to decrease in the California Current system during warming periods, but increase during cooler ones (Pearcy et al. 1985, Heitstuman 1994). Although comparable information for the Atlantic EBC systems is missing, it is clear that there is no "one-size-fits-all" explanation. Again, we need to be cautious.

In attempting to understand the likely effects of climate change on EBC systems, we cannot realistically ignore the simultaneous impacts of fisheries, especially for small pelagic fishes. And the text highlighted above, in reference to the conclusions of Bakun et al. (2015), is a reference to the situation off Namibia in the northern Benguela Current system (Roux et al. 2013). However, it is by no means clear that all EBC systems would behave similarly. Using a 40-year time series (1972–2014), Quiñones et al. (2015) examined the response of *Chrysaora plocamia* to both environmental variability and fishing pressure in the northern Humboldt Current system at a number of different timescales. Their results show that fluctuations in the biomass of *Chrysaora plocamia* were related to the environment, but not with the landings of anchoveta. Jellyfish biomasses were high and variable during the El Viejo warm regime in the 1970s and 1980s but low during the La Vieja cold regime known during the 1990s and 2000s (Quiñones et al. 2015). At shorter timescales and within the El Viejo regime, the peaks of jellyfish abundance coincided with events related to El Niño Southern Oscillation (ENSO). Anchoveta landings and the number of annual trips in the industrial fishery increased by a factor of three in the 1990s and 2000s, when jellyfish were scarce, but during the period of the greatest jellyfish abundance (1970s and 1980s), fishing pressure was low (Quiñones et al. 2015).

The northern Humboldt Current system is unique in its susceptibility to extreme interannual disturbances associated with the ENSO phenomenon, yet re-accommodates and recovers quickly without any apparent lasting impact (Bakun & Weeks 2008). Part of the reason for this may lie not so much with jellyfish but with the balance of key pelagic components. In the northern Humboldt Current system, the main pelagic resource is the anchoveta, which reaches age of first sexual maturity at one year in Peru (Perea & Roque 2005). Their short life provides anchoveta populations with an in-built resilience in the face of significant exploitation. By contrast in the northern Benguela Current system, sardine become sexually mature at two years of age (van der Lingen et al. 2006). Jellyfish are not common in the southern Benguela Current system off South Africa, perhaps because there are several species of small pelagic fish (anchovy and sardine) that occupy a similar niche, whilst off Namibia there has characteristically been just one: sardine (Boyer et al. 2001). The southern Benguela Current system is characterized by a narrow shelf and already pronounced offshore advection, whilst the broader shelf off central Namibia is remarkable for its retention mechanisms: the latter contributing to the build-up of coastal jellyfish populations.

Gaps in knowledge and constraints

Attempts to understand any species in any system require a sound knowledge of population dynamics. Sadly, the lack of targeted support for research into jellyfish means that the data on which our understanding is based are primarily derived from the by-catch of targeted fisheries surveys (Flynn et al. 2012, Brodeur et al. 2016). While "beggars can't be choosers", using fisheries surveys that are not specifically designed to quantify the structure of jellyfish populations has its limitations. When and where fisheries surveys are undertaken, what depths are sampled, and which gears are used are all dependant on the fish population of interest – not on the by-catch of jellyfish! While the ecosystem approach to fisheries management requires that we change our perception of jellyfish, and indeed much of the information showcased here illustrates that attention, more can and should be done.

Condon et al. (2013) have emphasized the value of collecting data that can contribute towards time series, because it is only with time series that we can measure change. Of course, it would be ideal to have a common set of standards, but the reality is that we are collecting by-catch data from different fisheries using different methods at different times of the year. Attempts to reduce the resulting data to a common standard will be no less fraught than using relative data, which, given the size of the commercial fleets operating in EBC systems, can be easily collected (see e.g. Flynn et al. 2012). Such data would, through time, allow us to explore regional links between population dynamics and both oceanographic/atmospheric conditions and other resources, and would also allow us to track what is happening outside of the time of year when fisheries-independent surveys are conducted. Relative data can also be collected using various community science programmes, as has been quite successfully deployed both more widely (Canepa et al. 2016) and more specifically (Benedetti-Cecchi et al. 2015) in the Mediterranean Sea. However, for such programmes to be useful, it is vital that they be maintained for the long term (Tredick et al. 2017).

The role of jellyfish in an ecosystem may be examined using dynamic simulations incorporated into dynamic mass balance or end-to-end models of whole systems. Although jellyfish were often omitted or underrepresented in early holistic ecosystem models (Pauly et al. 2009), recent iterations have included more robust estimates of abundance and trophic impacts and have shown the importance of this group to many systems globally (Lamb et al. 2019). Such models have been developed for the some of the systems examined here (e.g. Ruzicka et al. 2007, 2012, Brodeur et al. 2011, Robinson et al. 2014, Chiaverano et al. 2018) and have been used to examine different scenarios of increasing or decreasing jellyfish biomass on system functioning. While dynamic ecosystem models are in their infancy and subject to valid criticism (e.g. Boero 2013), our understanding of jellyfish roles in upwelling ecosystems can only benefit from a more complete incorporation of realistic jellyfish biomass and physiology.

Similarly, the role of jellyfish (and other gelatinous zooplankton) in carbon flux throughout the global ocean also requires more robust estimates of jellyfish abundance, physiology and trophic ecology. Recent evaluations indicate that the role of cnidarians, ctenophores and pelagic tunicates in marine carbon export to the benthos (through both carcass depositions and faecal flux) is likely to have been substantially underestimated (Wright et al. 2020), particularly for larger organisms not included in sediment trap estimates of carbon flux (Luo et al. 2020). Thus, a more accurate assessment of the role of jellyfish and other gelatinous zooplankton in EBC foodwebs is important to improving climate models and evaluating the role of carbon cycles in marine systems processes for climate change evaluation (e.g. Pauly et al. 2009).

As Gibbons & Richardson (2013) point out, studies of macromedusae are fraught because of their often-large size. This means that estimates of physiological parameters, especially those associated with feeding, are either based on more tractable, small individuals (e.g. Hansson et al. 2005) or on indirect measures (e.g. Purcell 2009, 2010). Efforts to address this shortcoming are desperately needed, as they would not only provide empirical validation of model outputs but also generate more explicit information about the interactions between species. Although stable isotopes ($\delta^{15}N$, $\delta^{13}C$) are potentially useful tools that can be used to place jellyfish in the context of their trophic environment, there are controversies over fractionation (Post 2002 *cf* D'Ambra et al. 2014), which serve to question their value (e.g. Wang et al. 2020).

We also know little about the interaction between life-history traits and population dynamics over different spatial and temporal scales. In fact, we tend to ignore the life cycle of jellyfish altogether (e.g. Wright et al. 2020), primarily because we know almost nothing about polyps. Indeed, polyps can be regarded as the "elephants in the room", which make jellyfish so different from other members of the plankton (Boero et al. 2008). While they are relatively easy to obtain by artificial means (e.g. Widmer 2008a) and are amenable to laboratory experimentation (e.g. Lucas et al. 2012), they have never been found *in situ* in any EBC system. Experiments on planula settlement have been widely conducted (Lucas et al. 2012), and there is an intuitive understanding of where polyps should be located, but as yet no serious searches have been conducted. However, we should be emboldened by Serrano's (2016) success in using settling plates to study *Chrysaora quinquecirrha* in Barnegat Bay, New Jersey, and renew our efforts. But if studies on polyps *in situ* cannot be conducted (Di Camillo et al. 2010), we could (at least) work on ephyrae as proxies for polyps, since they are identifiable in some of the EBC systems considered here (Widmer 2008b, Skrypzeck 2019). That said, with the exception of the very localized studies conducted off Namibia, routine and regular plankton collections are not being made. We do not deny the great advances in plankton ecology that have been made using the data collected by e.g. the California Cooperative Oceanic Fisheries Investigations (CALCOFI) (Gallo et al. 2019), but in truth, these samples are not collected close enough to the shore to yield useful information on ephyrae. While we remember that the CALCOFI programme was designed to answer questions relating to the interactions between the environment and economically valuable fish resources, the mismatch between fish needs and jellyfish needs is nevertheless frustrating. At the end of the day, however, without a knowledge of polyps *in situ*, we are denied an opportunity to fully understand wild populations (Gibbons et al. 2015). And this is a problem because, as the management of marine systems moves towards Ecosystem-Based Management, jellyfish may serve as an important indicator species for changing ecosystems worldwide (e.g. Samhouri et al. 2010).

But perhaps one of the biggest challenges facing jellyfish science in EBC systems relates to a lack of human capacity. The current number of specialists is too low to cover such a vast region, and the number of specialists on particular taxa is even lower. We believe that training in the taxonomy and ecology of gelatinous zooplankton, and stretching the gap between researchers from different fields (jellyfish researchers, physical oceanographers and fishery biologists), fishers, journalists and policymakers are essential to develop a better understanding of the ecological roles of jellyfish in the marine ecosystems. Such integration will be a critical element in the development of an ecosystem-based approach to fisheries management and to understand the importance of jellyfish in ecosystem functioning.

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Notes

1. Thirty-four specimens of Aequorea forskalea were, however, washed up stranded in the lagoon during January 2014: they ranged in sizes of 8–22 cm, with one specimen being 3 cm.
2. But see also Mohamed et al. (2019) for information on early gametogenesis in *Carybdea murrayana*
3. Podocysts are cysts that form at the base of the polyp that can then remain dormant when environmental conditions are inhospitable and that will form polyps when conditions are favourable.
4. Detailed information on the morphology and development of ephyrae of *Chrysaora fulgida* and *Chrysaora africana* can be found in Skrypzeck (2019), who noted six distinguishable ephyral stages. Stage 0 are newly released and least developed, while Stage 5 are most developed. As an individual grows and increases in size, so it develops increasingly more complex and medusa-like. A meta-ephyra stage is observed immediately before the individual becomes a medusa.
5. https://www.nwfsc.noaa.gov/research/divisions/fe/estuarine/oeip/g-forecast.cfm#TableSF-02.
6. Neither the Humboldt nor the Benguela LMEs were included in the analysis of Abboud et al. (2018).

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MARINE BIODIVERSITY IN KOREA: A REVIEW OF MACROZOOBENTHIC ASSEMBLAGES, THEIR DISTRIBUTIONS, AND LONG-TERM COMMUNITY CHANGES FROM HUMAN IMPACTS

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Abstract The present review provides a historical overview of the macrozoobenthos that supports Korean marine biodiversity set against a regional introduction to the oceanography and diverse marine habitats of Korean seas. We constructed a comprehensive meta-dataset of Korean macrozoobenthos to provide an up-to-date ecological inventory. In particular, we address faunal characteristics with respect to species occurrence, composition, and distributions along the Korean coasts. The ecology of the Korean macrozoobenthos is described in order of the West Sea, South Sea, and East Sea following the regional description of oceanography settings, in a consistent manner. Later, the impacts of anthropogenic pressures, such as coastal reclamation and oil spills, on long-term benthic community changes are also highlighted. We accounted for a total of 1915 macrozoobenthos species, belonging to 17 phyla, in the Korean marine environments. The most dominant phylum was Mollusca (670 species), followed by Annelida (469 species), Arthropoda (434 species), and Cnidaria (103 species). The most diverse communities inhabit the South Sea (1103 species), followed by the West Sea (829 species) and the East Sea (621 species). The highest regional numbers in each sea are comparable, in the West Sea (Taean: 510 species), South Sea (Jejudo: 511 species), and East Sea (Ulleungdo: 562 species). Subtidal areas, especially in the West Sea and South Sea, constituted the habitats with the greatest faunal occurrence, including predominantly soft bottom invertebrates. Polychaetes were the most widely distributed taxa, followed by bivalves, across the three seas. In general, the faunal assemblages and distributions seemed to reflect the typical habitat profiles for the environments, including well-developed tidal flats in the West Sea, rocky shoreline in the East Sea, and mixed features in the South Sea. Interestingly, the remote island of Jejudo was found to have a distinct faunal composition among the South Sea coastal areas, presumably as a consequence of its geographical and ecological isolation. Case analyses of the ecological impacts of coastal reclamations revealed long-term benthic community alterations in Lake Sihwa and the Saemangeum tidal flats. An analysis of faunal distributions over decadal periods showed substantial community alterations, particularly during periods of new dike construction. Signs of benthic community deterioration were evident in both areas, including the increased occurrence of opportunistic species and enriched organic indicators, which persisted even after the completion of dike construction. Although water quality seems to have recovered recently in Lake Sihwa owing to seawater circulation, the Saemangeum flats have yet to recover. Finally, we demonstrate the long-term ecological impacts of the 2007 Hebei Spirit Oil Spill (HSOS), the largest spill in South Korean national history, by analyzing 10 years of monitoring data. The HSOS disaster collapsed the entire marine ecosystem along the Taean coast and in nearby habitats, particularly mud bottoms. Although recovery pace varied across localities, the benthic community fully recovered after ~6 years, except

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for the limited hotspots, reaching ambient species baseline levels in terms of population, composition, abundance, and diversity index. The relatively fast recovery of marine ecosystem in Taean coast, say compared to the Exxon Valdez case, might suggest that the macrotidal West Sea coastal ecosystem is quite resilient. Overall, the present review supports the conclusion that Korea retains high marine biodiversity despite severe human impacts on coastal ecosystem sustainability. Although South Korean government agencies have long practiced ecosystem-based management efforts, their success has been limited to some extent by a fragmented approach. In the future, a holistic management strategy and framework for protecting organisms and habitats, as one ecosystem, would support the conservation of high marine biodiversity around the Korean Peninsula and elsewhere in the adjacent seas of East Asia.

Keywords: Biodiversity, Biogeography, Ecological checklist, Marine benthic invertebrates, Human impacts, Management and conservation

Introduction

Backgrounds and overview

South Korea (from here forward, Korea for simplicity) is located in the far eastern part of the Eurasian continental mass, between China and Japan; it is protected from the open Pacific Ocean by Japan (NGII 2016). The three-sided coasts of the Korean Peninsula, with west-, south-, and east-facing coastlines abutting the West Sea, South Sea, and East Sea, respectively, have some unique topographical and geographical characteristics (representative seascapes of the Korean coasts described in Table 1). Because the Korean economy and culture rely heavily on marine products, including artisanal and commercial fisheries and aquafarming sectors, the socioeconomic value of marine resources is highly significant (Koh & Khim 2014). The seas around Korea are affected by distinct regional natural conditions, including seasonal changes associated with the monsoon climate and dynamic oceanographic settings shaped by local macrotidal environments and the active mixing by warm and cold currents.

The dynamic marine environments around the Korean Peninsula are associated with high marine biodiversity. The 2015–2020 national marine ecosystem monitoring survey conducted in the three seas surrounding Korea catalogued the presence of 7619 marine species (MEIS 2021). These findings are consistent with the prior Census of Marine Life (Costello et al. 2010) in which the exclusive economic zone of South Korea was ranked as the most species-rich region in the world with some 32.3 species per unit area. Our recent reviews further highlighted high marine biodiversity for marine invertebrates in the Korean tidal flats along the western coast of Korea (Park et al. 2014a) and around the island of Dokdo (Song et al. 2017).

A notable unique feature of the Korean coastal waters is the convergence of diverse microhabitats from the three surrounding seas into a dynamic ecosystem. For example, along the upper intertidal zone of the West Sea, well-developed salt marsh beds with various halophytes, such as *Phragmites* and *Suaeda* plant species, provide nursery grounds for many marine organisms. Frequent blooms of microphytobenthos inhabiting the soft bottoms of the West Sea also support the upper trophic ecosystem. Our recent studies indicated that benthic primary production in the West Sea was quite high from a global perspective, supporting the high marine diversity in Korea-adjacent seas (Kwon et al. 2020). The rocky shoreline environment that prevails along the East Sea coast is home to diverse hardbottom plants and animals. Our recent review reporting the high occurrence of macrozoobenthos in the remote island of Dokdo (578 species; Song et al. 2017) revealed a major global biodiversity hotspot, with diversity comparable to that reported for the entire coastal span of the West Sea (624 species) (Park et al. 2014a), while the biodiversity on the South Sea, including the coastline of the island of Jejudo, has not been yet documented systematically.

Marine biodiversity is an index of ocean health that represents both species richness and habitat diversity. The maritime health status of South Korea, according to the 2019 Ocean Health Index

Table 1 General oceanographic conditions and socioeconomic information of Korean[a] coastal areas

Environmental characteristic	West Sea	South Sea	East Sea
Coastal landform	Submerged coast (Rias type)	Submerged coast (Rias type)	Emerged coast
Bottom topography	Sea bed gently slopes seaward (west to east) with tidal flats	Sea bed slopes gently seaward (northwest to southeast) with many islands	Sea bed deepens sharply from coast to seaward (east to west)
Coastal Location	126–127°E, 34–37°N	126–129°E, 34–35°N	128–129°E, 35–38°N
Coastline length, km	2450	2484	687
Tidal range, m	Megatidal (4.0–10.0)	Mesotidal (1.3–4.3)	Microtidal (0.2–0.5)
Ocean currents	Kuroshio Warm Current	Kuroshio Warm Current	Kuroshio Warm Current, Liman Cold Current
Seawater parameters			
Depth, m[b]	51 (124)	71 (198)	1497 (2985)
Transparency, m	1.6 (0.1–14)	5.4 (0.0–20)	9.4 (0.5–26)
Temperature, °C	14.3 (1.06–33.1)	15.8 (1.75–32.4)	10.6 (1.23–33.1)
Salinity, ‰	31.9 (27.7–91.0)	33.4 (12.4–36.1)	33.8 (28.9–36.7)
pH	8.06 (6.73–8.82)	8.10 (6.07–9.98)	8.04 (0.18–8.93)
DO, mg L^{-1}	8.62 (3.40–16.6)	7.85 (1.73–15.0)	8.60 (4.28–13.8)
COD, mg L^{-1}	1.25 (0.02–8.98)	1.01 (<0.01–8.29)	0.88 (0.01–6.36)
NH_3-N, µg L^{-1}	21.4 (<0.01–1030)	18.6 (<0.01–1060)	19.3 (<0.01–337)
NO_2-N, µg L^{-1}	7.18 (<0.01–117)	6.66 (<0.01–442)	3.98 (<0.01–224)
NO_3-N, µg L^{-1}	113 (<0.01–626)	64.5 (<0.01–1720)	66.4 (<0.01–579)
DIN, µg L^{-1}	142 (0.80–1080)	89.5 (<0.01–1800)	89.5 (0.80–597)
TN, µg L^{-1}	381 (67.4–2500)	286 (15.0–2520)	215 (16.0–1590)
DIP, µg L^{-1}	16.9 (<0.01–163)	14.7 (<0.01–524)	12.7 (<0.01–207)
TP, µg L^{-1}	47.1 (5.50–686)	31.2 (<0.01–2510)	26.8 (1.70–1010)
SiO_2-Si, µg L^{-1}	300 (<0.01–1730)	335 (3.80–2710)	266 (3.80–1680)
SS, mg L^{-1}	35.0 (0.10–512)	11.3 (0.10–200)	4.63 (<0.01–31.6)
Chl-*a*, µg L^{-1}	2.83 (<0.01–67.2)	1.81 (<0.01–61.4)	1.16 (<0.01–25.2)
Provinces (population size)	Gyeonggido (13.7 M), Chungnamdo (2.1 M), Jeollabukdo (1.9 M), Jeollanamdo[c] (1.9 M)	Jeollanamdo[c] (1.9 M), Gyeongsangnamdo (3.4 M)	Gyeongsangbukdo (2.7 M), Gangwondo (1.6 M)

[a] Data were collected along South Korean coasts, except for those from North Korea, from 1997 to 2019.

[b] Water depths are reported as mean (maximum); other parameters are given as mean (range).

[c] Jeollanamdo region is located across west and south coasts.

Abbreviations: DO, dissolved oxygen; COD, chemical oxygen demand; NH_3-N, nitrogen ammonia; NO_2-N, nitrite; NO_3-N, nitrate; DIN, dissolved inorganic nitrogen; TN, total nitrogen; DIP, dissolved inorganic phosphate; TP, total phosphate; SiO_2-Si, silica dioxide; SS, suspended solid; Chl-*a*, chlorophyll-*a*; M, million.

(OHI) assessment, was ranked 48th (76 points) in the world out of 221 countries and territories (global mean = 71 points) (OHI 2019), while the neighbouring three countries showed relatively low ranking in comparison: Japan 125th (66 points); China 158th (63 points); and North Korea 193rd (58 points) (Figure 1). It is noteworthy that Korea also received a higher biodiversity index ranking (5th, 96 points) than other East Asian countries.

Sustainable management of coastal habitats should be acknowledged as an important contributing component for preserving high marine diversity. However, it is obvious that large areas of Korean coastal habitats have been undergoing long-term anthropogenic destruction. Representative

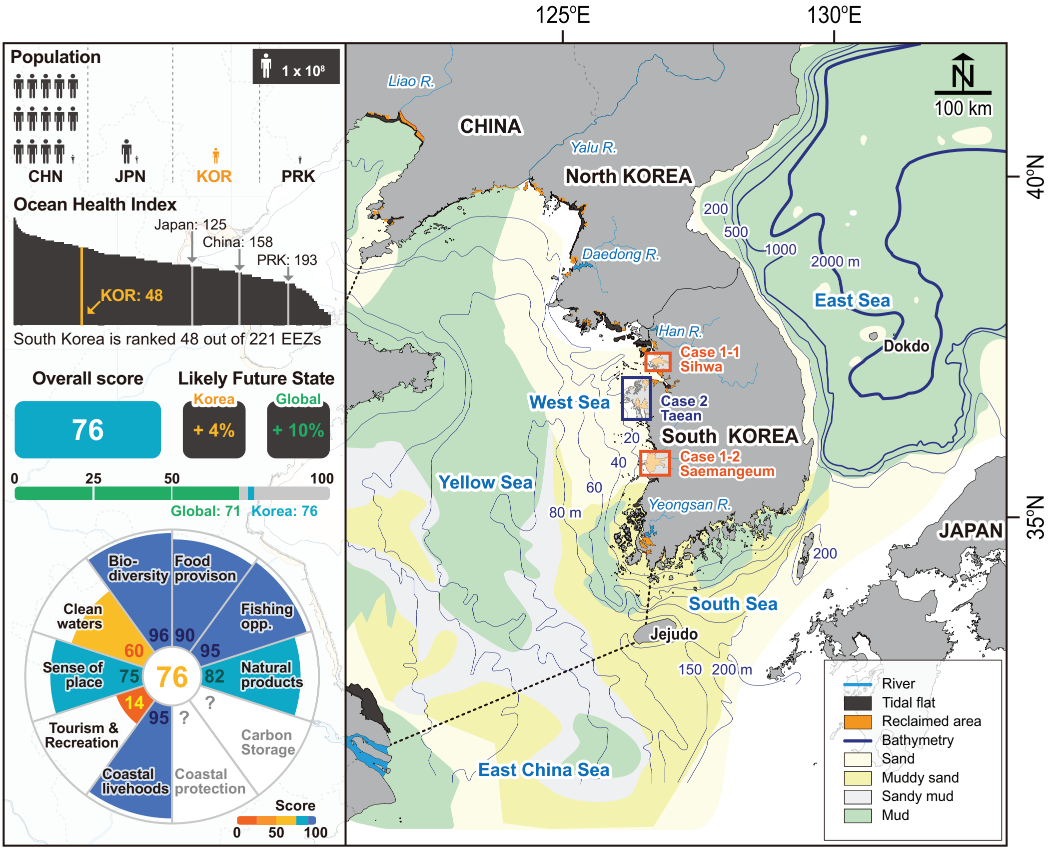


Figure 1 Map showing geographical setting of the Korean peninsula, populations of (South) Korea and its surrounding countries (China, Japan, and North Korea), and Ocean Health Index scores for Korea.

examples of the most destructive activities include large-scale coastal reclamations conducted in Korea over the past 40 years, which have resulted in a 40% loss of natural tidal flats along the West Sea coast (Yim et al. 2018). The loss of microhabitats due to dike construction, which is followed by changes in oceanographic conditions, has had adverse impacts on marine biodiversity. Another issue for biodiversity loss is coastal pollution (Khim et al. 2018), which is caused by eutrophication, land-derived pollutants, oil spills, etc. The event most destructive to the coastal region was the 2007 HSOS, which occurred in the West Sea. Continuing efforts to improve coastal management would benefit from a systematic assessment of the current status of marine biodiversity along the entire coasts of the Korean Peninsula.

In the present review, we first provide a regional overview of the Korean seas to improve understanding of these coastal environments. The basic characteristics of these environments, including seascapes, topography, geography, sedimentology, tides and currents, and water quality are summarized briefly. Then, we focus on the germane marine biodiversity literature and provide an overview of the relevant issues and history. The meta-data analyzed here were constructed from taxonomic and ecological studies of macrozoobenthos performed in Korea from a holistic perspective. The main goal of this review was to provide an up-to-date ecological inventory of Korean macrozoobenthos. In particular, we delineated the assemblages and distributions of macrozoobenthos in the three seas of Korea and describe their regional distributions. As part of this review, we sought to address human impacts on Korea's marine biodiversity, with in-depth analyses of three representative cases.

Two of these cases, namely Lake Sihwa and Saemangeum, were chosen to access the impacts of coastal reclamations. The third, Taean, was chosen to obtain data related to the environment's long-term recovery from the HSOS accident. Finally, we discuss limitations, implications, and future management directions for sustainability of the Korean marine ecosystem and biodiversity.

Oceanographic settings around the Korean Peninsula

The west coast of Korea encompasses well-developed tidal flats (~2500 km^2 in South Korea) and plays an important role in the maintenance of a large marine ecosystem in East Asia. It is characterized by a ria-type coastline with diverse coastal morphology and sea floors of the West Sea slope gently toward the greater Yellow Sea (of which it is a part). The total length of the western coastline in Korea is estimated to be 2450 km (Table 1). The West Sea is a shallow subtidal area within the Korean exclusive economic zone, spanning the area inclusive of longitudes 126–127°E and latitudes 34–37°N (Figure 1). The West Sea has been designated as part of the Yellow Sea Large Marine Ecosystem (YSLME) and is a large semi-closed bay with shallow water depth (~50 m). It has a very large tidal range and extensive tidal flats. The tidal range of the west coast decreases from a maximum of 10 m at its northern end in Incheon City to a minimum of 4 m at its southern end in Mokpo City, located at the south-end of the west coast.

The south coast of Korea lies on a northern boundary line of the East China Sea and is connected geographically to the southeastern Yellow Sea. The south coastal area has a generally flat topography in the west, but deepens southeast of the island of Jejudo. The south coast, the most complicated coastline in Korea geomorphologically, is a submerged coast with an archipelago consisting of over 2200 islands; it has with a total length of 2484 km (Table 1). The South Sea encompasses an area inclusive of longitudes 126–129°E and latitudes 34–35°N. It forms part of the Asian continental shelf and the Korea Strait located between the Korean Peninsula and Japan (Figure 1). The South Sea has a mean water depth of 71 m, and its maximum depth is 198 m near Jejudo. Its mesotidal environment has a depth range of 1.3–4.3 m, and its tidal range decreases eastwards.

Unlike the west and south coasts, the east coast of Korea is characterized by very deep water, a steep sea-floor slope and a very simple coastline. The East Sea is a small marginal sea of the Northwestern Pacific Ocean. It is enclosed by multiple countries, including principally Russia, Korea, and Japan. The East Sea is a shallow area along the east coast of the Korean Peninsula covering an area encompassing longitudes 128–129°E and latitudes 35–38°N. It has a mean depth of 1497 m and a maximal water depth of 2985 m near Ulleungdo (Figure 1). There are 687 km of well-developed sandy beaches along the coastline. However, the local sea bed topographies and microtidal amplitudes below 50 cm prevent the development of tidal flats on the continental shelf (Table 1).

The main currents affecting the Korean Peninsula are the Yellow Sea Warm Current, the East Korean Warm Current, and the Tsushima Warm Current, which are all branches of the Kuroshio Current (Figure 2). The Kuroshio Current, a western boundary current, is the second largest warm current after the Gulf Stream (NGII 2016). It starts from the north equatorial current by turning at the Coriolis reflection and flowing northward along the western boundary of North Pacific Ocean, passing eastern Taiwan, and then, finally, flowing to northern Japan. The Kuroshio Current has a characteristic water mass of high temperatures (20–30°C) and high salinity (34–35 psu) (NGII 2016).

The Tsushima Warm Current branches northwestward from the Kuroshio Current, forming the Yellow Sea Warm Current which passes into the Yellow Sea through the Liaodong Peninsula of China across the Heuksan-do and Baengnyeong-do of Korea, and reaches Bohai Bay (China) when it strengthens in the summer. The Yellow Sea Warm Current weakens as it enters the southern coastal waters of Korea during the fall, with marginal eastward flows along the Jeju Strait. The Tsushima Warm Current branches off the Kuroshio Current into the East China Sea and flows into the East Sea through the Korea Strait and the Tsushima Strait. The East Korean Warm Current branches northward off the Tsushima Warm Current at the east end of the Korea Strait and flows

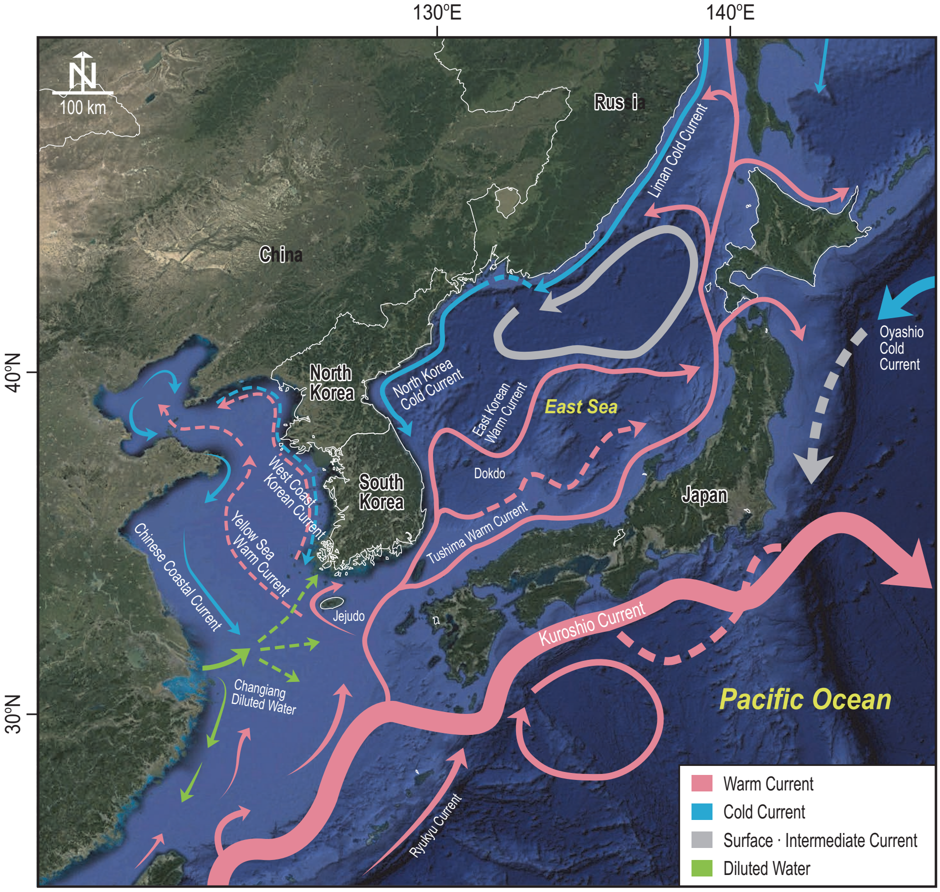


Figure 2 Map showing ocean currents and bathymetric topography around the Korean Peninsula (modified from Hwang et al. 2014 and NGII 2016).

north along the southeast coast of the Korean Peninsula. The East Korean Warm Current makes contacts with the North Korean Cold Current at latitudes in the range of 36–38°N and consequently changes its flow direction such that it flows toward the central East Sea. The boundary between the two currents changes continuously and forms a large eddy in the East Sea. The East Korean Warm Current shifts direction to flow northeast, finally joining the Tsushima Warm Current.

The Liman Cold Current begins in the vicinity of the Russian Tatar Strait and flows southward along the Eurasian Continent to the East Sea. The North Korean Cold Current is an extension of the Liman Cold Current that flows southwest along the east coast of North Korea. During the summer, the Liman Cold Current reaches the Wonsan area of North Korea. The North Korean Cold Current is strengthened during the winter, when it thus has more southward effects as far south of Korea. In the summer, the diluted waters of the Changjiang (Yangtze) River are dispersed eastward or southeastward, reducing seawater salinity along the Jejudo coast and southwestern Korean Peninsula coast; these waters flow south along the east coast of China in the winter (Hwang et al. 2014).

Because of the geomorphology of the Korean Peninsula, most of the major rivers in Korea flow into the West Sea or South Sea. The shoreline of the west coast is very complex with many rivers that flow through highly urbanized coastal cities and thus are exposed to substantial anthropogenic pressures. These rivers deliver large amounts of terrestrial organic matter to the West Sea and South Sea. Our analysis of long-term monitoring data of seawater parameters (20 years, 1997–2019) showed a clear gradient of marine environmental conditions from the west coast to the east coast based on Table 1. Relatively low water column transparency, salinity, and chemical oxygen demand (COD) were observed for the west coast, reflecting a strong influence of (in)organic matter through riverine and estuarine inputs to the West Sea. Consequently, relatively high primary production levels have been evidenced by high concentrations of chlorophyll *a* and a high nutrient potential from re-suspended sediments, which contribute to the maintenance of primary producer abundance available to upper trophic levels in the west coast ecosystem.

Historical overview on the macrozoobenthic studies in East Asia

To provide international research on the ocean environment of East Asia, a mini-review on three major ocean topics, namely seafood, pollution, and biodiversity, was conducted targeting the countries of China, Taiwan, and Japan, in addition to Korea (Figure 3). Of these countries, Japan had the most intensive marine research activities from the 1950s to the 2000s, after which research from China increased drastically (post-2000s). Similarly, there has been a marked increase in relevant publications from Korea since the 2000s, which reflects significant recent advances in ocean science.

Among the three aforementioned targeted topics, seafood science has long been pursued in all four countries. Japan has led in this area of science since the early 1950s. It should be noted that rapid increases in seafood science are evident after the early 2000s across all four countries, particularly for China and Korea in more recent years (Figure 3A). According to global fishery data reported by the FAO (Food and Agricultural Organization of the United Nations), there has been a substantial increase in catch volumes since the mid-1990s following soaring increases in demand for seafood in China (Pauly & Liang 2019).

Following increases in human activities affecting the marine environment, a number of environmental issues arose concurrently, especially in East Asian countries that have undergone dramatic socioeconomic development. Accordingly, research into marine pollution has been on the rise since the 2000s (Figure 3B). In particular, China has seen a noticeable increase in marine pollution research since the 2010s, with a major focus on the tremendous coastal development along the Yellow Sea coastline. Our recent studies on the topic of coastal and marine pollution in the Yellow Sea revealed severe ongoing pollution along the YSLME coast (Tian et al. 2020, Yoon et al. 2020, Shi et al. 2021). Of note, there is a relative lack of marine pollution studies in Taiwan, where there has been a decreasing trend in recent years. Meanwhile, there has been a steady increase of marine pollution studies in Korea from the 1990s to present. Indeed, various environmental issues in the coastal marine ecosystems have become more extensive and intense since the 1990s due to increasing coastal reclamations and land-driven marine pollutions along the Korean coasts (Koh & Khim 2014).

The concept of sustainable marine environment management also began to emerge in the 2010s, concurrent with a surge in publications on the topic of marine biodiversity (Figure 3C). Although the Yellow Sea coast is known as a biodiversity hotspot globally, there have been relatively few studies of this region in Korea, compared to China and Japan. Accordingly, more intensive research efforts on the subjects of marine biodiversity and biogeography in South Korea would be timely and important. The high marine biodiversity of Korea features an especially high species diversity of macrozoobenthos inhabiting diverse coastal habitats. For example, in our previous intensive meta-data analysis focused on the West Sea (Park et al. 2014a), we documented the occurrence of 624 macrozoobenthos. The present review shows that former macrozoobenthos studies were limited by unbalanced study efforts for limited target species, limited surveyed localities, and non-standardized monitoring methodologies.

Further, the Scopus mini-review on macrozoobenthic studies around the Korean Peninsula revealed a large contribution of macrozoobenthos diversity to the marine biodiversity in East Asia (Figures 4A). A substantial portion of the studies reported examined the Chinese and Russian seas nearby the Korean Peninsula. The network analysis bore out this trend, revealing clustering toward

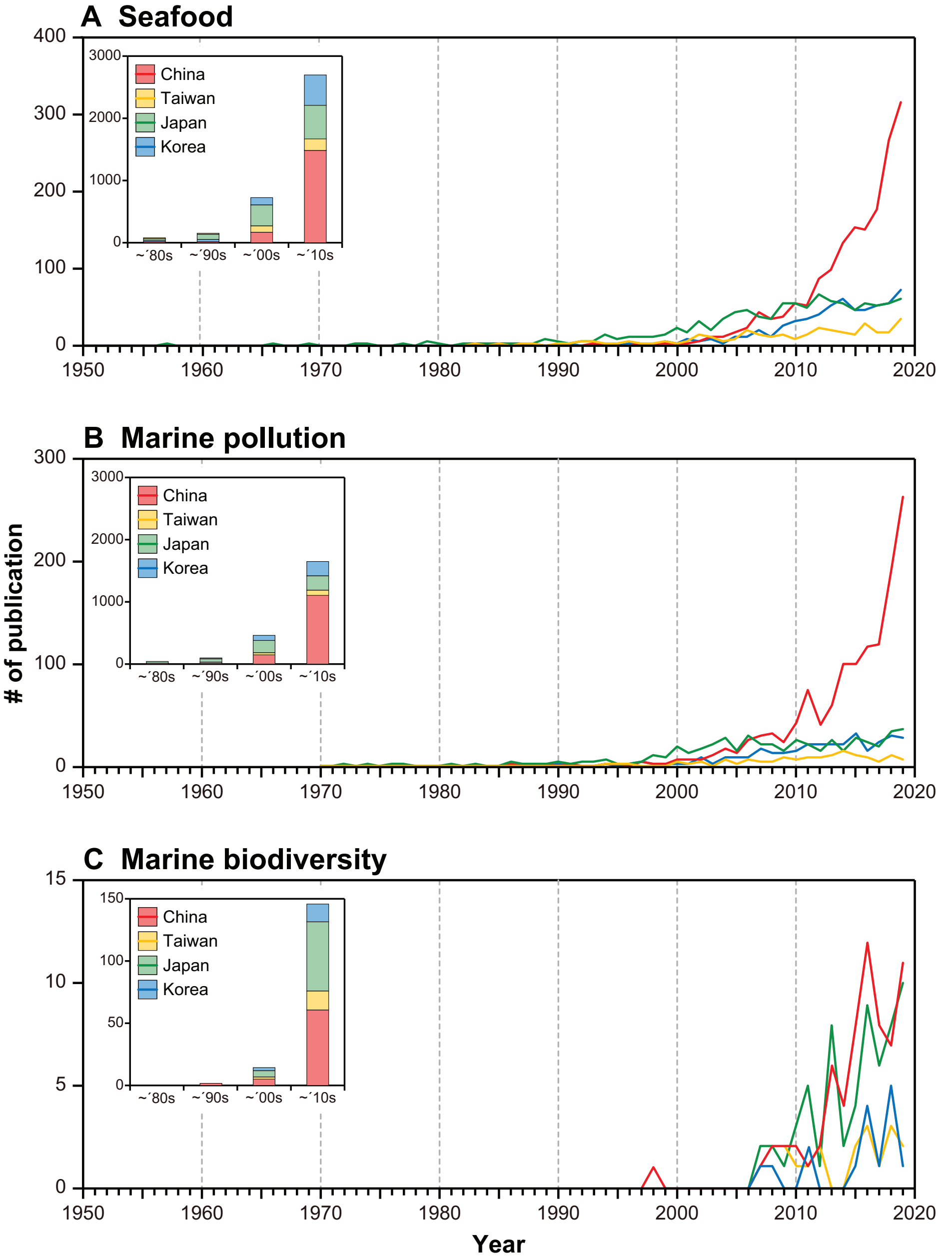


Figure 3 Historical studies on (A) seafood, (B) marine pollution, and (C) marine biodiversity in the East Asian countries of China, Taiwan, Japan, and Korea. The publications include original research articles, reviews, book chapters, books, and letters collected in the Scopus database (title, abstract, keywords) from 1950 to 2019.

two major keywords: the East Sea and the Yellow Sea. More recent ecological studies of macrobenthos have tended to deal with a greater variety of taxa along the Korean coasts (Figure 4B and C). Of note, the South Sea of Korea was not included among the 30 keywords in our analysis, evidencing a lack of study efforts in the region (8 documents of a total of 124). Finally, the results indicated a growing interest in macrozoobenthic research in the Yellow Sea and the East China Sea. Overall,

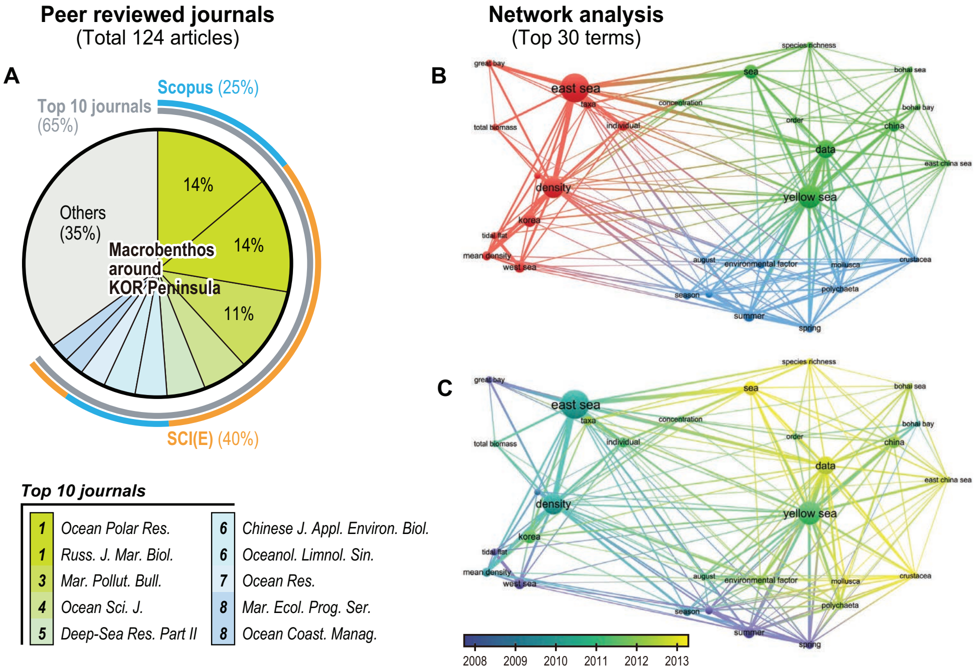


Figure 4 Publications related to the Korean Peninsula macrobenthos from 1970 to 2019. A total of 124 publications in 44 journals, including SCI(E) and Scopus, are included. (A) Top 10 journals accounting for 65% of the collated documents ($n=80$). To construct and display a terminological map, (B) cluster and (C) chronicle network analyses were carried out based on words in the titles and abstract fields of 124 publications.

holistic study efforts focused on the long-term monitoring of marine biodiversity in the Korean Peninsula are necessary to address the above knowledge gaps.

Methods and materials

Meta-data collection

We provide an up-to-date ecological inventory of macrozoobenthos, practically defined as the invertebrate species of >1 mm mesh size living in or on the sediment and hard substrates, observed along the Korean coasts (Supplementary information of Tables S1 and S2). Faunal species compositions and distribution were analyzed based on meta-data collected from previous studies during the past 50 years. Based on the Scopus and Korean local journal database, we identified a total of 128 peer-reviewed articles relating to macrozoobenthos ecology studies conducted along the Korean coasts. Taxonomic contributions only reporting new species to science or newly recorded species in the Korean waters were excluded because they do not have ecological implications in line with the focus of the current review.

A total of 128 peer-review articles were compiled, including 42 reported in international journals and 86 in Korean domestic journals, related to the community ecology of the Korean macrozoobenthos (Table S3, Figure 5). The first and early benthic ecological studies appeared in the 1970s and the number of studies increased over time. Two pioneering studies dealing with polychaete assemblages were conducted in the early 1970s (Paik 1973, Oh & Kim 1976), representing the emergence of marine ecology of macrozoobenthos in Korea. Many of the early macrozoobenthos studies focused on describing newly recorded taxa or new species in taxonomy; ecological studies joined

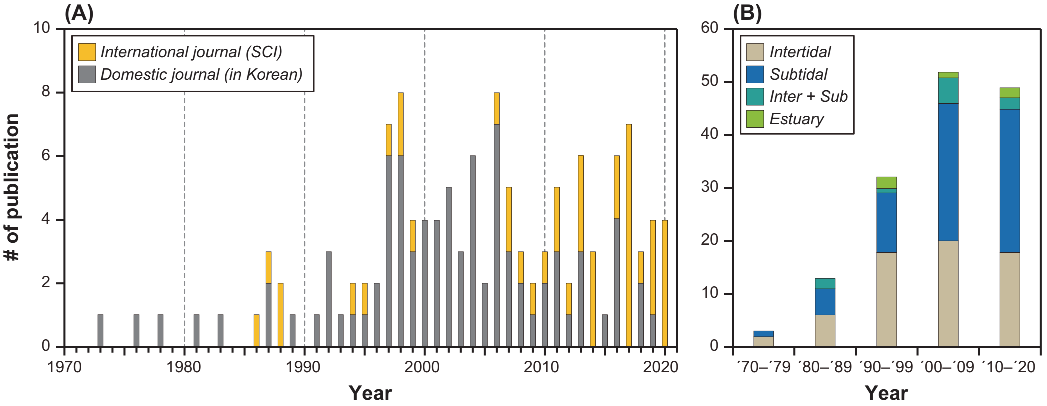


Figure 5 Overview of macrozoobenthos studies conducted in Korea from 1970 to 2020. Only peer-reviewed articles published in international (SCI) and domestic (Korean) journals were considered. (A) Publications each year for the past 50 years. (B) Decadal number of publications on specified benthic habitats (intertidal, subtidal, and estuary).

the literature in the 1980s (Lee et al. 1983, Lee 1987). The early ecological studies reported the distribution patterns of some macrobenthic organisms, with ecological studies increasing rapidly in the 1990s, documenting many aspects of structure and function in marine invertebrates across the diverse Korean habitats (Figure 5). It should be noted that the majority of the ecological studies performed since the 1990s have focused on intertidal and/or subtidal marine macrozoobenthos, while there have been relatively few that have focused on estuaries.

Data analyses

To understand the regional distributions of macrozoobenthos, meta-data were organized based on macrozoobenthos occurrence in a total of 38 subregions along the Korean coasts. The west coast includes 16 subregions (W1–W16), the south coast (including Jejudo) has 10 subregions (S1–S10), and the east coast has 12 subregions (E1–E12) (Figure 6). The subregion boundaries were based on the survey standards provided by Korean National Environment Monitoring (Koh & Khim 2014). The northern limit of the west coast was set as the Han River (W1) because data on the benthic ecosystems in North Korea were not readily available due to the political situation of the Korean Peninsula.

The region of Korea given the most previous research attention (~70%, 88 documents) is the West Sea (especially the tidal flats), followed by the South Sea (27 articles), and East Sea (17 articles). Although this regional inequity might introduce a bias in proportional random sampling, the general features of the macrozoobenthos studies are unlikely to be overly biased considering the substantial amounts of documents available for each region. Also, some documents were reviews, which already encompassed many individual reports and articles. Thus, the presently constructed meta-dataset should be sufficient to address the regional distribution characteristics of the Korean macrozoobenthos within a time frame of 50 years. Under such limitations on meta-data, we tried to evaluate the status of the macrozoobenthic biodiversity across the three seas of Korea, using a number of species and ecological indices of taxonomic distinctness (delta +) (Ryu et al. 2016).

Apart from updating the ecological checklist of Korean macrozoobenthos, the mini-review on the long-term community responses of macrozoobenthos under anthropogenic pressures was given to highlight human impacts on macrozoobenthos. The three representative case areas targeted in the West Sea are relevant for national-level concerns and have associated with them substantial accumulated data in relation to coastal reclamation (Lake Sihwa and the Saemangeum tidal flats) and the HSOS (Taean). There have been a large number of reports documenting environmental

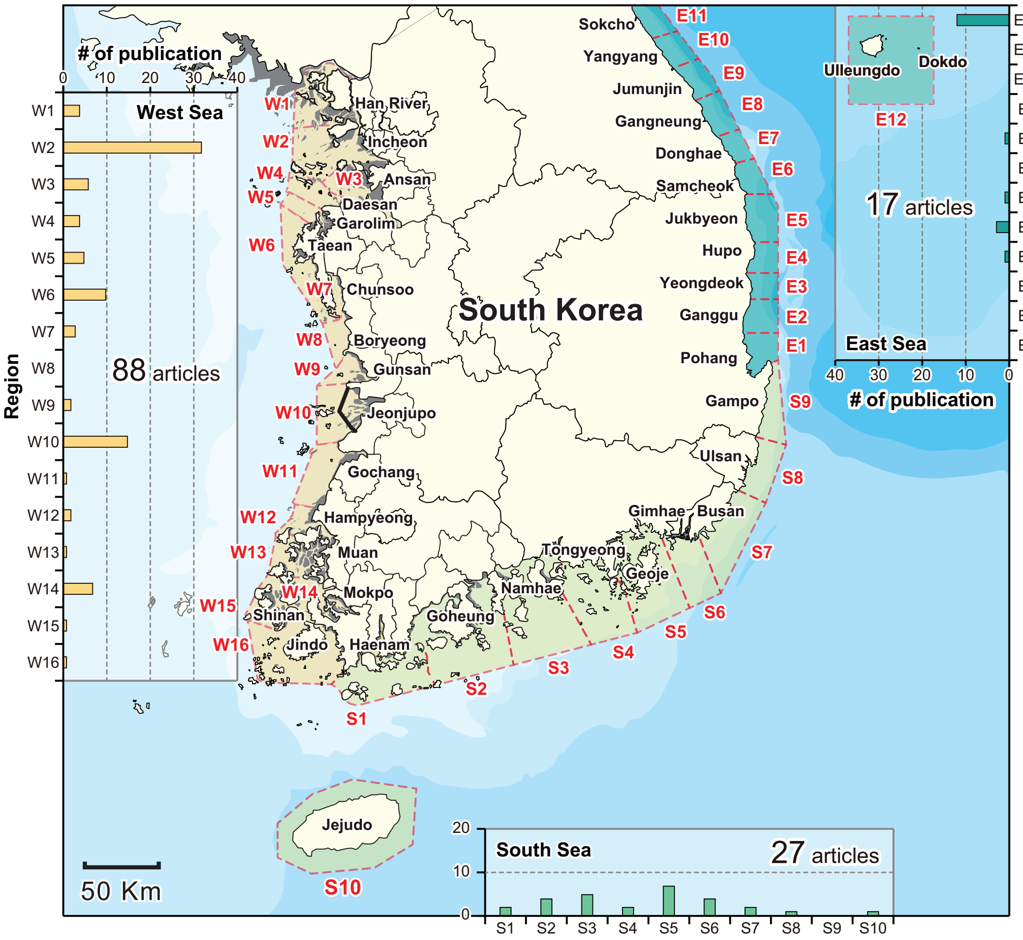


Figure 6 Coastal map of Korea (west, south, and east coasts in the southern parts of the Korean Peninsula), showing total numbers of relevant published articles on the West, South, and East Sea.

and ecological degradation related to these marine pollution issues; debates remain regarding some points. The present review is focused on the deterioration of key environments, such as water and sediment quality, and addresses long-term benthic community changes in macrobenthic faunal structure and its recovery.

Over 60% of the compiled relevant works were published in Korean domestic journals (Figure 5) and international documents increased in more recent years. As part of data quality assurance, we reexamined the macrozoobenthos data published in the domestic Korean journals carefully and validated species identifications using comparisons with the World Register of Marine Species (WoRMS) database and other appropriate taxonomic literature, seeking advice from experts as needed.

The meta-data produced in the present work may provide an overview of scientific efforts and advancement in marine ecology relating to the Korean macrozoobenthos. These efforts provide critically important background information for past and present assessments of the status of benthic community health, and further provide a reference for future monitoring. The present review is the first comprehensive compilation of Korean marine ecology research. It encompasses important aspects of taxonomy and ecology in relation to marine biodiversity. The findings are useful for guiding future research directions in relation to coastal and marine biodiversity monitoring and ecosystem management in the Korean coastal waters from an international perspective.

Biodiversity of macrozoobenthos in Korean coastal water

Overview of faunal assemblages and regional distributions

A faunal inventory of Korean macrozoobenthos, including ecological information, was constructed from the meta-dataset collated for the present review (Table 2). The meta-data analysis revealed that a total of 1915 species or subspecies and 1135 genera belonging to 488 families from 17 phyla occurred in the Korean coastal waters (Table S1). This updated list is comparable to those of previous reports. For example, the recently reported number of macrozoobenthos species from the National Marine Ecosystem Survey conducted in 2015–2019 was 1666 marine invertebrates from coastal locations (Table 2). When counted the species numbers from the tidal flat locations, the NMES number would be around the presently reported species number of 1915 species. Meanwhile, it is noteworthy that the Marine Bio-resource Information System documented a total of 5670 marine invertebrate species as of 2020, supporting the documented high biodiversity of the Korean macrozoobenthos. Regardless, public access to national monitoring data is limited, and taxonomic reconfirmation is required for utilization in a meta-analysis. A species list of all macrozoobenthos constructed, analyzed, and documented in the present review is provided in Table S2 for future public use.

Another mini-review of the global macrozoobenthos inventory indicated that Korea has comparatively high macrozoobenthic diversity (Table 3). The highest macrozoobenthos biodiversity was found in Australia including deep sea (24,854 species), which could be indicative of Australia's exceptionally high marine biodiversity (Costello et al. 2010). Given the lack of global inventory data for specific taxa, efforts to establish a global inventory of coastal marine invertebrates at national or regional sea levels would be beneficial.

With respect to faunal composition, the Korean macrobenthic communities were composed primarily of five dominant taxonomic groups: Mollusca (670 species), Annelida (469 species),

Table 2 Macrozoobenthos species richness in Korean coasts documented over the last two decades and summarized by taxa and/or coastal regions and based on fauna data from National Marine Ecosystem Survey (NMES), Marine Bio-resource Information System (MBRIS), and this study

Program	NMES				MBRIS	This study
Habitat type	Tidal flat			Coast	Marine	Tidal flats and coasts
Year	1999–2005	2008–2012	2015–2018	2015–2019	2019	1973–2020
Macrozoobenthos[b]						
Mollusca	54	185	–	–	1764	670
Annelida	228	213	–	–	361	469
Arthropoda	205	240	–	–	2016	434
Echinodermata	5	30	–	–	213	79
Others	9	49	–	–	1316	263
Total	**501**	**717**	**639**	**1666**	**5670**	**1915**
Coastal region						
West coast	–	–	474	1050	–	829
South coast	–	–	452	1107	–	1103
Jejudo coast	–	–	70	557	–	511
East coast	–	–	55	626	–	621
Total	**501**	**717**	**639**	**1666**	**5670**	**1915**

[a] *MBRIS (2020) data based on the National Marine Biodiversity Research Institute of Korea's species collection list;*
[b] *Total number of species in Korean coasts*

Table 3 Comparison of species richness of macrozoobenthos present in selected global coasts and regional seas; species richness was summarized by macrozoobenthos taxa (references given including this study)

Locality	British Isles	Australia (including deep sea)	Western Turkey	North Pacific (subtidal trawl)	Arctic (subtidal)	Korea (coasts)
Macrozoobenthos						
Mollusca	192	8525	227	255	392	670
Annelida	54	1558	–	–	668	469
Arthropoda	109	6365	116	128	847	434
Cnidaria	93	1754	18	–	–	103
Echinodermata	47	1594	50	85	228	79
Others	35	5058	274	108	501	160
Total	**530**	**24,854**	**685**	**576**	**2636**	**1915**
References	Marine Life Information Network	Butler et al. (2010)	Gönülal and Güreşen (2014)	Volvenko et al. (2018)	Inniss et al. (2016)	This study

Arthropoda (434 species, mostly crustaceans), Cnidaria (103 species), and Echinodermata (79 species) (Table S1). These five faunal groups collectively accounted for >91% of the total macrozoobenthic species (Figure 7A). Annelida was the most dominant taxa, representing ~35% of the total species, followed by Mollusca (30%) and Arthropoda (26%). The relatively diverse polychaete annelids were recorded more frequently along the west coast than along the other two coasts, presumably because of the much extensive shallow mudflat habitats on the west coast (Yim et al. 2018).

Of the three coasts, the south coast had the most faunal species, numbering 1103, and the proportions of the three major taxa differed from those of the west coast. The most diverse taxa were Mollusca (416 species, 38%), followed by Annelida (274 species, 25%) and then Arthropoda (210 species, 19%) (Table S1). The number of molluscan species was the highest in the south coast. Although the east coast showed the lowest total number of species (621 species) among the three Korean seas, the composition of three major phyla did not differ greatly among the three seas, reflecting faunal commonness across the region. Along the east coast, Mollusca were predominant (190 species, 31%), followed by Annelida (149 species, 24%) and Arthropoda (142 species, 23%). Although phylum Cnidaria was ranked as the fourth dominant faunal group (55 species; 9%), the cnidarians were the dominant taxa only within a limited region (Ulleungdo and Dokdo) not diverse in the other regions. Phylum Echinodermata had low species richness (31 species, 5%).

Next, the distribution patterns of macrozoobenthos species richness along different habitat types (intertidal, subtidal, and estuarine) were analyzed (Figure 7B). Not surprisingly, the subtidal environment showed the highest number of macrozoobenthos species (1325 species, >69% of the total). Interestingly, a third of all molluscan species observed (437 species) were found in the subtidal zone, where they account for ~70% of species present. Large portions of the polychaetes species (82%) and arthropod crustacean species (64%) observed in the Korean seas were present in subtidal habitats. Species diversity was relatively moderate in the intertidal area (875 species) and relatively low in estuarine areas (244 species). Of note, about 6% of macrozoobenthic species co-occurred across all three habitats (123 taxa); these organisms are euryhaline or salinity-tolerant species.

Unfortunately, the habitat information for some species was not provided in the original articles. In particular, the habitat information was often lacking for studies conducted along the east coast, especially around Dokdo. Overall, the results indicated a high proportion of habitat overlap in faunal occurrence. Broadly, these co-occurring species across the habitats encompass all observed taxa, including Mollusca (128 species, 20%), Annelida (209 species, 45%), Arthropoda (111 species, 28%), and Cnidaria (17 species, 17%).

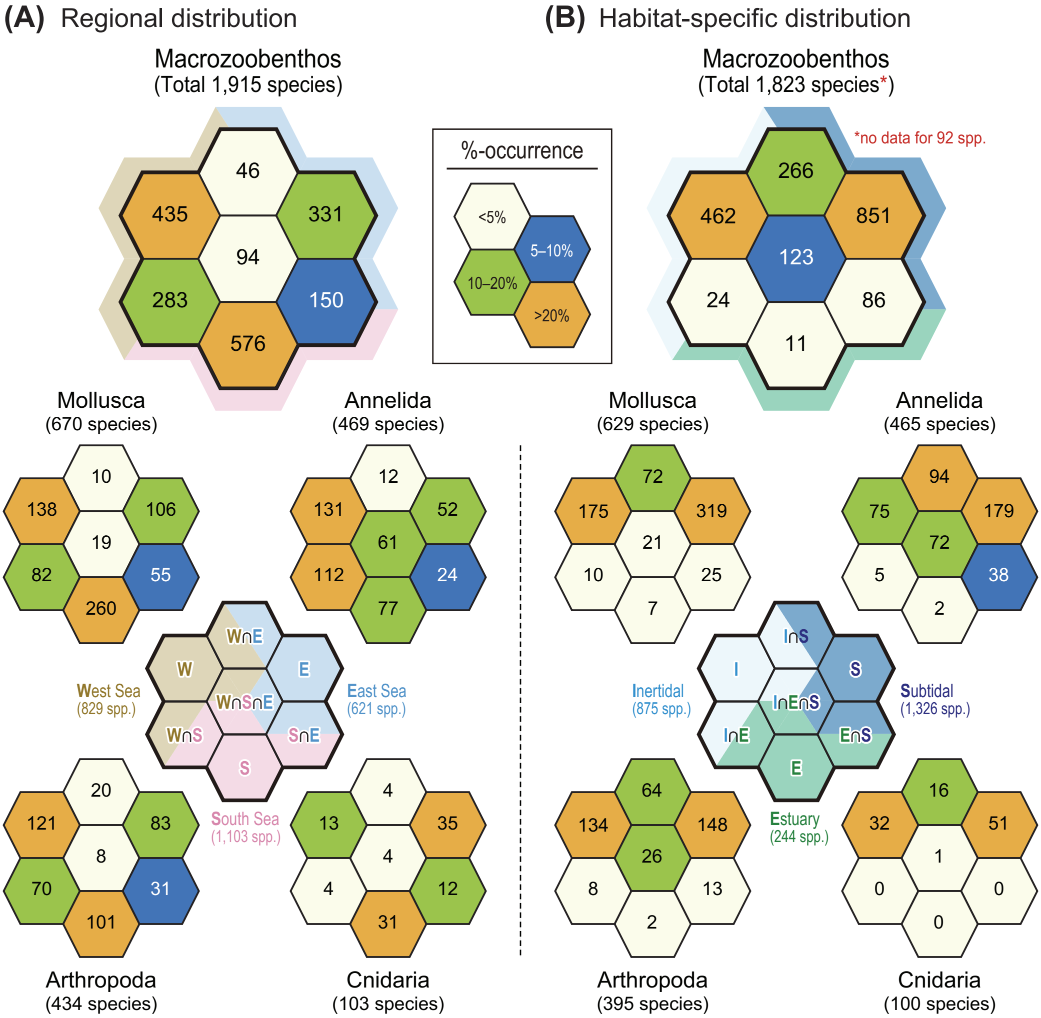


Figure 7 The occurrence of macrozoobenthic species showing intra- and inter-regional and habitat-specific distributions in Korea. (A) Regional patterns for all 1915 species and 4 major taxonomic groups present in the West Sea, South Sea, and East Sea, (B) habitat patterns for 1823 species and 4 major taxonomic groups present in intertidal, subtidal, and estuary areas (92 species were excluded due to there being no habitat information).

The limited information on benthic community structure from the original meta-data made it difficult to address the overall ecological quality at present. Under the limitation, the analysis of taxonomic distinctness indices across the three seas indicated the regional characteristics in benthic ecological quality (Figure 8). In general, the high taxonomic diversity was evident, ranging from delta+values of 65–95, across all the three seas. When depicted the delta+against the number of species, three groups could be featured by representing biodiversity hotspots, estuarine regions, and regions close to the highly populated cities (Figure 8).

Another aspect of regional biodiversity could be explained by variations in delta+and number of species across the subregions in each sea. Considering the significance of both factors to overall biodiversity, the five grades (I–V; from excellent to good, moderate, poor, and bad) across the number of species and delta+are suggested to represent benthic ecological quality (Figure 9). Most of the subregions showed moderate to excellent benthic ecological quality based on the suggested

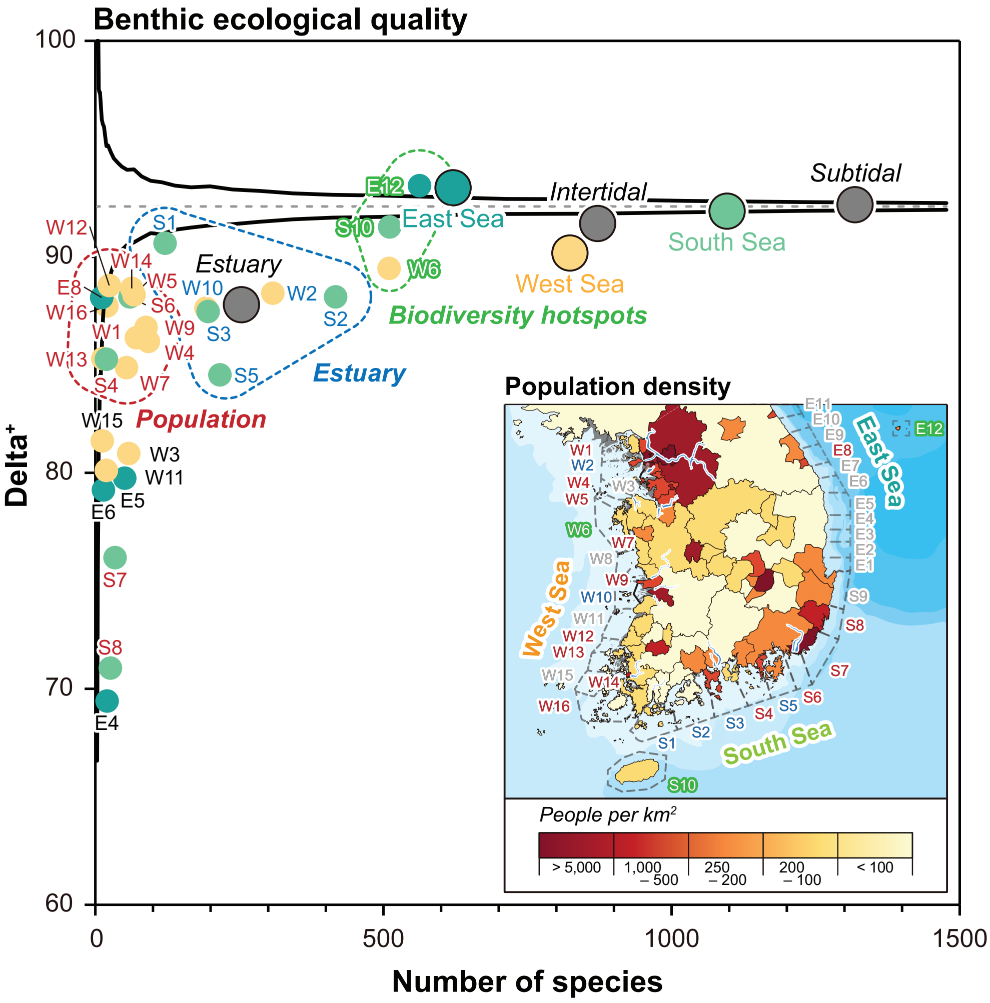


Figure 8 Spatial benthic ecological quality (delta+) results for number of occurred species in 30 coastal areas of Korea (West: 15 regions, South: 9 regions, East: 5 regions; regions in which less than one species appeared were excluded from the analysis). The 95% probability lines represented the delta+values obtained from 1000 independent simulations of the 1915 macrozoobenthic species.

index. It should be noted that subregions with high delta+value may not be always considered as excellent biodiversity if the number of species are relatively low. Overall, the ecological quality analysis reflected general and specific features of macrozoobenthos biodiversity across the three seas and specific habitats and/or conditions.

Faunal composition and distributions in the West Sea

The West Sea was divided into 16 subregions (W1–W16) along the western coast of Korea. The Taean coast (W6) exhibited the most diverse fauna (510 species), with a predominance of polychaetes (192 species), followed by crustaceans (154 species) and molluscans (124 species) (Figure 10 and Table S1), approximately two-thirds of the total number of reported species (829 taxa) from all 16 subregions. The Taean coast was confirmed to be a hotspot of macrozoobenthic biodiversity, which may reflect, at least in part, the intensive sampling efforts that were made following the HSOS in 2007.

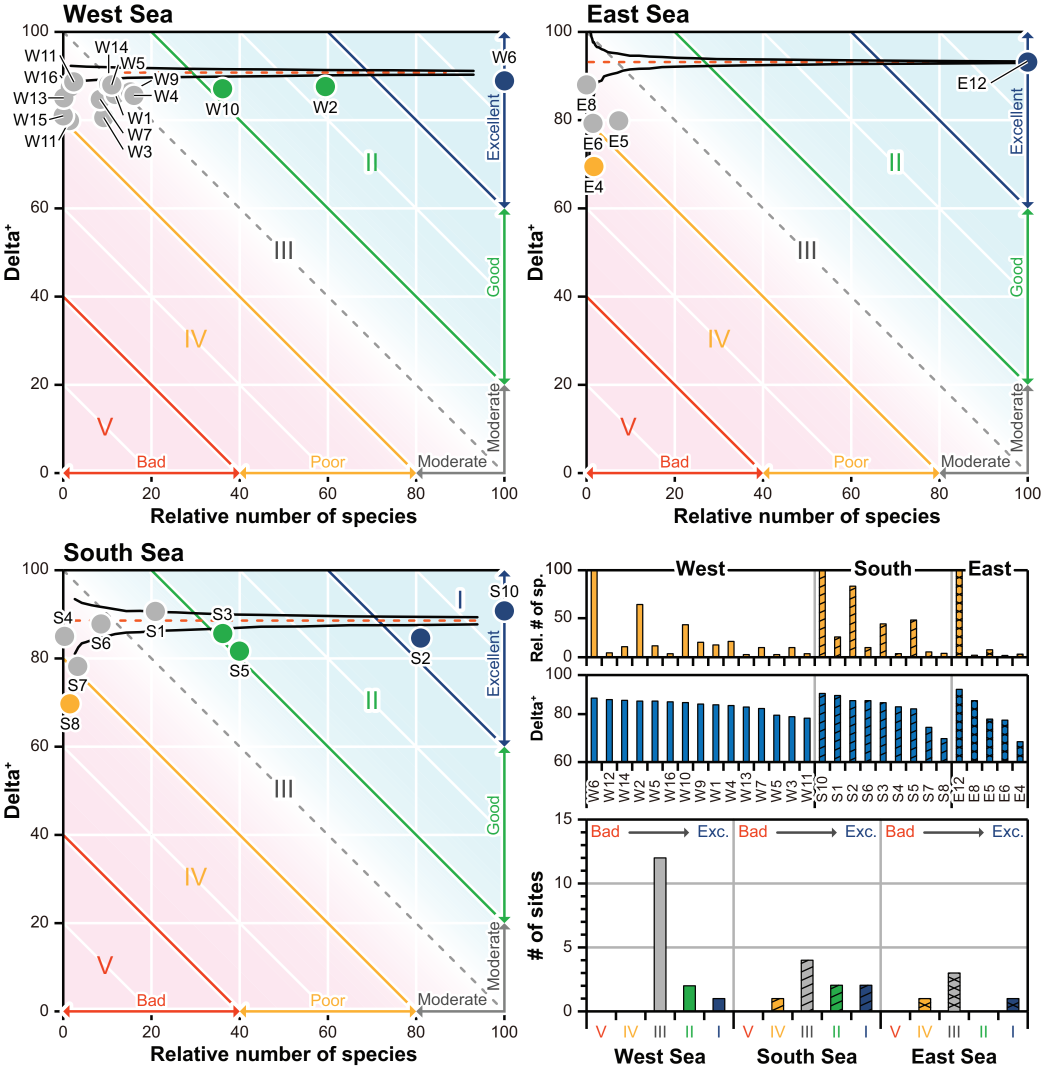


Figure 9 Benthic ecological status of 30 coastal areas in Korea (West: 15 subregions, South: 9 subregions, East: 5 subregions). The criteria used to rate benthic ecological quality included delta + and relative number of species (set 100 for the maximum number of species occurred in each sea). The five grades representing 20% each across two factors ("I: Excellent", "II: Good", "III: Moderate", "IV: Poor", and "V: Bad") are suggested as a proxy guideline in overall assessment of benthic ecological quality.

The Incheon coast (W2), which has attracted intense research interest (35 studies), showed high species richness (308 species). It encompasses an extensive harbour near the megapolitan city of Seoul and various industrial complexes, including an electric generation power plant and an international airport. The area includes Lake Sihwa and several representative tidal flats, which have attracted high sampling efforts, and it is considered to have high natural marine diversity.

The Jeonjupo coast (W10) also showed relatively high species abundance with 193 species. Annelid species were the dominant taxa (46%), reflecting the typical mud bottoms around inertial flats. Interestingly, the community structure in the Jeonjupo coast was similar to that found in the Incheon coast, with polychaetes accounting for over half of the total species number. The Jeonjupo coast includes the former Saemangeum tidal flats, where extensive tidal flats (~180 km^2)

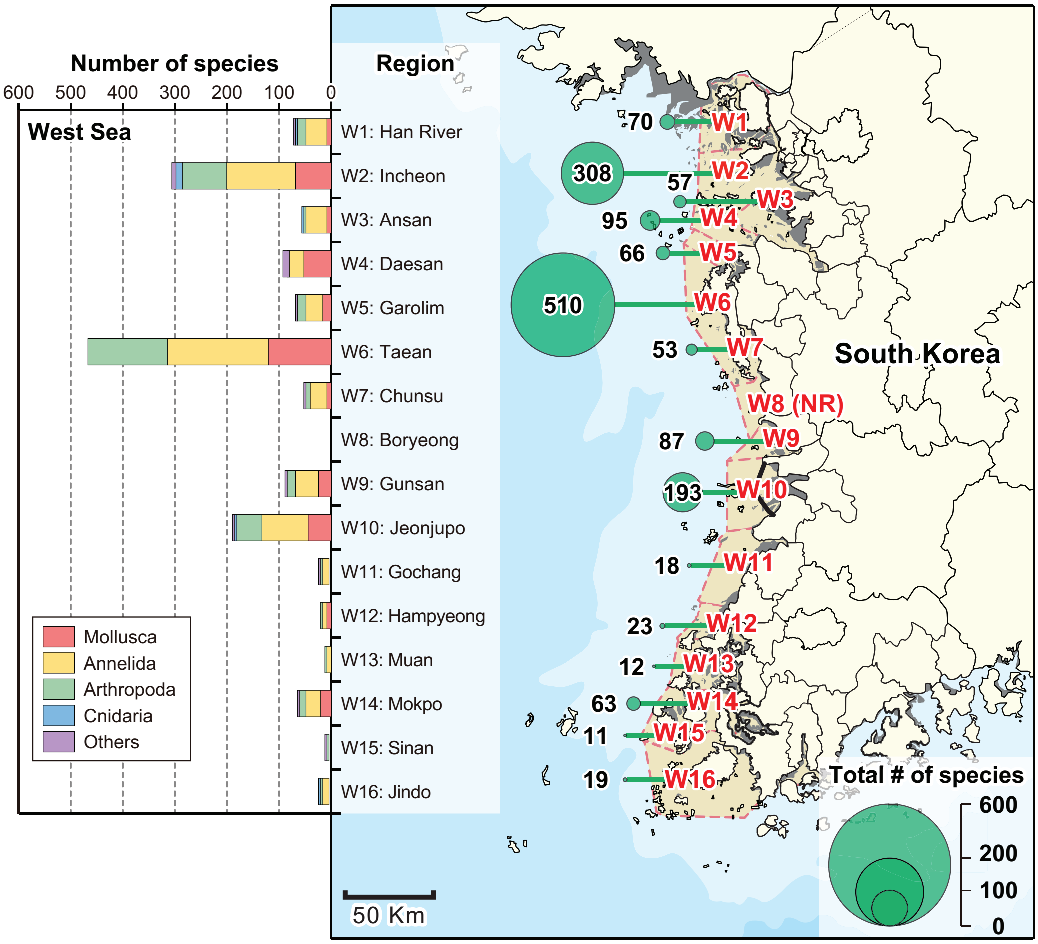


Figure 10 Map of the Korean West Sea showing the total number of recorded species over 16 subregions and the faunal composition of the macrozoobenthos in each region.

had developed before sea-dike construction was undertaken (Ryu et al. 2014). For this reason, many studies have been conducted in the Saemangeum region before and after construction to monitor the marine environment and ecosystem, with a major focus on faunal distributions.

The next most notable ecological hotspots are Daesan (W4) and Gunsan (W9), which had relatively large numbers of recorded species (95 and 87, respectively). The Daesan coast showed a predominance of molluscs (57%), and the Gunsan coast was occupied primarily by annelids (51%). The Gunsan coast contains a major estuary that is fed by the very large Geum River, resulting in an environment distinct from that of the Daesan coast. This distinction seemed to underlie the dissimilarity in faunal composition between these regions.

Examining the regional co-occurrence of macrozoobenthos in the West Sea, it was observed that many macrozoobenthos (>500 species; ~58%) occupied only a single region (Figure 11). There are two possible explanations for this high proportion of uni-regional presence. First, a considerable number of macrozoobenthic species are confined geographically by the dented shoreline and embayment system. Such oceanographic settings on the west coast may thus hinder the coastal migration of macrozoobenthic larvae and favour their site-specific settlement, as described previously by Koh & Khim (2014). Second, it is possible that biased regional sampling could have provided incomplete occupation records.

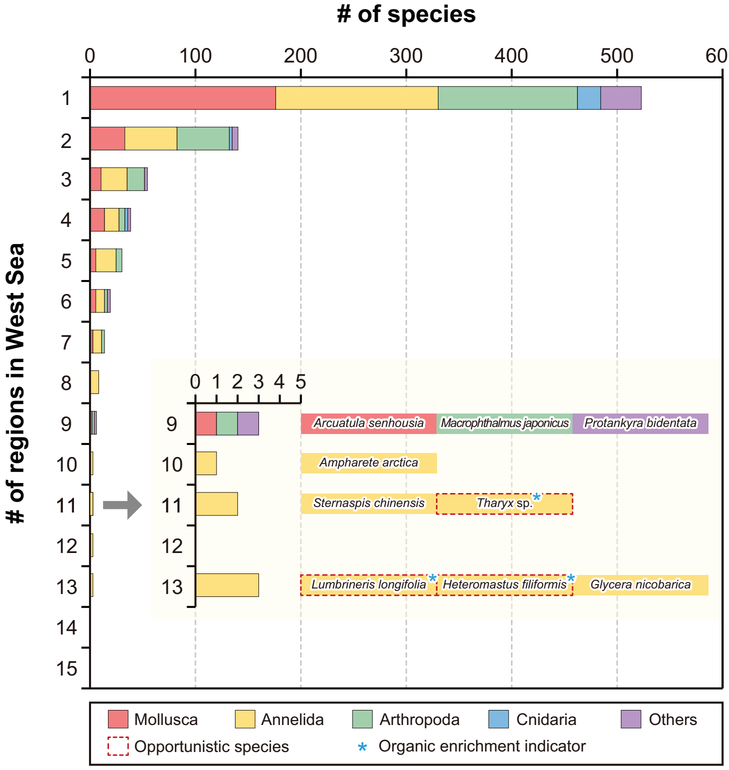


Figure 11 Number of macrozoobenthos species observed in one or more Korean West Sea subregions simultaneously. The inset shows the most common species found in more than 9 subregions. Some opportunistic or organic enrichment indicator species based on their life history traits are denoted.

Among uni-subregional species, molluscs were predominant (178 species, 32%), followed by polychaete annelids (154 species), crustacean arthropods (134 species), and cnidarians (22 species). Macrozoobenthic species observed in two subregions include 147 taxa, consisting mostly of crustacean and annelid species with subequal species numbers (50 and 49 species each), followed by molluscs (34 species). The number of regionally co-occurring species decreased as the number subregions in common increased, as expected. No species were found to be co-occurring in more than 14 subregions. It is notable that of the nine species found to co-occur across at least nine West Sea subregions, three were opportunistic species and organic pollution indicators (*Tharyx* sp., *Heteromastus filiformis*, and *Lumbrineris longifolia*) (Figure 11).

Further analysis of these nine species to characterize each taxon's site specificity (Figure 12) indicated that three polychaete species (*Glycera nicobarica*, *Heteromastus filiformis*, and *Lumbrineris longifolia*) were found in 13 of the 16 regions in the West Sea, affirming their broad spatial distribution across the west coast. Three additional polychaete species were quite broadly distributed: *Glycera chirori* (12 regions), *Sternaspis chinensis* (11 regions), and *Tharyx* sp. (11 regions). Interestingly, but not surprisingly, polychaetes occurred most broadly along the west coast. Three non-polychaete species co-occurred in nine regions, including the bivalve *Arcuatula senhousia*, the crustacean decapod *Macrophthalmus japonicus*, and the holothurian *Protankyra bidentata*. Although there is little information on the distributions of these nine wide-spread macrozoobenthos species, these species seemed to be able to inhabit essentially all coastal areas regardless of habitat preference. Of these species, eight spanned three types of habitat (e.g. intertidal, subtidal, and estuarine area); the exception was a polychaete annelid, *Ampharete arctica*.

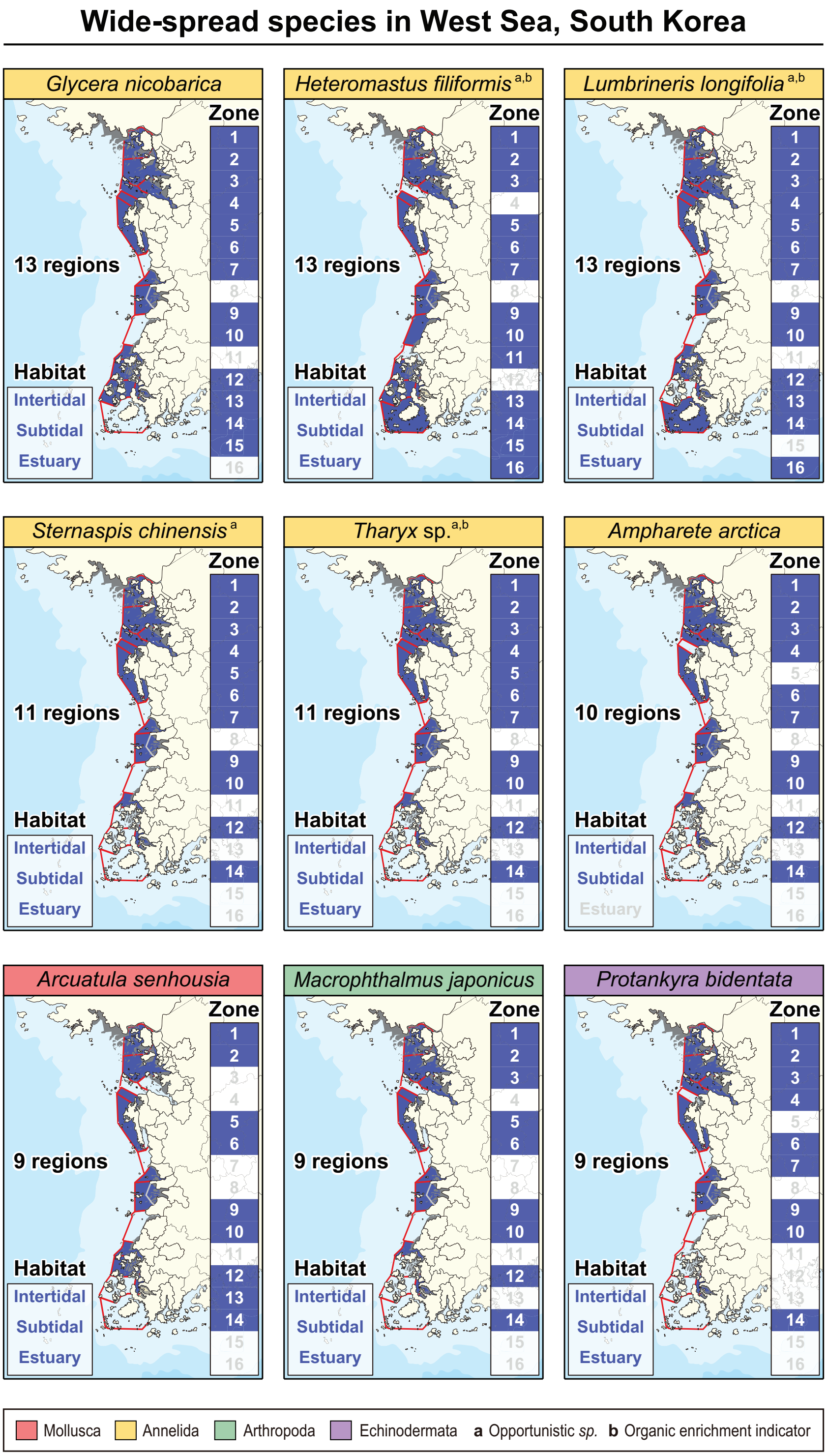


Figure 12 Distribution patterns of nine macrozoobenthic species occurring in more than nine subregions along the West Sea of Korea. Their occurrence regions and habitat types are indicated by blue colour in the map and row of boxes, respectively.

Faunal composition and distributions in the South Sea

The South Sea encompasses 10 subregions including nine (S1–S9) along the southern coast and one subregion around the island of Jejudo (S10). The Jejudo coast showed the most diverse faunal assemblages with 511 species, all of which were recorded by Ko et al. (2016). Molluscan species showed predominance with 254 species (50%), followed by crustaceans and annelids with 70 and 31 species, respectively (Figure 13). This quantity of 511 accounted for about half of the total number of reported species (1103 species) in the South Sea. Notably, the Jejudo coast had an unusual predominance of molluscans, which accounted for over 60% of the total number of mollusc species found in the South Sea. Indeed, the Jejudo coast sustains the most diverse assortment of molluscs among all of the Korean coast regions.

The Goheung coast (S2) was found to be next in species diversity (417 species) despite a low sampling intensity. The taxonomic composition of the Goheung coast differed from that of the Jejudo coast. About half of the total macrozoobenthos, 193 species, were polychaetes, followed by subequal numbers of crustacean arthropods and molluscs (101 and 95 species, respectively). The

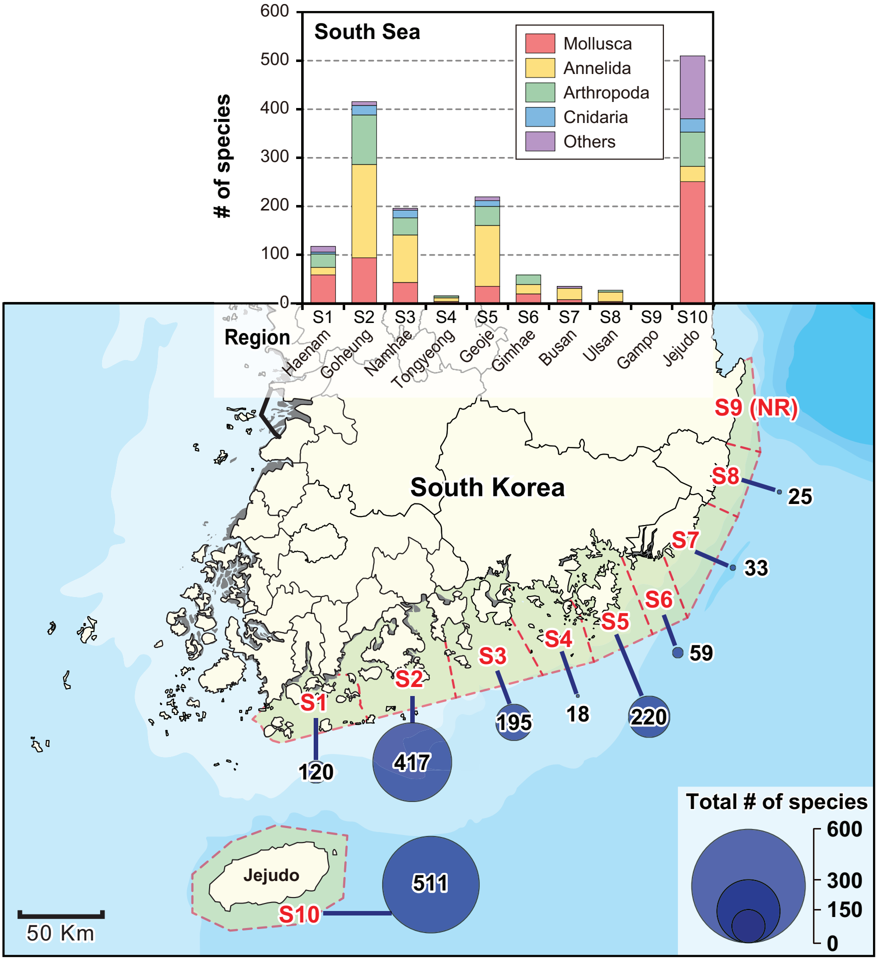


Figure 13 Map of the Korean South Sea showing the total number of recorded species over ten subregions and the faunal composition of the macrozoobenthos in each region. NR: not reported.

Goheung coast exhibited the highest diversity for annelids and crustacean arthropods among all regions of the South Sea.

The next most species-rich hotspot found in the South Sea was the Geoje coast (S5). Among the 10 subregions in the South Sea, S5 had the highest sampling effort, owing to the pursuit of many benthic community studies. The area includes several sediment contamination hotspots, such as Masan Bay and Jinhae Bay, where there has been elevated concern regarding benthic community health in recent decades (Hong 1987, Choi & Seo 2007, Seo et al. 2014a, Bae et al. 2017). Indeed, despite a high sampling intensity and the publication of seven studies focused on the Geoje coast, only 220 species were reported. This relatively low benthic faunal diversity reflects the impacts of sediment pollution (Khim & Hong 2014). Annelid species were the predominant taxa in subtidal bottoms (>58% of total species). There were relatively low numbers of crustacean arthropods (43 species) and molluscs (32 species). All other South Sea subregions had <200 macrozoobenthic species documented, likely reflecting a relative lack of research across the region.

Regional co-occurrence analysis indicated that some 779 macrozoobenthos species in the South Sea (~70%) were found in only a single region (Figure 14). Hence, there were even more uni-subregional species found in the South Sea than were found in the West Sea. These limited ranges may likewise be due to local geographical characteristics and, perhaps in part, sampling bias. Of the species present in only a single subregion of the South Sea, 44% were molluscs (340 species); this quantity of species is nearly double that found in the West Sea (178 species). The next compositional taxa include crustacean arthropods (146 species), polychaete annelids (114 species), and cnidarians (50 species). Only 213 species were found to co-occur in two subregions, including 95 annelid species, followed by 61 mollusc species and 42 crustacean arthropod species. Co-occurrence in more than three subregions much reduced. Of 10 polychaete species found to co-occur across five or more subregions, five were opportunistic, namely *Capitella capitate*, *Tharyx* sp., *Heteromastus filiformis*, *Lumbrineris longifolia*, and *Magelona japonica* (Figure 14). Also, five species were organic pollution indicator species, namely, *Theora lata*, *Capitella capitate*, *Tharyx* sp., *Heteromastus filiformis*, and *Lumbrineris longifolia*.

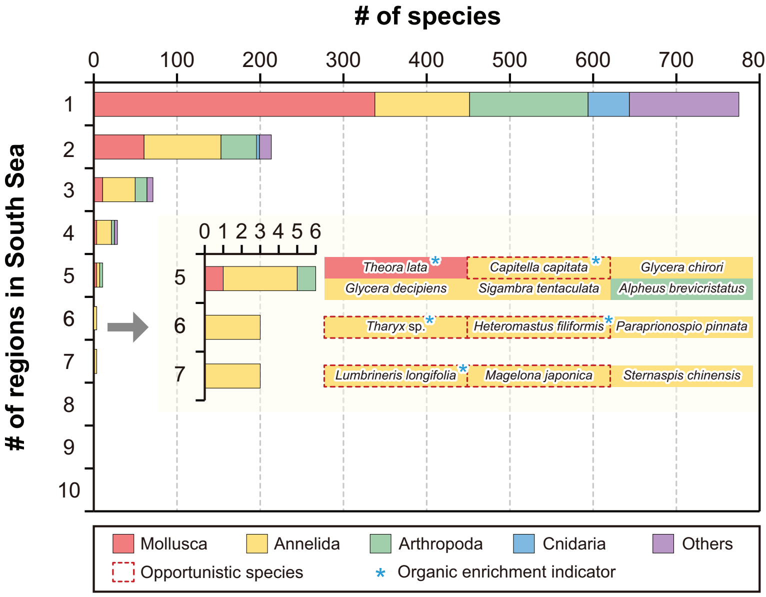


Figure 14 Number of macrozoobenthos species observed in one or more Korean South Sea subregions simultaneously. The inset shows the most common species found in more than 6 subregions. Some opportunistic or organic enrichment indicator species based on their life history traits are denoted.

Next, we described the distribution of selected taxa, seven annelid species and one molluscan species, that co-occurred in more than five subregions to characterize the commonly occurring species along the extent of the South Sea coast (Figure 15). Three polychaete species (*Lumbrineris longifolia*, *Sternaspis chinensis*, and *Magelona japonica*) were found crossing the seven subregions, indicating their wide-spread distribution on the southern coast. Three polychaete species (*Tharyx*

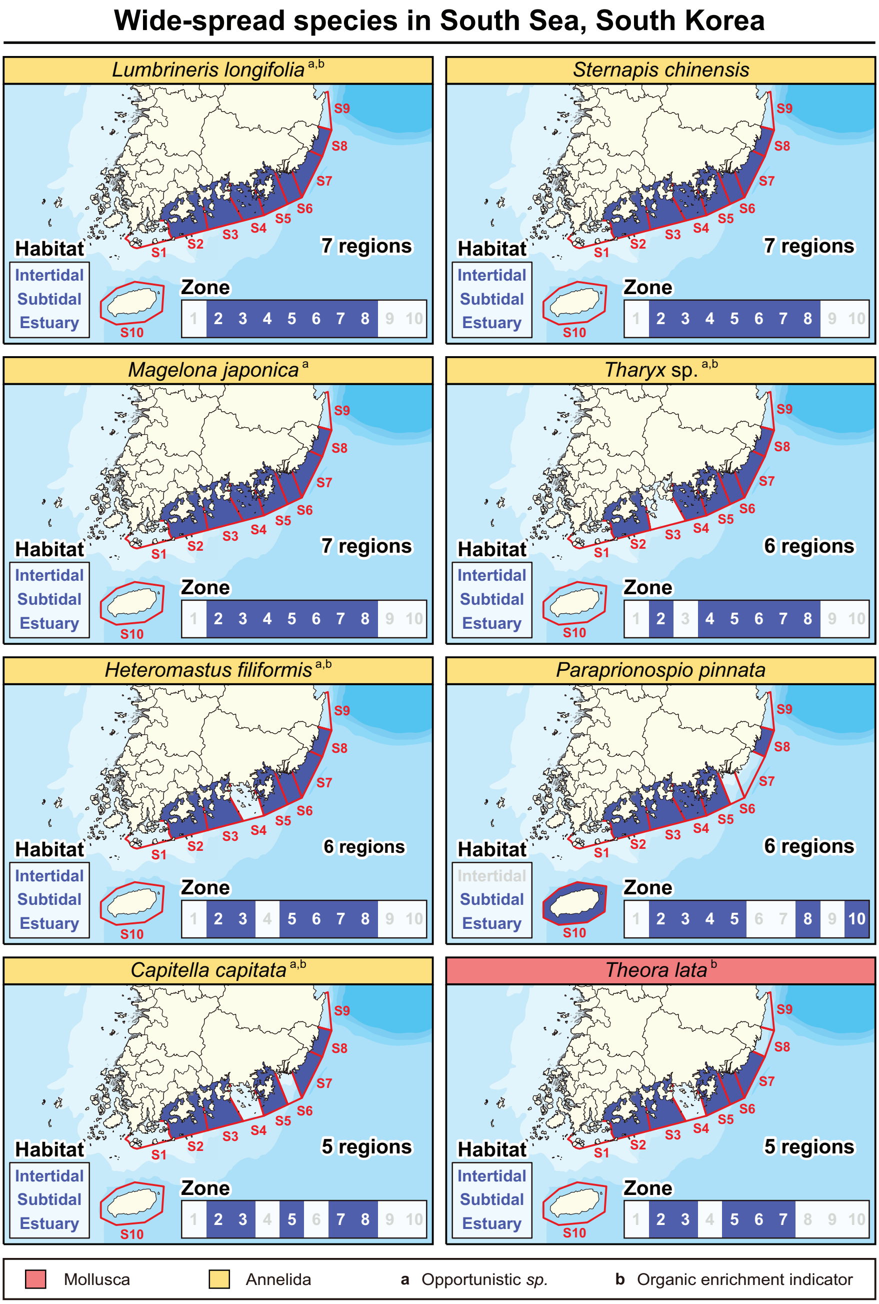


Figure 15 Distribution pattern of eight macrozoobenthos species occurring in more than five subregions along the South Sea of Korea. Their occurrence regions and habitat types are indicated by blue colour in the map and row of boxes, respectively.

sp., *Heteromastus filiformis*, and *Paraprionospio pinnata*) were found to co-occur in six subregions. Five of the aforementioned species showed a widespread presence along the consecutive coastline encompassing S2 to S8 (exceptions: *Tharyx* sp. not at S3 and *Heteromastus filiformis* not at S4). Interestingly, among the cosmopolitan polychaetes, only *Paraprionospio pinnata* showed co-occurrence around the remote island of the Jejudo coast, reflecting an especially wide geographical distribution. In terms of faunal distribution by habitat type, seven of the eight wide-spread cosmopolitan macrozoobenthos species inhabited across all three habitats (intertidal, subtidal, and estuary areas); the exception was *Paraprionospio pinnata*.

Faunal composition and distributions in the East Sea

The East Sea is characterized by its comparatively simple shoreline and a rapidly increasing water depth from the coast toward offshore. Its coastal habitats feature well-developed vast sand beaches and rocky shores. Despite its unique topographical features and varying habitat types, biodiversity research has been concentrated (>75% studies) around the Ulleungdo coast (E12). The few remaining works to date were carried out in the Hupo coast (E4), Jukbyeon coast (E5), and Samcheok coast (E6).

The Ulleungdo coast is a remote volcanic island far from the Korean Peninsula, including the Ulleungdo and Dokdo islands and associated small islets. This subregion was found to exhibit an extraordinarily diverse faunal assemblage with 562 species, a species number close to the total number of species reported for the East Sea (621 species). Our recent review documented a total of 578 macrozoobenthos species from 12 phyla at the Dokdo coast, including the intertidal and subtidal zones (Song et al. 2017). However, we excluded 16 taxa documented from Dokdo in the meta-data of the present review for the following reasons: they were treated as (merged into) one "species" because they were only identified to the genus level; double-counted species were excluded owing to synonyms or typos in the original reports and treated as one taxon according to a taxonomic update in WoRMS.

Among all of the recorded benthic organisms, molluscans were predominant with 183 species (33%), followed by crustaceans and annelids, with 132 and 112 species, respectively (Figure 16). Despite the distance of the island of Dokdo from the mainland and relative inaccessibility, its marine biodiversity was first introduced publicly via reports identifying two new crustacean decapods, *Pagurus similis* and *Pachygrapsus crassipes*, in the early 1960s (Kim 1960). Dokdo's high biodiversity has been recognized internationally by three dedicated works in the last decade (Ryu et al. 2012, Song et al. 2017, Kim et al. 2020). The total number of macrozoobenthic species reported in the Ulleungdo subregion was only 226, based on a recent review (Song et al. 2017).

The other subregion in which studies were conducted, other than the Ulleungdo coast, showed very low species diversity of macrozoobenthos (<100 species), reflecting a lesser variety in habitat diversity. Only 50 species have been documented in the Jukbyeon coast (E5), likely due to low sampling efforts (only three studies). Annelid species were the relatively dominant group in the subtidal area with 35 species, followed by crustacean arthropods and molluscs with eight and five species, respectively. Of note, the Jukbyeon coast, which is well known for public concerns between conservation and development, is home to various marine institutes and eco-tourism but faces potential risk due to the largest nuclear power plants in Korea. Finally, two prior investigations were conducted in the Hupo coast (E4) and Samcheok coast (E6), one study each, yielding the documentation of quite a few marine species (20 and 13 species, respectively).

Regional macrozoobenthos co-occurrence analysis indicated that 598 species have been found only a single region of the East Sea (Figure 17). The results obtained for the East Sea were consistent with those found for the West Sea and South Sea, with biased sampling efforts representing the main reason for there being so few co-occurring species. Among uni-subregional species, molluscs were predominant (189 species, 32%), followed by similar numbers of crustacean and annelid species (139 and 130 species, respectively). Due to the lack of sampling effort in other subregions in the East Sea, these co-occurrence records may not reflect the actual span of the species.

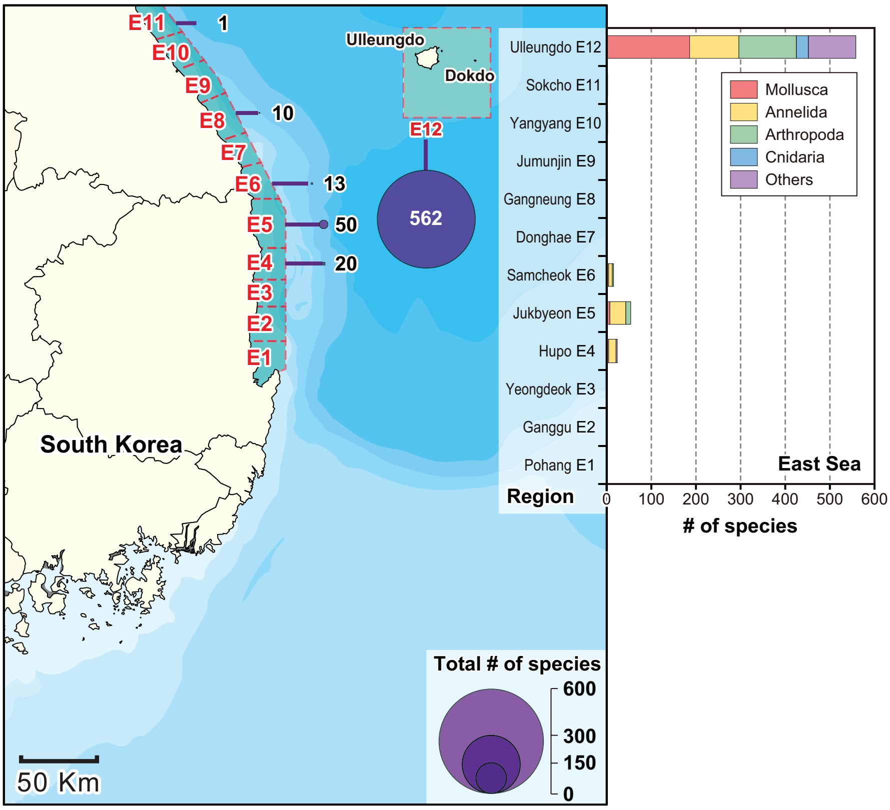


Figure 16 Map of the Korean East Sea showing the total number of recorded species over 12 subregions and the faunal composition of the macrozoobenthos in each region.

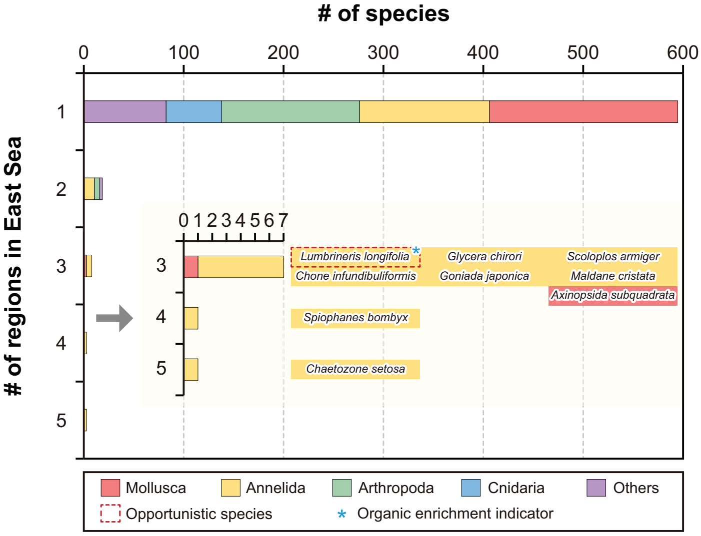


Figure 17 Number of macrozoobenthos species observed in one or more Korean South Sea subregions simultaneously. The inset shows the most common species found in more than 3 subregions. Some opportunistic or organic enrichment indicator species based on their life history traits are denoted.

Notwithstanding, given the presently available data, it was found that a total of 14 macrozoobenthos species co-occurred at two or more subregions, of which most were annelids (11 species). The number of co-occurring species across 3, 4, and 5 subregions were 7, 1 (*Spiophanes bombyx*), and 1 (*Chaetozone setosa*), respectively. Only one of the polychaete species, *Lumbrineris longifolia*, was found to be opportunistic and organic enrichment indicator at this time.

Finally, to characterize the commonly occurring species, we analyzed the distribution patterns for the nine wide-spread species found to occur in three or more subregions of the East Sea (Figure 18). The polychaete species *Chaetozone setosa* spanned five East Sea subregions (E4, E5, E6, E8, and E12), with its widest observable distribution along the eastern coast and Dokdo. The next widely distributed species, *Spiophanes bombyx*, is also a polychaete; it was observed in four subregions. Next, six polychaete annelids (*Lumbrineris longifolia*, *Glycera chirori*, *Scoloplos armiger*, *Chone infundibuliformis*, *Goniada japonica*, and *Maldane cristata*) and one molluscan species (*Axinopsida subquadrata*), co-occurred in three subregions. Most co-occurring species found inhabited three habitat types (intertidal, subtidal, and estuary). The exceptions were *Spiophanes bombyx* (intertidal and subtidal); *Chone infundibuliformis* (subtidal and estuary); and *Maldane cristata* and *Axinopsida subquadrata* (subtidal only).

Long-term human impacts on marine ecosystem: Sihwa reclamation

Backgrounds and overview of Sihwa issue

Coastal habitat destruction (or alteration) is recognized as the main issue relating to marine ecological quality in East Asia, particularly in the Northwest Pacific Action Plan region encompassing Korea, China, Japan, and Russia (Khim et al. 2018). Coastal reclamation has long been an environmental issue, especially in China and South Korea. Its blocking effect on tidal connectivity has contributed to the loss of valuable coastal habitat and loss of marine biodiversity. Lake Sihwa, formerly a natural tidal flat, is a well-known example of ecosystem deterioration due to large-scale coastal reclamation. Lake Sihwa has been isolated from the offshore marine environment by the construction of a 12.7 km sea-dike constructed in 1994. The original purpose of the Sihwa reclamation project was to provide a freshwater supply to nearby industrial and agricultural areas via seawater desalinization (Lee & Khim 2017). After the dike construction, however, the water quality of the lake deteriorated drastically, with a COD approaching 20 $\text{mg}\cdot\text{L}^{-1}$, a level far above standard good water quality guidelines (2 $\text{mg}\cdot\text{L}^{-1}$) in Korea (Hong et al. 1997, Kim et al. 2002).

The failure of the Sihwa project can be attributed to underestimation of three ecological aspects. First, important ecological functions of the natural environment were not considered prior to sea-dike construction, which resulted in a rapid deterioration of water quality followed by a drastic reduction in benthic faunal diversity. Consequently, a huge budget was consumed to implement an uncertain water quality improvement technique (Lee et al. 2014, Lee & Khim 2017). Second, the volume of annual freshwater flowing into Lake Sihwa was very low, thus necessitating a long time for full desalination, which was not adequately predicted in the initial planning (KWRC 2005). Third, the regional watershed was not adequate to meet increasing volume demands for wastewater and freshwater consequent to rapid expansion of the adjacent industrial and agricultural areas. In response to the unexpected water quality deterioration that occurred within two years of the dike's construction (1996), several short-term temporary measures were applied by the Korean government to address the water quality issue (Table 4), including a simple discharge of wastewater to the outer sea by seawater circulation (Lee et al. 2014). Despite such efforts, good water quality did not recover to the regional ambient level until 2000.

After 2000, the Korean government abandoned its original plan to convert Lake Sihwa into a freshwater reservoir and then constructed a tidal power plant, which allowed seawater circulation

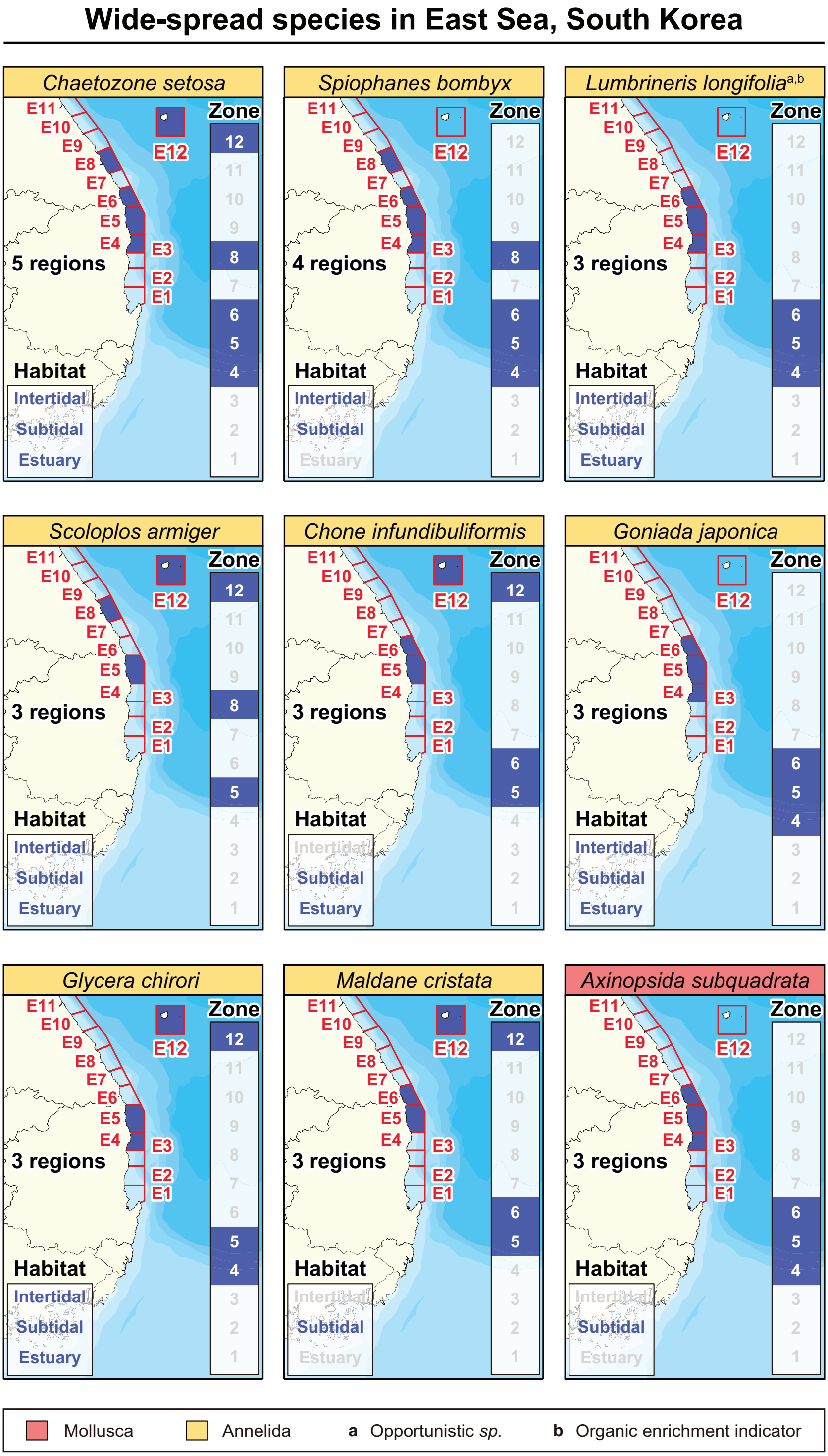


Figure 18 Distribution pattern of nine macrozoobenthos species occurring in more than three subregions along the East Sea of Korea. Their occurrence regions and habitat types are indicated by blue colour in the map and row of boxes, respectively.

Table 4 Summary of progress on political and sociological issues, environmental conditions, and ecological responses to Lake Sihwa reclamation from 1986 to the present

Year	Issues	Major management measures	Environmental conditions	Ecological responses
1986	Developed industrial complexes			
1994–1996	Construction of Sea dike	Establishment of special WQ management measures (96)	Highlighted Lake Sihwa pollution (96)	Brackish water species predominated Opportunistic species dominated
1997–1999	Seawater circulation began	Test sluice operation to increase seawater circulation	Great concentrations of NPs found	Outbreak (>90%) of opportunistic species, *Nitzschia* species dominated
2000	Abandonment of plan to keep Lake Sihwa as a freshwater reservoir	Designation as a SMA (00) Implementation first phase of SCR EMMP (01~06) Construction of wetland to reduce nonpoint pollution ($1.04\,km^2$) (02)	Great concentrations of NPs found Inland sediment highly polluted	Dominant taxa changed and opportunistic fauna decrease
2004	Initiation of TPP	Improvement of sewage treatment plant (03~04)	PFCs originated from surrounding activities	Brackish species and organic indicators still dominant
2007–2010		Second phase of SCR EMMP Stream sediment dredging and marine debris cleanup	Mercury in sediment showed great concentrations; PBDE concentration was the highest in the world	*Acartia* species dominated seasonally, density increased toward the dike
2011	Completion of TPP	Test operation of TPP ($32\text{-}160 \times 10^6 m^3 d^{-1}$)		
2012–2016		Third phase of SCR EMMP Full STPP operation ($160 \times 10^6 m^3 d^{-1}$) TPLMS implementation (13)		Brackish species and organic indicators still dominant
2019–Present		Fourth phase of SCR EMMP		

Abbreviations: TPP, Tidal Power Plant; WQ, water quality; SCR EMMP, Sihwa Coastal Reservoir Environmental Management Master Plan; TPLMS, Total Pollution Load Management System; NPs, nonylphenols; PEDEs, polybrominated diphenyl ethers.

between the lake and outer sea. Since 2011, the Sihwa Tidal Power Plant (TPP) has been operating with two purposes: electric power generation and water quality improvement via maintenance of water circulation. Although tidal circulation has improved Lake Sihwa's water quality somewhat, various land-based environmental pollutants—such as dioxins/furans, organochlorines, perfluorinated chemicals, and alkylphenols—have long contaminated the lake water and bottom sediments due to the limited artificial seawater circulation (Khim & Hong 2014). More recently, to keep land-based pollutants in Lake Sihwa below set levels, the Korean government launched the Total Pollution Load Management System (TPLMS) policy program. A historical overview of environmental issues and the Korean government's action plans was provided here to highlight efforts to improve the water quality in Lake Sihwa in recent decades.

Long-term changes in the environments of Sihwa

Sea-dike construction at the Sihwa site began in 1987 and ended in 1994. The dike's original purpose was to provide a supply of freshwater from the artificial lake for agricultural and industrial uses. The maximum water capacity of Lake Sihwa was designed to be 330 × 10^6 m^3, with a storage volume of 180 × 10^6 m^3. After the dike construction, water quality parameters for lake bottom waters showed rapid deterioration (Figure 19). Notably, COD, which was less than 3.5 ppm in 1992

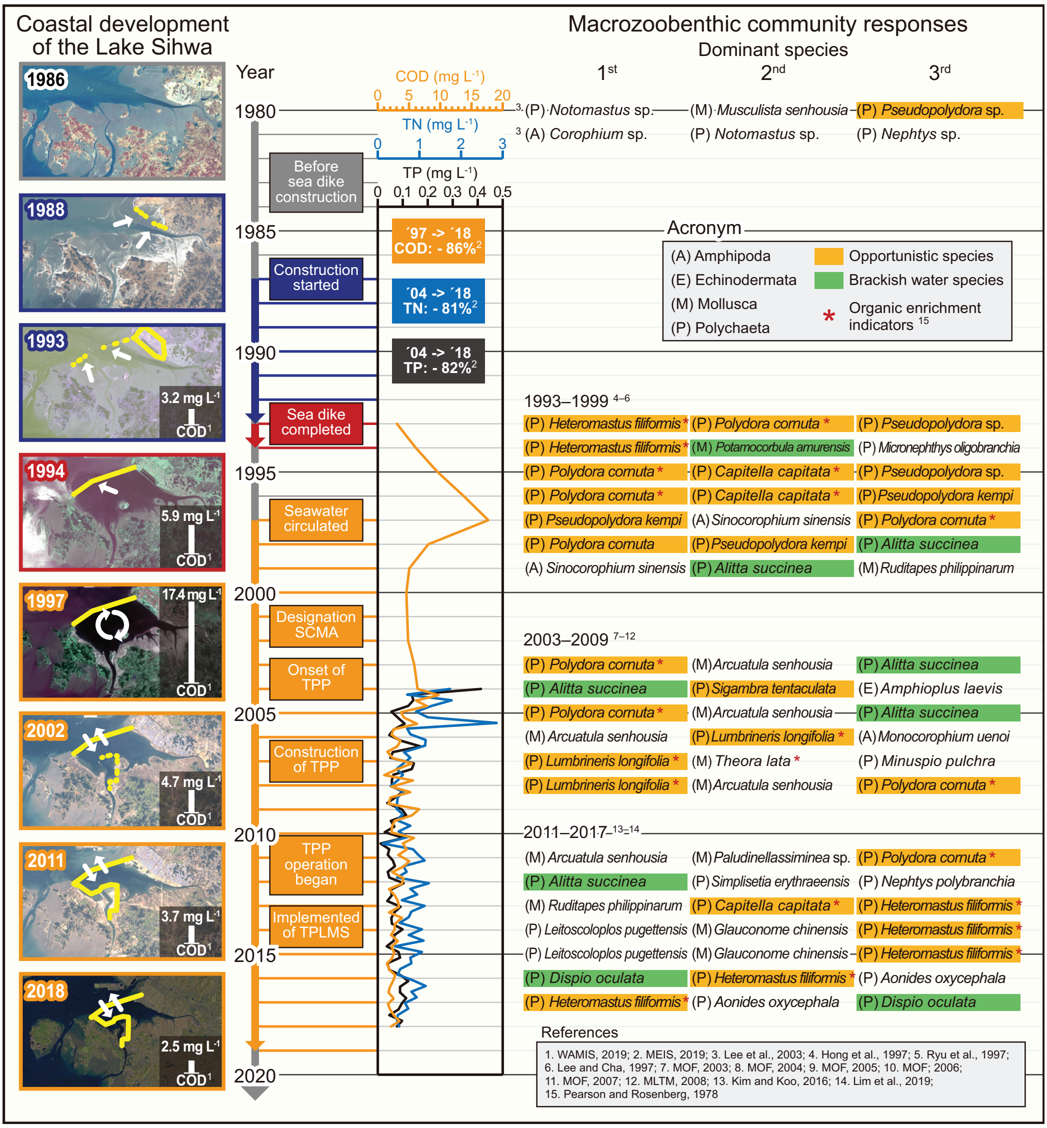


Figure 19 Top three dominant macrozoobenthos found in Lake Sihwa over time. Data are shown over the past 30 years (meta-data extracted from 14 references given), starting from before the Sihwa reclamation project. Species belonging to taxonomic groups with opportunistic species, brackish water species, and organic enrichment indicators that were found to occur in Lake Sihwa are highlighted. A brief summary of the history of the reclamation project, highlighting historical embankment activities with basic water quality data (COD, TN, and TP).

before the dike was functional, increased dramatically from 5.9 mg·L^{-1} in 1994 to 17. 4 mg·L^{-1} in 1997. Although several short-term treatments applied in response to this water quality deterioration did achieve a rapid decline of COD levels in 1997, this course correction began to plateau in 1998. Subsequently, COD levels remained around 5~6 mg·L^{-1} until 2004, after which further significant reductions in COD levels were finally achieved with the use of a sluice.

Opening of the sea-dike sluice gates allowed outside seawater to flow into the lake, thereby mixing the polluted seawater of Lake Sihwa with backfilling seawater. Although this strategy was helpful to some extent, it was not sufficient to fully circulate the lake water with seawater. Thus, construction of the TPP was proposed and implemented by the Korean government in 2004. Because the original sluice gate for Lake Sihwa was situated at the southern corner of the dike, a new gate for the TPP was required to enable the exchange and circulation of seawater and to enable electric power to be generated in a more efficient manner. Accordingly, the TPP was constructed in the middle of the dike, and it became operational finally in 2011 (Figure 19). Thereafter, COD proceeded to decrease to 2.5 mg·L^{-1} by 2015, where it has been roughly maintained until recently. The TPLMS has been exercised to reduce the input of organic materials to the lake by controlling the amounts of COD and total organic carbon levels flowing into the adjacent sea, but efficiency and management system issues have persisted.

Total nitrogen (TN) and total phosphate (TP) concentrations showed temporal patterns similar to that of COD. Although increased seawater circulation seemed to improve water quality in Lake Sihwa, the power of circulation was not enough to improve water quality satisfactorily in the whole lake (Lee et al. 2014). In terms of sedimentary pollution, among coastal Korea areas, Lake Sihwa showed the greatest concentrations of some persistent toxic substances after the completion of dike construction (Lee et al. 2014). In 2006, perfluorinated chemicals (perfluorooctane sulfonate and perfluorooctanoic acid) in the upper stream of Lake Sihwa were present at the highest levels in the world (651 and 62 ng·L^{-1}, respectively) (Rostkowski et al. 2006). Indeed, Lake Sihwa has been suffering from environmental deterioration due to land-based pollution since the early 1990s due to point sources of adjacent industrial complexes and highly populated nearby cities (Khim et al. 1999, Hong et al. 2016). Despite the partial improvement of water quality in Lake Sihwa since the commencement of TPP operation in 2011 (Lee et al. 2014), lake water quality and bottom sediment quality have remained unsatisfactory due to continuing pollution from inland industry sources and densely populated cities (Hong et al. 2016).

Long-term changes in Sihwa benthic communities

The macrozoobenthic community in Lake Sihwa changed in response to habitat condition alterations primarily attributable to the new dike. To determine the ecological responses of the macrozoobenthic community, macrozoobenthos species dominance was analyzed over the past 36 years (Figure 19). The benthic community at Lake Sihwa was significantly affected by hypoxia or anoxic bottom conditions, seemingly due to organic enrichment (Lee et al. 2014, Lee & Khim 2017). There were clear changes in dominant macrozoobenthos species following sea-dike construction. Opportunistic species, such as *Heteromastus filiformis*, *Pseudopolydora kempi*, and *Capitella capitata* were more abundant after construction of the sea dike.

Several previous studies demonstrated clearly that dike construction and sluice closure caused various adverse ecological effects due to limited tidal mixing (decrease in assimilative capacity), water stratification, eutrophication, algal blooming, and increased pollutant load from the watershed (Lee et al. 2014, Lee & Khim 2017). Of note, the COD in Lake Sihwa reached 17.4 mg·L^{-1} in 1997, at which time the direct waste treatment plant's discharge outlet was moved to outside of the lake. Rapid COD increases were associated directly with low tidal mixing after sluice closure. However, after commencing active seawater circulation through the sluice in the late 2000s, COD levels began to decrease rapidly in the 2010s, reaching levels last seen in the early 2000s.

The benthic community of Lake Sihwa would have been directly affected by the sedimentary pollution concomitant with the observed water quality deterioration. Indeed, brackish water species, such as the polychaete *Alitta succinea*, became dominant during the period of limited tidal mixing (Figure 19). The combination of blocked tidal connectivity and continuing freshwater input seemed to alter the composition of the lake's macrofauna. Subsequent long-term changes in dominant species tended to reflect the historical sedimentary pollution (Lee et al. 2014, Lee & Khim 2017).

In terms of species richness and evenness, macrozoobenthos diversity decreased while a small number of opportunistic species exhibited rapid population increases (Lee et al. 2014). Specifically, a prevalence of polychaetes emerged after dike construction, with the numbers of opportunistic polychaetes (e.g. *Pseudopolydora kempi* and *Polydora cornuta*) increasing drastically right after the dike was constructed in 1994 until the COD peak in 1997. The predominance of opportunistic species and organic enrichment indicators seemed to decline after the TPP became operational in 2005. However, they are still present, reflecting long-term polluted bottom conditions. Positive effects of TPP operation have been acknowledged in some aspects of water quality, though the status of benthic community recovery in the lake continues to be debated. Continued monitoring of the benthic community is needed to fully address the long-term effects of the coastal reclamation in Lake Sihwa.

Long-term human impacts on marine ecosystem: Saemangeum reclamation

Backgrounds and overview of Saemangeum issue

Estuaries are ecological hotspots and buffering zones; they support and contribute to various ecological processes across terrestrial, brackish, and marine ecosystems in an integrated manner (Gray 1997). Tidal flats that develop in the critical transition zones constituted by estuaries play an important socioecological role in supporting diverse marine ecosystems (Levin et al. 2001, Wall et al. 2001). However, about half of the Korean estuaries situated along the west and south coasts of Korea have been blocked at the estuarine mouth and/or in the upper rivers by seawalls and/or dams. The worst example of coastal reclamation in Korea is the Saemangeum project, which was designed to achieve a massive inland land-gain of 400 km^2 (about 2/3 the size of Seoul, which is ~600 km^2) for urban development by estuarine filling.

In 2006, two large estuaries at Mangyung River and Dongjin River in the Saemangeum tidal flat area were isolated from ocean waters by the world largest seawall (33.9 km). The Saemangeum seawall was built in four sectors. Sector III (2.7 km, Sinsido to Yamido) was completed in 1994. Sector I (4.7 km, Buan to Garukdo) was completed in 1998. Sector IV (11.4 km, Yamido to Gunsan) was completed in 2003. And finally, Sector II (9.9 km, Garukdo to Sinsido) was completed in 2006 (Figure 20). The former tidal flats that had developed in these estuaries extended seawards some 5~10 km, covering an area of ~180 km^2 and constituting the largest tidal flat area in Korea. The entire marine and estuarine ecosystems of these areas are expected to be destroyed consequent to water quality deterioration and sedimentary pollution due to limited seawater circulation and tidal mixing, as was experienced previously in the Sihwa reclamation case. Rich and productive benthic communities were documented before the dike construction, and observations of benthic community changes, from microphytobenthos to macrozoobenthos, were reported during and after the construction of the dike (Ryu et al. 2014).

The Saemangeum project was launched by a commitment that the president of Korea made in the late 1980s. Work commenced in 1991 with political support. The environmental issues and Korean government's actions at Saemangeum from 1991 to the present are summarized in Table 5. There have long been social conflicts between proponents for and antagonists against such projects involving central and local governments as well as varying stakeholders from local residents to

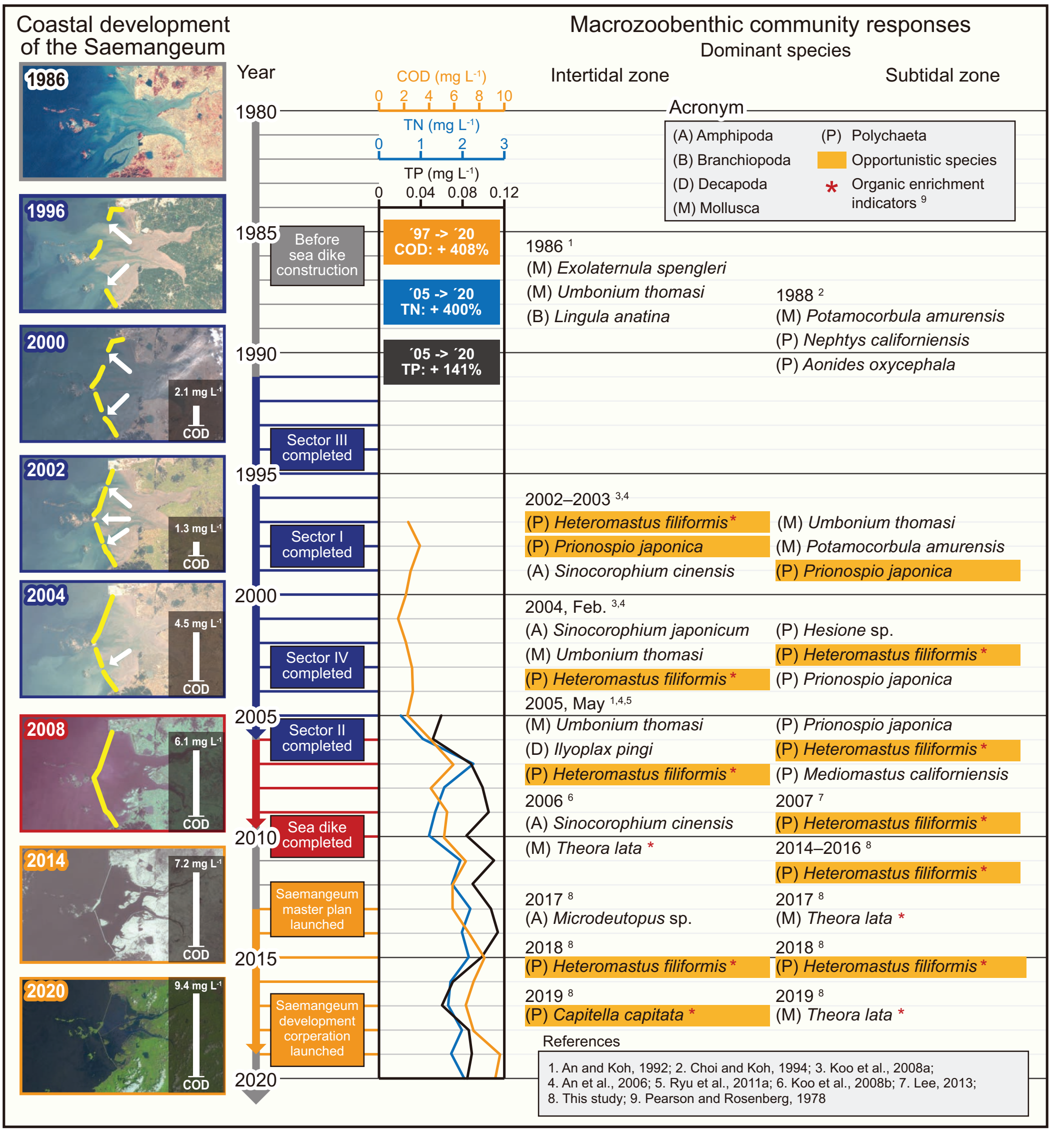


Figure 20 The dominant macrozoobenthos found in the Saemangeum tidal flats since during the Saemangeum reclamation project, over the past 30 years (meta-data extracted from nine references given). Species belonging to five taxonomic groups with opportunistic species, and organic enrichment indicators in the intertidal and subtidal zones of the Saemangeum area are highlighted. A brief summary of the history of the Saemangeum reclamation project is shown, highlighting historical embankment activities with basic water quality data (COD, TN, and TP) in the Saemangeum area.

environmental NGOs. Conflict over the Saemangeum project arose in light of the lessons of Lake Sihwa reclamation case described above. In the middle of project, construction was paused for re-evaluation of the project's feasibility in 1999 and then resumed in 2001 based on a top-down order from the Korean government.

Debates on the Saemangeum project continued, culminating in a remarkable public movement in 2003 led by religious leaders wherein more than 8000 participants chanted *Samboilbae* ("three steps and one bow"). The participants completed a walk of about 300 km from the Buan tidal flat of Saemangeum

Table 5 Summary of progress on political and sociological issues, environmental conditions, and ecological responses to the Saemangeum reclamation project

Year	Progress	Political and sociological issues	Environmental conditions	Ecological responses
1991	Sea-dike construction began			
1994–1995	Sector III completed (2.7 km, 94)	SMG industrial complex plan announced (95)		
1996–1998		Highlighted Lake Sihwa pollution (96); Argued reasonable fishery compensation (97)		Shellfish catch sharply decreased (91–98)
1999	Construction stopped	SERP organized holding for dike construction	>95% reduction in land-based nutrient loading in tidal flats	
2001–2002	Construction resumed (01); environmental monitoring (02–12)	Sustainable, stepwise developmental planning followed by continuing construction (01)		
2003–2005	Sector IV completed (11.4 km, 03)	“Three steps and one bow” campaign against reclamation (03); government lost first trial, but won appeal to SAC (05)	Organochlorine pesticides from two rivers widely distributed in seawater and sediments	Macrofaunal assemblages in intertidal areas were changed and/or altered (Ryu et al. 2011a; 04–05)
2006–2008	Sector II completed (9.9 km, 06) Sea-dike construction completed (06)	Government won at the Supreme Court (06) Established the Special Act for promotion of the SMG Project (07)	Sedimentation increased and strong erosion (06) River inputs induced stratification in waters inside dike	Shorebird composition clearly changed (06) Great decrease of species number and density in tidal flat (Koo et al. 2008b; 08)
2011–2013	SMG Master Plan launched (11) Launched the Korea Agency for SMG Development and Investment (13)			30% reduction in fishing boats (11), and >200 finless porpoises died, due to freezing water surfaces within dike (11)
2016–2018	Operation of SCTP Cogeneration Plant SMG New Port Breakwater Completion	Launch of SMG Development Corporation Amendment to establish SMG Development (18) Corporation with juristic personality (18)		

Abbreviations: SMG, Saemangeum; SERP, Saemangeum Expert Review Panel; SAC, Seoul Administrative Court; SCTP, Saemangeum Cogeneration Thermal Power Plant.

to the Presidential Blue House in Seoul, Korea. This protest caused a great sensation and led to a historic change in the Korean public view, which shifted to favour conservation over development.

The project itself was subjected to legal actions. However, upon winning the final court decision in 2006, the government resumed the project, which led to the loss of the once majestic natural tidal flats of Saemangeum. In 2007, the Special Act on the Promotion of the Saemangeum Project was passed, and the Saemangeum Master Plan was established to further promote the development of the landfilled area in 2011 (Table 5). The Saemangeum area is being developed currently, but the plan continues to be debated.

The Saemangeum case shows a policy failure with respect to protective estuary and coastal management in Korea. The natural value of the flats, ecologically and socioeconomically, was underestimated (Koh et al. 2010). All five major rivers flowing into the sea are now effectively closed estuaries due to seawalls at the river mouth or multiple upstream dams. The mouths of the estuaries of the Han River and Seomjin River are open to the sea, but they have water and sediment quality problems due to upstream dams. Although some development of limited dams is necessary, large-scale coastal reclamations involving seawalls should not be acceptable given their enormous socioeconomic cost and the associated loss of ecosystem services.

Long-term changes in Saemangeum environments

Environmental deterioration consequent to the Saemangeum reclamation has been anticipated since the late 1990s, before the dike was completed, based on several early signs. Water quality and sediment quality deterioration was already evident in 1999–2000. First, water quality parameters (COD, TN, and TP) for bottom waters changed dramatically in the interior of the dike (Figure 20). In particular, COD concentrations increased rapidly after the completion of Sector IV in 2003; these increases can be attributed to water column stratification due to limited tidal mixing (Figure 20). Although there are no COD data available for the pre-dike Saemangeum area, a continuously increasing COD trend has been observed since the completion of the dike in 2006, with data from the most recent year available, 2019, indicating that COD levels in the Saemangeum reached 9.7 $mg{\cdot}L^{-1}$. This level far exceeds the standard water quality guidelines for COD in Korean coastal and marine areas, indicating that the situation is highly concerning.

After Sector II was constructed in 2006, TP concentrations increased sharply and they have remained high for almost 10 years. From 2014 to 2017, TP concentrations fell gradually, perhaps owing to the temporary measures of the water quality improvement project implemented by the local government in Jeollabukdo. By 2017, TP concentrations had decreased to about 52.9% of 2011 levels. However, since 2017, TP concentrations in the Saemangeum have again been increasing due to increased nutrient input and particulate organic matter from river inflows. Lower density freshwater and summer heating favour the formation of a thermocline and vertical stratification in the water column interior to the dike. TN levels have remained relatively constant since their peak in 2007, not yet reflecting water quality improvement.

The direct effects of the Saemangeum dike seem to be to reduced volume, velocity, and duration of tidal inflows, effects that would be expected to alter benthic geochemical conditions (Park et al. 2014b). Furthermore, the dike and the altered tidal currents associated with its presence stimulate surface sediment erosion (Lie et al. 2008). These physical regime shifts can alter natural biogeochemical cycles, including those related to benthic community structure and function. In particular, the concentrations and fluxes of particulate organic matter in coastal areas within and outside the Saemangeum dike have changed dramatically in recent years (personal observation by the first author in 2020).

Long-term changes in benthic communities of Saemangeum

The benthic community structure was altered during the dike construction (2002–2006), due to bottom layer hypoxia associated with water column stratification as well as changes in sediment faces owing to altered sedimentary dynamics (Ryu et al. 2014). In addition, many fishermen have reported fishery reductions in harvestable shellfishes and fishes in tidal flats and coastal areas since completion of the dike. For example, increased deposition of fine sediments on tidal flats near Sector IV resulted in decreased macrozoobenthic diversity and increased opportunistic species in

2002–2003 (Koo et al. 2008a). Numerous adverse ecological effects of the Saemangeum dike construction have been documented for numerous marine organisms, including microbiota (Choi & Noh 2008), zooplankton (Lee et al. 2009), and waterfowl (Jin et al. 2010, Kang et al. 2011).

In the present review, we collected long-term macrozoobenthos data from the Saemangeum area and then analyzed benthic community changes longitudinally in response to environmental changes (Figure 20). Fortunately, before the Saemangeum project began, studies on macrozoobenthos (An & Koh 1992) and microphytobenthos (Oh & Koh 1995) had been conducted, establishing the natural baseline benthic community conditions for the area. In general, the macrobenthic faunal composition showed two clear temporal trends. First, increases in proportions of polychaetes, particularly in the subtidal zone, occurred after the dike was constructed. Second, increased proportions of opportunistic species and/or indicator species for organic pollution/enriched sediments were evidenced during and after dike construction, in particular the predominance of two opportunistic polychaete species, *Heteromastu filiformis* and *Prionospio japonica*. *H. filiformis* was a widespread polychaete species in the West Sea (Figure 20), whilst *Prionospio japonica* could be an opportunistic local species associated with the Saemangeum reclamation event.

After dike construction in the Saemangeum, the population density of previously dominant species in the intertidal zone, including a molluscan species, *Exolaternula spengler*, and a brachiopod species, *Lingula anatina*, decreased dramatically (Ryu et al. 2011a,b). Dominant species in the subtidal zone also showed a pronounced temporal change in the faunal composition of macrozoobenthos, and such temporal change might reflect more dynamic environmental changes that are directly linked to long-term benthic community alterations.

Macrozoobenthic community data for the Saemangeum tidal flats evidenced long-term and ongoing alterations in macrozoobenthic community responses to environmental deterioration. There remains a knowledge gap regarding long-term benthic community changes to fauna and flora. Likewise, there are limited data available from before the dike was constructed. We realize, and would like to emphasize, the critical importance of baseline and monitoring data to address long-term ecological changes, particularly in the Saemangeum case (Reise 2012). Without such basic long-term data, it would be difficult to address the status and trends of marine biodiversity in the Saemangeum region, and elsewhere, adequately. Considering the ongoing events affecting the Saemangeum flats, further accumulation of benthic community data is needed.

Long-term human impacts on a marine ecosystem: Taean oil spill

Backgrounds and overview of the Taean case

The HSOS occurred on the 7 December 2007, less than 10 km offshore of Taean County on the west coast of Korea. Approximately 13 million liters of crude oils, including three types of oils (Iranian Heavy, United Arab Emirates Upper Zakum, and Kuwait Export), spilled into ecologically sensitive areas of the coastline near Taean (Hong et al. 2014, Yim et al. 2017). The spilled crude oil reached the nearby shore within 14 h of the spill; the oil slick was 33 km long, 10 m wide, and 10 cm thick after two days (Sim et al. 2010), and it was distributed in intertidal areas, covering pacific oyster farms and natural beaches (Kim et al. 2017). Historically, the HSOS was the largest oil spill in the Korean waters and remains one of the largest recent oil spills in the world, second only to the DEEPWATER HORIZON oil spill in the Gulf of Mexico in April 2010.

The Korean Government and local authorities responded to the HSOS immediately by placing tremendous efforts on implementing a comprehensive cleanup over several months (Table 6) (MLTM 2009, Hong et al. 2014). There was an intensive human endeavor (>2.1 million people) that included some 1.2 million volunteers and 0.9 million residents, military personnel, and others, during the cleanup period (Hong et al. 2014). Cleanup activities at sea and in the onshore areas of

Table 6 Summary of the Hebei Spirit Oil Spill (HSOS) accident and HSOS cleanup activities in marine and coastal area

HSOS occurrence	Location	~10 km off Taean County	
	Month/Day/Year	December/07/2007	
	Amount of spilled oil	12,547 kL	
	Type of spilled oils	Kuwait Export Crude Iranian Heavy Crude UAE Upper Zakum	
	Polluted areas	375 km of Korean west coast (total 1300 km^2)	
Cleanup activities	Ships	KCG	6630
		KOEM	889
		Navy	723
		Others	11,968
		Total, units	20,210
	Heavy machinery	Truck	9991
		Excavator	5559
		Tractor	1304
		Others	12,119
		Total, units	28,973
	Personnel	Volunteers	1,226,730
		Residents	566,343
		Military personals	152,695
		Public officers	76,684
		Others	249,884
		Total no. of individuals	2,122,296
	Cleanup materials	Oil boom, km	47
		Oil absorbent, kg	493,127
		Dispersant, kL	298
	Cleanup cost	USD	~330 M
Oil collection	Liquid oil	At sea	2360
		On shore	1815
		Total (kL)	4175
	Oil wastes	At sea	1034
		On shore	31,040
		Total (Tons)	32,074
Research	Fund and duration	US ($)	~23 M, 10 years

Source: Modified from KCG (2008) and Hong et al. (2014).

Abbreviations: KCG, Korean Coast Guard; KOEM, Korea Environment Management Corporation; M, million.

Taean were officially terminated in October 2008. However, oil persisted in the deeper subsurface sediments (>20 cm below the surface) and in the most heavily affected intertidal areas of Taean for at least 24 months after the spill (Hong et al. 2014).

Oil spills can cause a wide range of adverse ecotoxicological effects by way of physico-chemical pollution of diver marine environments with effects across habitat areas (intertidal and subtidal) and sediment types (muddy, sandy, and rocky shore), thereby affecting resident organisms. The short-term environmental impacts of an oil spill can be severe, including the infliction of serious physiological distress and mortality upon individual marine organisms. Indeed, the intertidal and nearby shallow subtidal ecosystems of Taean are healthy and productive encompassing diverse habitats such as rocky shores and sand beaches, but most oil-sensitive marine organisms were eradicated immediately by the spill (Yu et al. 2013, Seo et al. 2014b). Fortunately, due to the open coastal regime with high tidal energy together with extensive initial cleanup activities after the spill, the coastal ecosystem recovered faster than ecosystems impacted by other oil spills, such as the EXXON VALDEZ case (Yim et al. 2020). Notwithstanding, contamination hotspots are still found in intertidal areas, where residual oils still remain in subsurface layers until present day, underscoring the need for continued monitoring (Yim et al. 2012).

The present macrozoobenthos meta-dataset was collected from long-term ecological monitoring data for the HSOS and some independent ecological studies of the HSOS effects. In the present review, we delineated the recovery timeline of macrozoobenthos in four typical coastal areas of Taean, encompassing intertidal sandflats, intertidal mudflats, intertidal rocky shores, and the subtidal zone over a period of about seven years.

Long-term changes in Taean coast environments

Crude oil is composed mainly of hydrocarbons, including aromatic hydrocarbons, such as volatile organic compounds (VOCs) and polycyclic aromatic hydrocarbons (PAHs). Aromatic hydrocarbons accounted for approximately 30% of the spilled oils from the HSOS (Ha et al. 2012). All of the VOCs evaporated within a few days after the accident as follows: benzene – 10 hours; toluene, ethylbenzene, and xylene – 48 hours; and other VOCs – ≤4 days (Kim et al. 2012). Several carcinogenic compounds, including PAHs, remained for weeks to months; PAHs can be highly persistent in environmental media and thus can bioaccumulate over time (Lee et al. 2013).

The degradation of residual oil in the environments was strongly dependent on the media (water, sediments, or porewater) and substrates (grain size, organic carbon contents, etc.) (Natter et al. 2012). Other factors affecting degradation include microbial community and activity (Lee et al. 2019), natural energy (e.g. tidal flushing) (Hong et al. 2012), and even degree of initial cleanup activity (NOAA 2013). Residual oils are more persistent in sediments than in seawater, especially in low-energy regions (Hong et al. 2012, Yim et al. 2012, Kim et al. 2017). In addition, the adverse effects of residual oils on marine organisms depend on initial oil concentrations and the degree of oil weathering, which is further dependent on site-specific tide-associated exposure conditions (Hong et al. 2012). Indeed, in the Taean environment, oil weathering seemed to have a strong influence on the persistence of residuals and potential toxicities, particularly in intertidal benthic hotspots. Residual oil trapped in the bedrock along the rocky shores accumulated over long periods in the bottom layer, due to the lack of natural weathering.

Immediately after the HSOS, very high maximum concentrations of total petroleum hydrocarbons (1630 $\mu g{\cdot}g^{-1}$), PAHs (3350 $ng{\cdot}g^{-1}$) and alkylated PAHs (66,430 $ng{\cdot}g^{-1}$) were recorded (Figure 21). These peak concentrations would be expected to have direct adverse effects on intertidal organisms. The spatial distributions of PAHs in sediments varied widely, both regionally on the west coast and within Taean County, primarily due to the patchy distribution of spilled oil and non-uniform sediment characteristics (Hong et al. 2012). In general, PAH concentrations in intertidal sediments decreased over time—except for in hotspot areas, particularly in the intertidal zone—with relatively high concentrations being recorded in the subsurface layer (Hong et al. 2012; Hong et al. 2014) (Figure 21). For example, in March 2014, the concentrations of 16 PAHs and alkylated PAHs in sediments ranged from 0.42 to 74.8 $ng{\cdot}g^{-1}$ and from 0.56 to 50.9 $ng{\cdot}g^{-1}$, respectively. However, at the Sinduri and Sogeunri mudflats, high concentrations of alkylated PAHs were observed, remaining as oil contamination hotspots. Analyses of the compositions of alkylated chrysenes and dibenzothiophene homologues in mudflats with elevated PAHs showed that mudflats continued to be impacted by spilled oil residues. Six years after the HSOS, concentrations of PAHs and other chemicals settled into normal environmental levels in Taean and along the nearby coast, with the exception of the Sinduri hotspot.

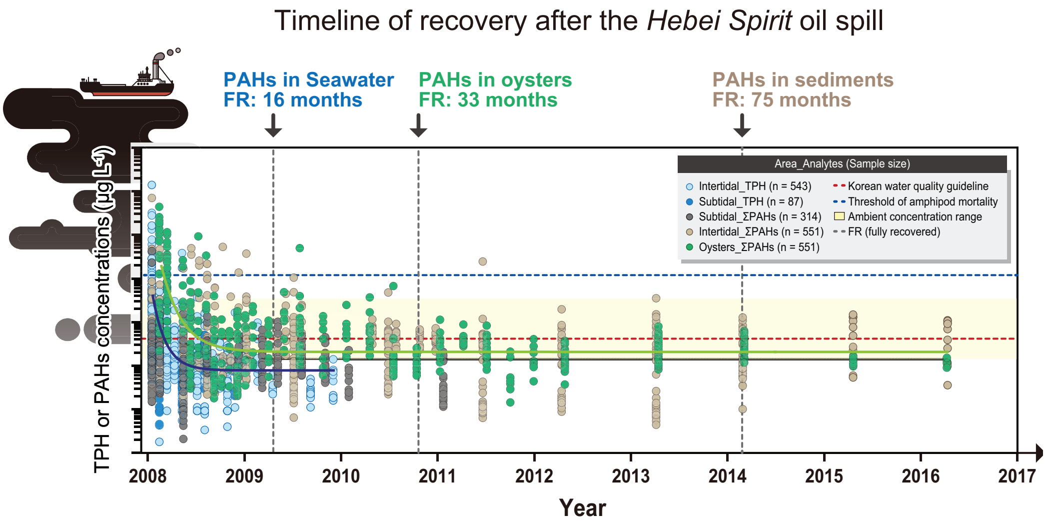


Figure 21 Temporal variations in residual oil concentrations in multiple environmental samples from different sources in the Taean coast, Korea. Concentrations of total petroleum hydrocarbon (TPH) and PAHs in seawater were checked after 16 months; those in sediment collected from intertidal and subtidal areas were measured after 75 months. Temporal variation in PAHs (including alkyl-PAHs) in oysters collected from intertidal areas in the Taean subregion was monitored. Fitted curves were obtained based on residual oil concentrations and the number of months after the oil spill using an exponential decay model. Yellow-shaded sections represent the ambient PAH concentration ranges in sediments on the west coast of Korea. The two dotted lines represent the Korean water quality guideline (red) and the threshold value of amphipod mortality (blue).

Long-term changes in benthic communities of the Taean coast

A dynamic marine environment shows substantial fluctuations in abundance and diversity as a feature of their normal functioning. These fluctuations evidence the strong capacity of marine environments for natural recovery from severe perturbations caused by natural phenomena as well as anthropogenic pressures, such as an oil spill. The HSOS impact has been evaluated extensively with respect to marine organism responses and recovery status. For example, a recent review indicated that the recovery period for macrozoobenthos varied across taxa and habitat, but generally spanned five to six years for the HSOS. The relative abundance of opportunistic bivalve species *Felaniella sowerbyi* had increased within eight months of the catastrophic mortality of the previous community (Figure 22). After other benthic species, such as polychaetes, expanded, the relative abundance of initial colonizers began to decline during the partly recovered stage. Over time, the initial community was seemingly eliminated through competition with species from higher trophic levels via complex biological interactions.

Four categories of habitat, namely intertidal sandflat, intertidal mudflat, intertidal rocky shore, and subtidal zone, were examined for macrozoobenthos community recovery at a population level (Figures 22–25). The number of macrozoobenthic species in the intertidal sandflat ranged from 94 to 114 during the sampling period, with a mean density of 1688 individuals (ind.)·m^{-2}. One year after the spill, the number of species and biodiversity of macrozoobenthos in the oil-impacted area continued to increase, but remained low compared to that of lesser oil impacted areas. After 2014, the density of macrozoobenthos increased in lesser impacted areas, but decreased in the oil impacted area. The most dominant species, *Felaniella sowerbyi*, which decreased at Sinduri and Mallipo in 2011 and 2012, respectively, increased in the oil impacted area after 2014. Two species that were dominant before the oil spill, *Umbonium thomasi* and *Scopimera globosa*, had low densities in the oil impacted area until 2014. Since 2010, the number of species has increased gradually, with current species diversity similar to non-polluted west coast areas.

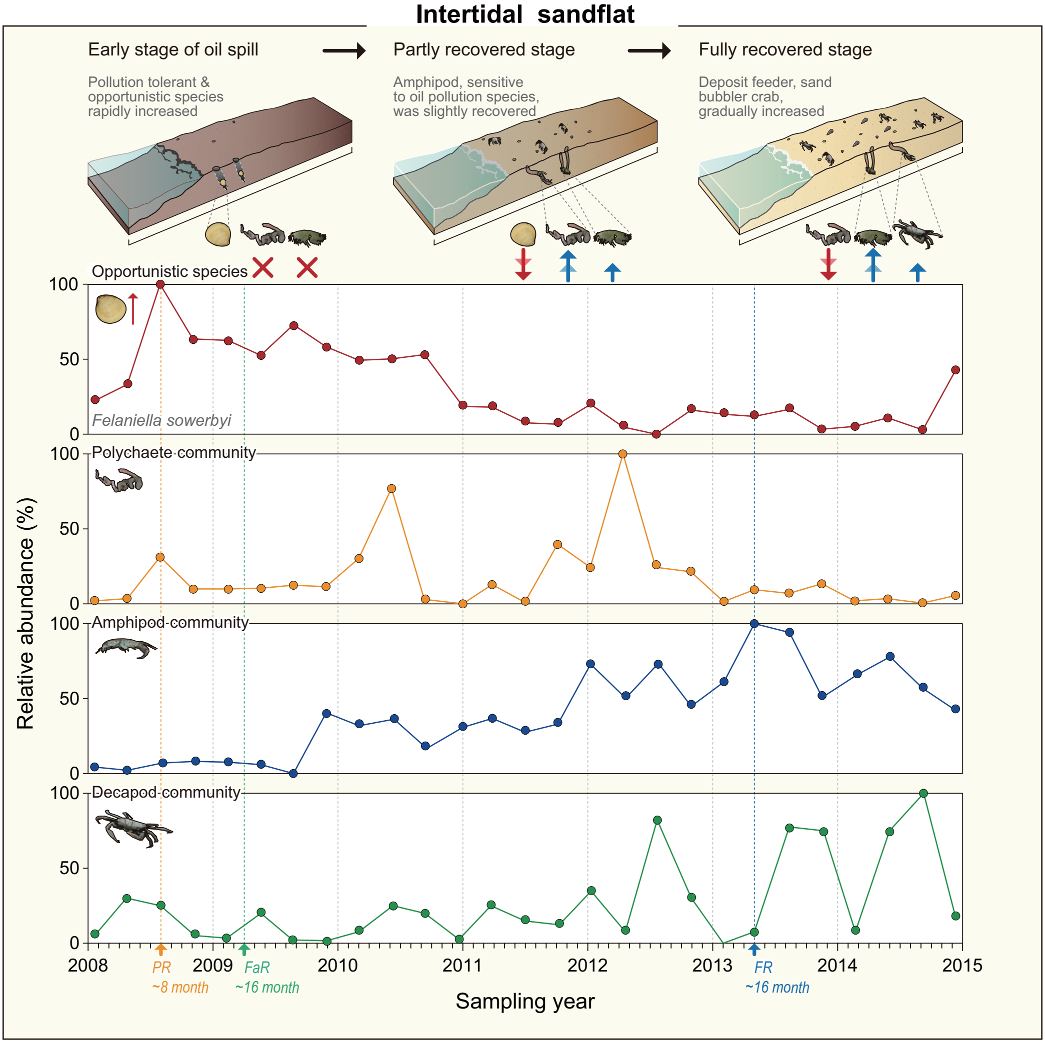


Figure 22 Schematic diagrams showing macrozoobenthic community recovery and colonization in oil spill-affected intertidal sand flats. Red/blue arrows indicate decreasing/increasing trends in relative abundance of benthic communities in the oil-contaminated environment.

Next, the impact of the oil spill on the macrozoobenthic community was assessed in the intertidal mudflat of Sogeunri (Figure 23). It was analyzed relative to the control area of Keunsoman. We found that the number of species, density, and diversity of macrozoobenthos at Sogeunri continued to increase after 2011, with signs of a strong recovery. The number of species and density differed between the two areas in 2014. Of note, the recovery at both areas showed some varied features depending on tidal conditions, such that differences in number of species or faunal density were observed only between upper to lower zones at Keunsoman. Although opportunistic species did not occur in the low tidal zone at Keunsoman, abundant *Ruditapes philippinarum* individuals were observed. Meanwhile, the nereid polychaete species, *Perinereis aibuhitensis*, was detected only at Sogeunri.

The intertidal rocky shore showed another feature in macrozoobenthos recovery. Macrobenthos on rocky shores in the mid-shore areas of polluted sites at Padori were analyzed (Figure 24). At the polluted sites, the ecological index increased gradually after 2009, with minimal fluctuations since

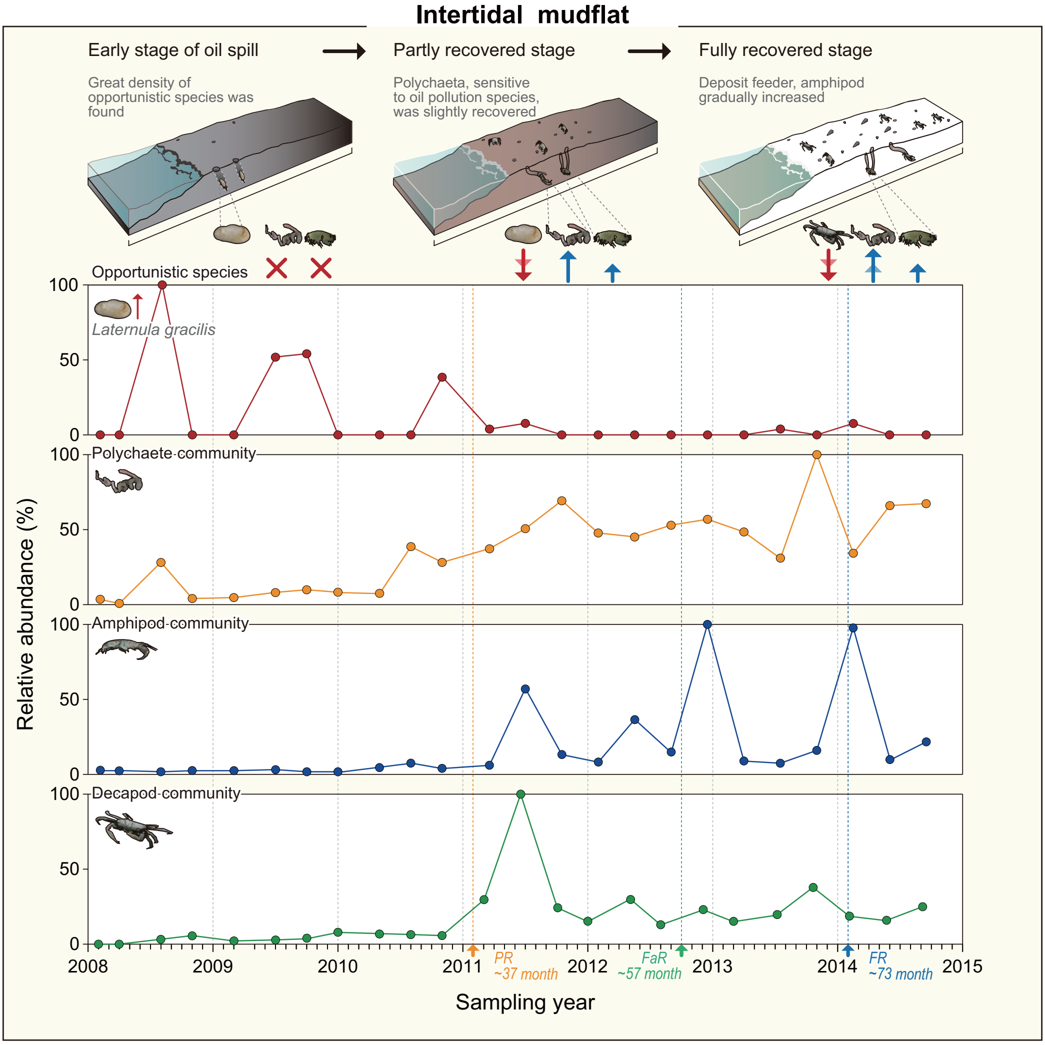


Figure 23 Schematic diagrams showing macrozoobenthic community recovery and colonization in oil spill-affected intertidal mudflat. Red/blue arrows indicate decreasing/increasing trends in relative abundance of benthic communities in the oil-contaminated environment.

2012, indicating a rapid recovery of diversity. However, the mean density remained below 50% of that at the control site, indicating partial recovery at the oil impacted rocky shore. By 2014, both diversity and density at the polluted sites were similar to (or higher than) those at the control site at Yeonpo, reflecting a full recovery. Correlational analyses of dominant species indicated that the recovery of *Crassostrea gigas*, a habitat forming bivalve, had an important influence on the overall recovery of macrozoobenthos on rocky shores. The proliferation of *Crassostrea gigas* in the oil spilled site can be regarded as one indicator of general ecosystem which is recovering in similar environments as it provides habitat for a diversity of other organisms.

Finally, the macrozoobenthos communities inhabiting soft subtidal bottoms were assessed to observe the impacts of the oil spill in the deep-water zone (Figure 25). We found that species richness decreased continuously from spring to summer of 2008, indicating adverse acute impacts of submerged oils on macrozoobenthic community health. However, the number of macrozoobenthic species and their density increased after the summer of 2009 at almost all locations. By July 2012,

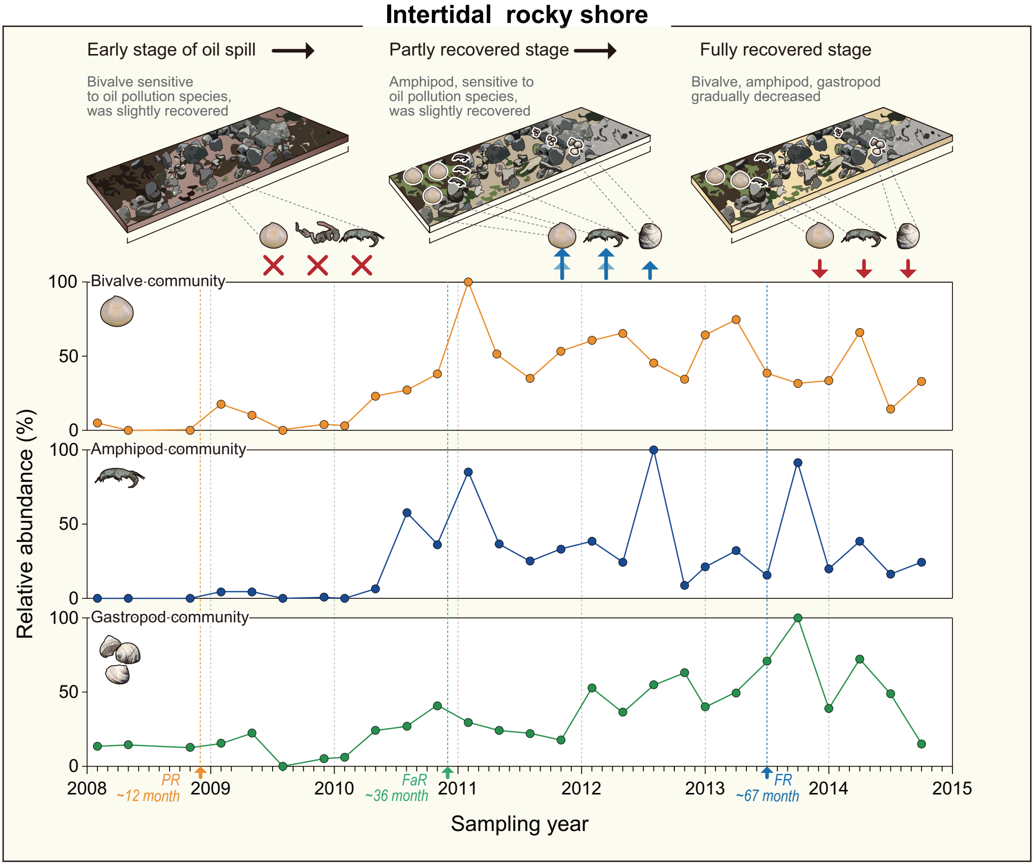


Figure 24 Schematic diagrams showing macrozoobenthic community recovery and colonization in oil spill-affected intertidal rocky shore. Red/blue arrows indicate decreasing/increasing trends in relative abundance of benthic communities in the oil-contaminated environment.

over 40 macrozoobenthic species occurred in the subtidal zone, with a density of 1769 ind.·m^{-2}, reflecting a more rapid recovery than in the intertidal mudflats. These numbers declined again after 2013, which might reflect a natural fluctuation rather than effects from residual oils.

Management of the Korean coasts and marine biodiversity

The legal framework of coastal management

The current conservation strategy for coastal areas in Korea was implemented primarily through the establishment of the Conservation and Management of Marine Ecosystem Act, Marine Environmental Management Act, and Wetlands Conservation Act. These three documents establish fundamental principles of ocean conservation policy at a national level. The shared purposes of these acts are (1) to protect marine ecosystems from artificial damage and to conserve or manage marine ecosystems in a comprehensive and systematic manner; and (2) to provide the resources necessary for marine pollution prevention, improvement, response, and recovery.

The aforementioned acts establish marine protected areas (MPAs), of which there are eight types, each of which serves a specific purpose. Currently in Korea, there are five Specially Managed Sea Areas (SMSAs), four Environmental Preservation Sea Area (EPSAs), eight Fishery

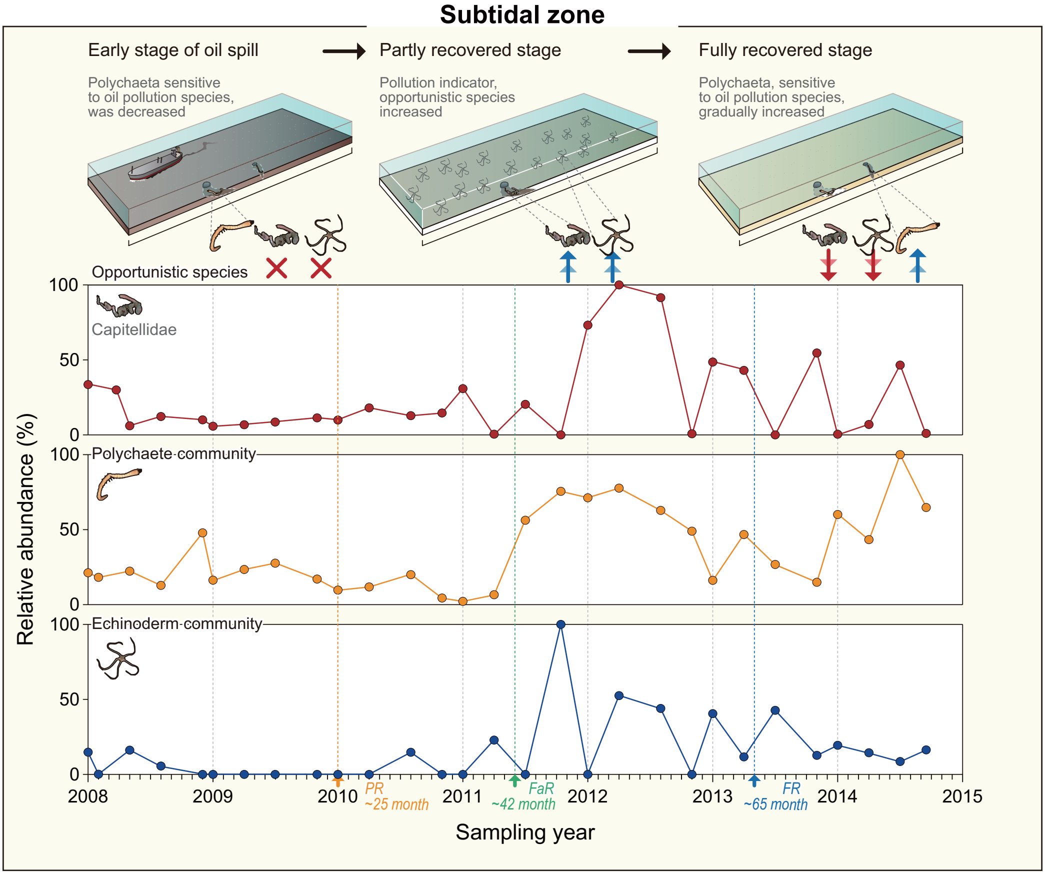
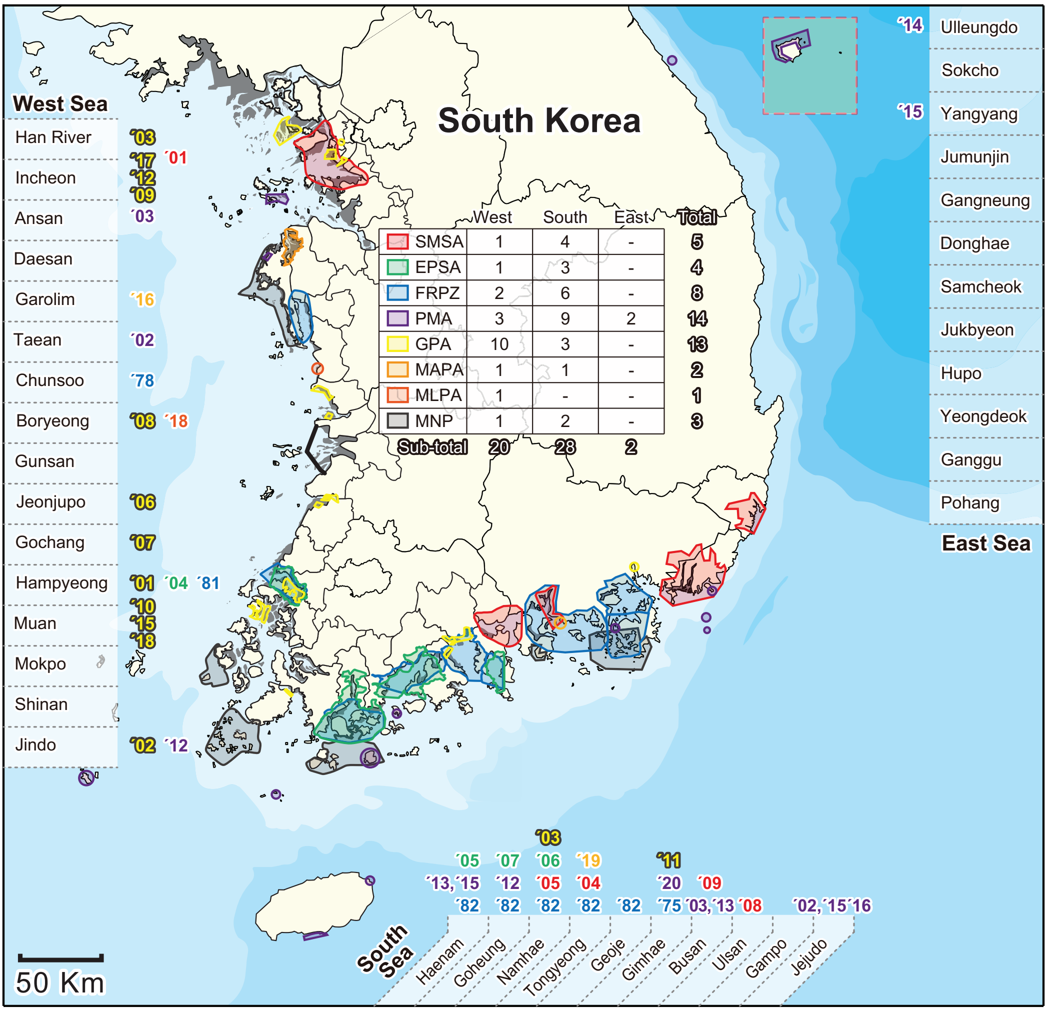


Figure 25 Schematic diagrams showing macrozoobenthic community recovery and colonization in oil spill-affected subtidal zone. Red/blue arrows indicate decreasing/increasing trends in relative abundance of benthic communities in the oil-contaminated environment.

Resources Protected Zone (FRPZs), fourteen Protected Marine Area (PMAs), thirteen Getbol (mudflat) Protected Areas (GPAs), two Marine Animal Protected Area (MAPAs), one Marine Landscape Protected Area (MLPA), and three Marine National Parks (MNPs). The locations and aerial coverage of these MPAs along the Korean coasts are shown in Figure 26.

A total of 50 MPAs (localities) have been designated along the coasts of Korea in the West Sea (20 areas), South Sea (28 areas), and East Sea (2 areas). The only two designated MPAs along the coast of the East Sea are Ulleungdo and Dokdo which were identified for protection first because they have high marine biodiversity and they provide valuable marine ecosystem services that need to be protected and managed for sustainability and second because they are in need of immediate attention due to past or ongoing ecological deterioration.

The six categories of MPAs (FRPZ, GPA, PMA, MAPA, MLPA, and MNP) address the first reason for protection mentioned above. That is, it is hoped that the marine biodiversity, ecosystems, and ecosystem services (e.g. fisheries and coastal seascape) of these areas can be sustained long term. Within the MPA strategy, GPAs have the longest history. A total of 13 tidal flat sites have been designated as GPAs since 2001: Muan (2001), Jindo (2002), Suncheon (2003), Boseong and Beolgyo (2003), Ungjin and Jangbong (2003), Buan and Julpo (2006), Gochang (2007), Seocheon (2008), Songdo (2009), Sinan (2010, 2015, 2018), Masan Bongam (2011), Siheung (2012), and Daebu (2017). These designations represent a fragmented approach to protecting and managing tidal flats in that



	West	South	East	Total
🟥 SMSA	1	4	-	5
🟩 EPSA	1	3	-	4
🟦 FRPZ	2	6	-	8
🟪 PMA	3	9	2	14
🟨 GPA	10	3	-	13
🟧 MAPA	1	1	-	2
🟥 MLPA	1	-	-	1
⬜ MNP	1	2	-	3
Sub-total	20	28	2	

Figure 26 Map showing the location and aerial coverage of eight types of protected areas on the coast of Korea. Each number represents the year when the protection area was designated.

selected localities are designated despite the tidal flats being extensively and continuously developed along the west and south coasts of Korea. This fragmentation reflects the independent management systems across local governments and perhaps weak policy management power. In terms of protection effectiveness and management philosophy, the Trilateral Cooperation on the Protection of the Wadden Sea—which involves Denmark, the Netherlands, and Germany—provides a model of integrated policy for the management of tidal flats.

Regarding the aforementioned need for immediate attention, two cases of coastal and marine pollution should be considered. First, an SMSA was designated to manage inland and adjacent coastal areas to control land-driven coastal pollution. Within this area, the land and coastal areas should be managed as one unit in an integrated manner. Five areas have been designated as SMSAs for this purpose: Sihwa (2001); Incheon (2001); Masan (2004); Gwangyang (2005); Ulsan (2008); and Busan (2009). These areas have long experienced severe land-driven pollution due to elevated industrial and urban activities in recent decades that have resulted in severe coastal and marine pollution (Khim & Hong 2014). EPSAs are designated in sea areas with direct susceptibility to marine pollution from lands to protect and manage coastal and marine resources, such as fisheries. The four bay regions have been designated as SMSAs: Wando and Doam Bay (2005), Gamak Bay (2006), Dukryang Bay (2007), and Hampyeong Bay (2009).

Management of marine biodiversity in Korea

Apart from spatial management, the Korean government seeks to protect ecologically important marine and wildlife species in marine ecosystems. These activities are conducted by the Ministry of Oceans and Fisheries (MOF), the Ministry of Environment (MOE), and the Cultural Heritage Administration (CHA) (Table 7). These agencies are charged with the protection or management of five categories of marine organisms: (1) marine organisms under protection; (2) harmful marine organisms; (3) organisms disturbing marine ecosystems; (4) endangered wild marine fauna species; and (5) cultural heritage species.

The term “marine organisms under protection” was established by the MOF in 2006 on the basis of the Conservation and Management of Marine Ecosystems Act (Article 2, Subparagraph 11). The MOF interprets this term as being inclusive of organisms in the following categories: (1) endemic species inhabiting Korean waters; (2) species with a marked decrease in their population size or density; (3) species with high academic or economic value; and (4) species with high international protection value. The MOF designated 46 protected species in 2007, and the number of protected species is presently 80. They include 16 mammals, 7 algae/sea grasses, 4 reptiles, 5 fishes, 14 birds, and 34 marine invertebrates (21 cnidarians, 3 molluscans, 1 polychaete annelid, 7 crustacean arthropods, and 2 echinoderms) (invertebrates presented in Table 7). Interestingly, one brackish water molluscan species, *Clithon retropictum*, is included in the species list of marine organisms under protection.

Korea’s national action plans related to harmful marine organisms were established by the MOF in 2016 on the basis of the Conservation and Management of Marine Ecosystems Act (Article 2, Subparagraph 13). The MOF considers harmful marine organisms to be any organisms that are harmful to life in nature or the property of human beings. Thus far, the government has designated 17 marine species as harmful marine organisms, including the following five macrozoobenthos: two echinoderms, *Asterina pectinifera* and *Asterias amurensis*, and three bryozoans, *Membranipora tuberculata*, *Tricellaria occidentalis*, and *Watersipora subovoidea* (Table 7).

The term “organisms disturbing marine ecosystems” was defined by the MOF in 2020 on the basis of the Conservation and Management of Marine Ecosystems Act (Article 2, Subparagraph 12). According to the ordinance, any marine organism can be designated as such when it meets either of the following criteria: (1) having been introduced from abroad intentionally or naturally, and causing (or being likely to cause) a disturbance to the balance of marine ecosystems; (2) causing (or being likely to cause) a disturbance to the balance of marine ecosystems due to being a genetically modified organism without natural control organisms. The government assigned a tunicate species, *Ciona intestinalis*, to this category based on its rapid population growth (Table 7). The animal was introduced from the Mediterranean and then became widely distributed throughout the coasts of Korea, including Jejudo. It is a sessile suspension feeder and a biofouling organism that inhabits mainly hard substrates, such as aquaculture farm facilities, ships, and bridge abutments, thereby causing damage to farms and boating equipment.

The Wildlife Protections and Management Act, established in 2012, allows for the designation of “endangered wild fauna and flora” based on the Protections and Management Act (Article 2, Paragraph 2) of the MOE. The government divided this category into Grade I and II, which currently include 50 and 171 species, respectively. The Grade I species include 12 mammals, 14 birds, 2 amphibians/reptiles, 11 fishes, 6 insects, 4 invertebrates, and 11 plants. Among the invertebrates, there are two marine species, including one molluscan (*Charonia lampas*) and one crustacean crab (*Pseudohelice subquadrata*) (Table 7). The Grade II species include 8 mammals, 49 birds, 6 amphibians/reptiles, 16 fish, 20 insects, 28 invertebrates, 77 plants, 2 algae, and 1 fungus

Table 7 Species list of marine invertebrates under legislative management by Korean governmental organizations, including the Ministry of Oceans and Fisheries (MOF), Ministry of Environment (ME), and Cultural Heritage Administration (CHA)

Authority		MOF ('19)			ME ('18)	CHA ('05)
Target species		Marine species			Wildlife species	
Category (purpose)		MOP[a]	HMO[b]	NIS[c]	EW[d]	NM[e]
# of targets		80	17	1	267	461
# of marine invertebrate species		34	5	1	23	2
Phylum	Scientific name					
Cnidaria	*Antipathes densa*	y				
	Antipathes dubia	y				
	Antipathes lata					y
	Cirrhipathes anguina	y				
	Dendronephthya alba	y			y	
	Dendronephthya castanea	y			y	
	Dendronephthya mollis	y			y	
	Dendronephthya putteri	y			y	
	Dendronephthya suensoni	y			y	
	Dendrophyllia cribrosa	y			y	
	Dendrophyllia ijimai	y			y	
	Dichopsammia granulosa	y				
	Echinogorgia complexa	y			y	
	Echinogorgia reticulata	y			y	
	Ellisella ceratophyta	y				
	Euplexaura crassa	y			y	
	Myriopathes japonica	y			y	y
	Myriopathes lata	y				
	Plumarella adhaerans	y			y	
	Plumarella spinosa	y			y	
	Synandwakia multitentaculata	y				
	Tubastraea coccinea	y			y	
	Verrucella stellata				y	
Arthropoda	*Chasmagnathus convexus*	y			y	
	Ocypode stimpsoni	y				
	Parasesarma bidens	y				
	Pseudohelice subquadrata	y			y[*]	
	Scopimera bitympana	y				
	Sesarmops intermedius	y			y	
	Uca lacteal	y			y	
Echinodermata	*Asterias amurensis*		y			
	Asterina pectinifera		y			
	Nacospatangus alta	y			y	
	Ophiacantha linea	y			y	
Bryozoa	*Membranipora tuberculata*		y			

(*Continued*)

Table 7 (*Continued*) Species list of marine invertebrates under legislative management by Korean governmental organizations, including the Ministry of Ocean and Fisheries (MOF), Ministry of Environment (ME), and Cultural Heritage Administration (CHA)

Authority		MOF ('19)			ME ('18)	CHA ('05)
Target species		Marine species			Wildlife species	
Category (purpose)		MOP[a]	HMO[b]	NIS[c]	EW[d]	NM[e]
# of targets		80	17	1	267	461
# of marine invertebrate species		34	5	1	23	2
	Tricellaria occidentalis		y			
	Watersipora subovoidea		y			
Mollusca	*Charonia lampas*	y			y*	
	Clithon retropictum	y			y	
	Ellobium chinense	y				
Annelida	*Paraleonnates uschakovi*	y				
Chordata	*Ciona intestinalis*			y		

[a] Marine organisms under protection

[b] Harmful marine organisms

[c] Non-indigenous invasive species

[d] Endangered wildlife species (Grade I* and II)

[e] Natural monument including animals, plants, minerals, caves, geological features, biological products and special natural phenomena, carrying great historic, cultural, scientific, aesthetic or academic values, through which the history of a nation or the secrets to the creation of the earth can be identified or revealed

(a mushroom). There are 21 Grade II marine invertebrates, including 1 molluscan, 15 cnidarians, 3 crustacean arthropods, and 2 echinoderms (Table 7).

Finally, the Cultural Heritage Protection Act, established in 1962 by the CHA, has thus far designated 70 organisms, as natural monuments for preservation and management; 12 mammals, 47 birds, 1 reptile, 4 fishes, and 2 marine invertebrates, 3 insects, and 1 plant. Two marine invertebrates are anthozoans, both designated in 2005: *Myriopathes japonica* (No. 160) and *Antipathes lata* (No. 457).

Conclusions

The present review confirms the high marine biodiversity of marine macrozoobenthos in Korea and provides an updated ecological checklist for macrozoobenthos in Korean coastal waters. Although overall species diversity remains high, site-specific distributions were highly variable across the regional seas (West Sea, South Sea, and East Sea) and across subregions along each coast. Both widely present species and site-dependent species were observed, reflecting the heterogeneous oceanographic setting along the coasts of Korea.

By region, the South Sea had the most diverse taxa, indicating its favourable coastal environments for marine organisms. This diversity might be explained by the convergence of West Sea and East Sea waters in the south. By habitat, subtidal areas were found to have the highest diversity of macrozoobenthos, which was principally attributable to large numbers of molluscs in the submerged zone. There was notable species co-occurrence across intertidal and subtidal habitats, indicating that there are extensive habitats under the dynamic macrotidal environment in the Korean coastal waters, particularly in the West Sea. By taxa, molluscs, polychaete annelids, and arthropods were predominant, followed by cnidarians. Their regional distributions varied across the three seas and three habitats greatly varied, reflecting their favoured habitats. It should be noted that regional diversity biases and unbalanced regional distributions of macrozoobenthos reflect sampling limitations, which should be addressed in future research efforts and activities.

Long-term benthic ecological studies in the Korean waters have been limited by a lack of trained professionals and the relatively short history of marine ecological science in Korea. Some long-term studies were conducted in response to the development of environmental issues, such as those described above at Lake Sihwa, Saemangeum, and Taean. Long-term studies of the benthos have also been conducted at Gwangyang Bay and Masan Bay, known pollution hotspots in Korea. The long-term macrobenthic community data that are available provide clear documentation of ecosystem deterioration in response to environmental changes and events, such as reclamations and oil spills. In each case, we observed diversity loss accompanied by a rise in the abundance of opportunistic species and/or organic enrichment indicator species. These effects were related to overall deterioration of water/sediment quality.

In conclusion, the macrozoobenthos in the Korean coastal waters support, contribute to, and play an important role in maintaining nearby communities. Benthic food webs and material flows are important ways in which macrozoobenthos contribute to the overall ecosystem functions. The benefits of local ecosystem health on human populations should be further examined. Continuing efforts in diverse scientific fields, including taxonomy, marine ecology, fisheries biology, pollution biology, environmental science, mathematical modeling, bioinformatics, and oceanography, are needed to elucidate, maintain, and protect the diversity and ecosystem services of the macrozoobenthos in coastal and marine environments. A holistic, integrated approach from multiple related fields, with balanced efforts and international perspectives, would support the development of sound marine science and biologically informed marine policies in Korea and elsewhere.

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WIDESPREAD *ZOANTHUS* AND *PALYTHOA* DOMINANCE, BARRENS, AND PHASE SHIFTS IN SHALLOW WATER SUBTROPICAL AND TROPICAL MARINE ECOSYSTEMS

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Abstract *Zoanthus* and *Palythoa* are benthic colonial zooxanthellate cnidarians common in shallow hard substrate marine ecosystems in subtropical and tropical regions, where they are an important component of coral and temperate reefs. However, recent studies have discovered areas where zoantharians dominate the benthos, potentially indicating a degraded or shifted reef state. In this review, we collated the available information on areas of high *Zoanthus* and *Palythoa* coverage. We found 34 reports from 19 locations and categorized them into three states: (1) "dominance"—dominant *Zoanthus* and *Palythoa* with no information on past states; (2) "barrens"—zoantharians have replaced another community, with no information on this state's persistence over time; and (3) "phase shifts"—zoantharians have replaced another state and have been present for five years or longer. The reports encompass all subtropical/tropical oceans of the world. We confirmed only one zoantharian phase shift and noted eight cases each of barrens and zoantharian dominance. Records spanned from the late 19th century to the current day, and 12 of 19 instances were associated with anthropogenic impacts, primarily decreasing water quality. A temporal shift in zoantharian communities was also apparent, with historical records before the 1990s largely reporting intertidal zoantharian dominance while records that are more recent note subtidal zoantharian barrens. With shallow hard substrate ecosystems undergoing increasing degradation, knowledge regarding different possible states of these ecosystems, including *Zoanthus* and *Palythoa* outbreaks, is needed in order to recognize and report such events and track them over time and space.

Keywords: Zoantharia; Zoanthid; Climate Change; Coral Reef; Anthozoa

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Introduction

In ecology, phase shifts are defined as an ecosystem's persistent and abrupt transition from one state to another due to some kind of disturbance (Done 1992, Dudgeon et al. 2010) (Table 1). In marine ecosystems, phase shifts have been reported across a wide range of habitats such as kelp beds (Ling et al. 2009, Filbee-Dexter & Scheibling 2014), rocky shores (Petraitis et al. 2009), and coral reefs (Davis 2018). These events have been reported to originate from both natural (e.g. hurricanes; Done et al. 2007) and anthropogenic causes (e.g. overfishing; Ling et al. 2009), ocean acidification (Kroeker et al. 2013), climate change (Wernberg et al. 2016), urbanization (Heery et al. 2018), and decreased water quality (Birkeland 1988, De'ath & Fabricius 2010). In particular, phase shifts in shallow subtropical and tropical reefs have gained much research attention, due to their high biodiversity, productivity, importance, as well as their susceptibility (Done 1992, Roberts et al. 2002, Norström et al. 2009, Wernberg et al. 2013, Abelson et al. 2016, Pecl et al. 2017). In the face of growing threats at local and global scales, there is a risk of phase shifts in subtropical and tropical reefs increasing in frequency and extent.

Phase shifts in shallow subtropical and tropical hard substrate (SHS) ecosystems

In seaweed beds, sea urchin barrens and phase shifts decimate macroalgae, often leaving only crustose coralline algae or bare rock, a term originating from Japan called "isoyake" (Fujita 2010). As the ecological balance and levels of various stressors on macroalgae-dominated ecosystems change in response to anthropogenic climate change, changes in communities are expected (Harley et al. 2012). On shallow subtropical and tropical coral reefs, many studies on phase shifts have focused on changes from zooxanthellate scleractinian coral dominance to macroalgal dominance, often triggered by various anthropogenic stressors causing coral decline and loss (Hatcher 1984, McManus & Polsenberg 2004, Norström et al. 2009). For example, on the Great Barrier Reef in Australia, hard coral losses between 1985 and 2012 were attributed primarily to increasing strengths of cyclones, to crown-of-thorns starfish *Acanthaster* outbreaks, and to coral bleaching (De'ath et al. 2012), all of which have been related to anthropogenic causes.

Table 1 Key terms in this work, their definitions, and relevant references

Key term	Definition as used in this work	Relevant reference(s)
Dominance	A benthic coverage higher than 25%, but without information about a different previous condition.	Bruno et al. (2009)
Barrens	An area of dominance by one taxon where there is evidence of change, but there is not enough time (>5 years) or data to confirm persistence.	Norström et al. (2009)
Phase shift	An abrupt change in community dominance persistence in time.	Done (1992); Dudgeon et al. (2010)
Zoantharian dominance	An area of zoantharian dominance.	Yang et al. (2013); this study
Zoantharian barrens	An area of zoantharian dominance replacing a previous condition.	Yang et al. (2013); this study
Zoantharian phase shift	A phase shift to zoantharian dominance.	Cruz et al. (2015a); this study
Outbreak	A rapid and noticeable increase in the population of a species or group of organisms.	Timmers et al. (2012)
Persistence	The maintenance of a dominant condition for at least a generation. However, in some cases it may take many years or decades to identify. Here, we use Norström et al.'s (2009) definition of 5 years of dominance.	Connell & Sousa (1983); Norström et al. (2009)

Table 2 Numbers of reports in the Web of Science of different types of phase shifts reported from shallow water subtropical and tropical hard substrate ecosystems

Search terms	Location(s) reported from	Example reference(s)	# of Web of Science papers*
Coral reef+phase shift	Worldwide	Hughes (1994), Norstrom et al. (2009)	1089
Macroalgae+phase shift	Worldwide	Bruno et al. (2009), Cheal et al. (2010)	442
Cyanobacteria+phase shift	Worldwide	Paul et al. (2005), Kuffner et al. (2006)	143
Porifera+phase shift	Worldwide	Rützler & Muzik (1993)	135
Anemone+phase shift	Taiwan	Tkachenko et al. (2007)	19
Corallimor[a]+phase shift	Palmyra Atoll	Work et al. (2008)	7
Zoanthid+phase shift	Worldwide (see Fig. 1)	see Table 3	8

Note: For details on Zoantharia phase shifts, see Table 3.

[a] As of May 30, 2020.

However, coral reef and other subtropical and tropical shallow water ecosystem phase shifts are not limited to scleractinian coral-algal changes (Norström et al. 2009), and there have been reports of outbreaks of many other benthic organisms including cyanobacterial sponges (e.g. *Terpios hoshinota*, Rützler & Muzik 1993, Fujii et al. 2011), corallimorpharians (Loya 2004, Work et al. 2008, Crane et al. 2016), and sea anemones (Chen & Dai 2004, Tkachenko et al. 2007) (Table 2). Despite the fact that individual causes of many of these phase shifts remain unclear, these phenomena are of concern as the impacts of global climate change in synergy with local impacts become more prevalent (Hughes et al. 2010, Gilmour et al. 2013).

Zoantharians are hexacorals most closely related to sea anemones (=order Zoantharia, also known as Zoanthidea). Zooxanthellate zoantharian species on SHS primarily belong to the genera *Zoanthus* (family Zoanthidae) and *Palythoa* (family Sphenopidae). Well known as common components of coral reefs and rocky shores, some species have the ability to increase their coverage rapidly at sites (Wee et al. 2017), have long-lived planktonic larvae (Ryland et al. 2000, Polak et al. 2011), and can raft on anthropogenic debris (Santos & Reimer 2018), indicating potential for dispersal and quick growth in new locations. There have been reports from various regions of the world (Figures 1 and 2, Table 3, references therein) that indicate some SHS may phase shift from zooxanthellate scleractinian coral or macroalgal dominance to *Zoanthus* or *Palythoa* dominance (="zoantharian barrens"; e.g. Cruz et al. 2015a,b; Tables 1–3). However, no worldwide overview of the state of knowledge of Zoantharia dominance, barrens, and phase shifts exists, and an understanding of the possibility and frequency of such events is lacking. With SHS ecosystems facing increasing degradation from anthropogenic stressors, knowledge on different possible states of these ecosystems is needed in order to recognize and report such events, and subsequently track them over time and space (Knowlton 1992).

Aims of this review

In this study, we collate the available scientific information on zooxanthellate zoantharian dominance, barrens, and phase shifts via a literature search and review, and supplement data with additional new information in order to provide marine researchers with an overview on this understudied phenomenon. We also discuss where zoantharian phase shifts may be observable in the near future as climate changes advances and identify areas where further research is needed. Finally, we provide guidelines for future observations. Thus, the aims of this review are to provide field workers and marine ecosystem managers with data on zoantharian dominance and outbreaks; to provide a baseline review to support future research; and to provide predictions on possible future zoantharian outbreaks.

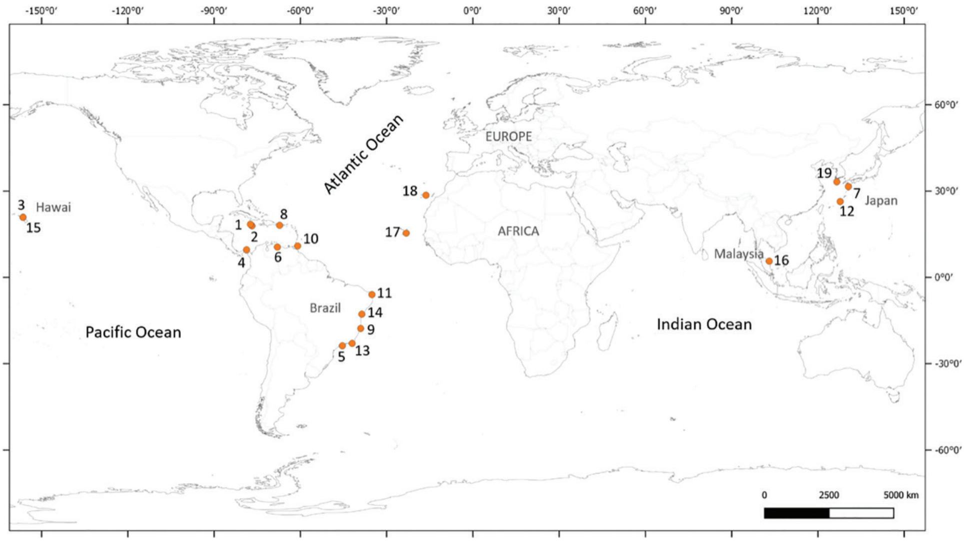

Figure 1 Global occurrences of zoantharian barrens analyzed in this study (Table 3 for details; numbers of locations correspond to those in Table 3).

Background

Focus taxa

Genera Zoanthus and Palythoa

The zoantharian genera *Zoanthus* and *Palythoa* are commonly observed on SHS throughout the world and are important benthic components of shallow water ecosystems. Both genera are within the suborder Brachycnemina, and the large majority of species are zooxanthellate, hosting endophotosymbiotic Symbiodiniaceae (Trench 1974). Species of the genus *Palythoa*, like most zoantharians, incorporate large amounts of sand and debris into their body wall (Haywick & Mueller 1997). Many species of the genus are known to contain potent palytoxin (PTX) (Moore & Scheuer 1971). Conversely, *Zoanthus* spp. do not incorporate sand and often contain high levels of fluorescent proteins (Remington et al. 2005). Like most other zoantharian genera, *Zoanthus* and *Palythoa* form colonies, with numerous clonal polyps connected with common coenenchyme tissue. Despite their frequent presence in SHS ecosystems, research on both genera is generally lacking, in part due to difficulties in accurate species identification (Burnett et al. 1997). Both genera contain numerous species, but the true number of these is a matter of debate (Burnett et al. 1995, 1997, Reimer et al. 2004), and even DNA barcoding molecular methods often provide somewhat ambiguous results (Sinniger et al. 2008).

Even though there are many described species of both *Zoanthus* and *Palythoa*, some generalizations about the genera can be made. Both genera include species that can be considered generalists in the widest sense of the term, with broad geographical ranges (Hibino et al. 2014), across a variety of different environments from high energy coral reef crests to inner bays and lagoons (Irei et al. 2011), and from intertidal to mesophotic depths (Kamezaki et al. 2013, Leal et al. 2016, Rosa et al. 2016). *Zoanthus* and *Palythoa* have very fast colony growth speeds compared to scleractinian corals that are limited by calcification rates (Silva et al. 2015, Wee et al. 2017) and have plastic morphologies able to adapt to different environments (Ong et al. 2013). Zoantharians can be voracious planktivores (Reimer 1971, Fabricius & Metzner 2004) that also utilize the energy supplied by their endosymbiotic Symbiodiniaceae (Trench 1974). Both genera are thought to be relatively

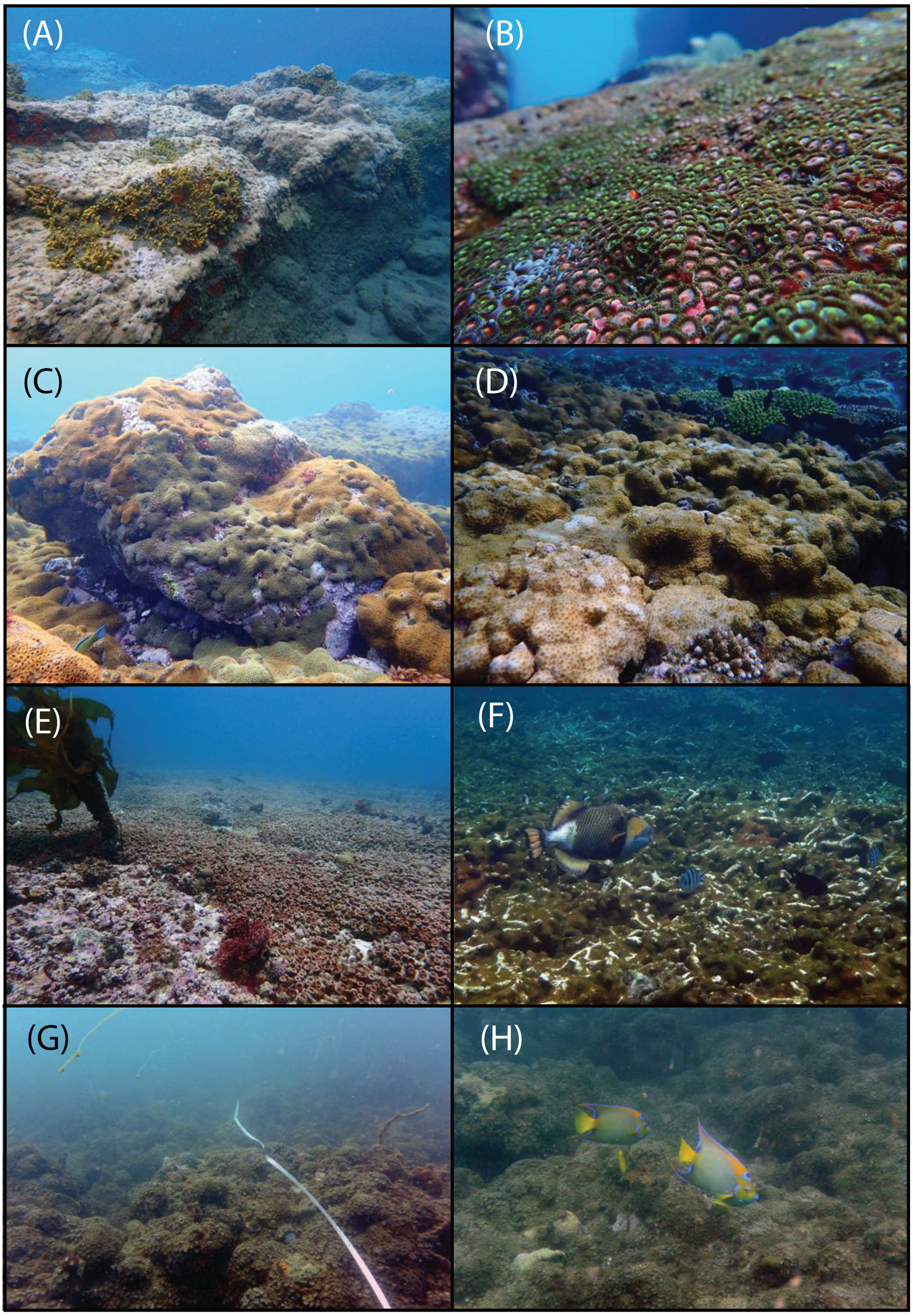

Figure 2 Images of zoantharian barrens from around the world, with location numbers corresponding to those in Figure 1. (A). *Palythoa caribaeorum* at La Gomera Island, Spain (location 18), depth 8 m, image taken November 2018. (B). *Zoanthus sansibaricus* at Koshiki-jima, Nagaki, Japan (not reported on in this work), depth 1.5 m, image taken September 2018. (C). *Palythoa caribaeorum* at La Palma Island, Spain (location 18), depth 3 m, image taken October 2018. (D). *Palythoa tuberculosa* at Okinawa, Japan (location 12), lower intertidal, image taken August 2020. (E). *Palythoa* cf. *mutuki* at Jeju Island, Korea (location 19), depth 4 m, image taken May 2018. (F). *Zoanthus* zone near Pulau Redang, Malaysia (location 16), depth <2 m, image taken July 2013. (G and H). *Palythoa* cf. *variabilis* at Todos os Santos Bay, Brazil (location 14), depth 5 m, images taken 2016.

Table 3 Overview of zoantharian dominance reports and information on location, ocean, genera/species involved, general and detailed causes, coverage details, depths, possible effects, category (dominance/barrens/phase shift), and relevant references

Location	Ocean	Genus/species	General Causes	Possible causes, notes	Maximum coverage, area	Depths	Possible effects	Category	Reference(s)
1. Kingston Harbor+Port Royal Cays, Jamaica	Atlantic	*Zoanthus* spp., *Palythoa* spp.	Natural	In shallow water, *Zoanthus* 1–2 fathoms, *Palythoa* 3 to 4 fathoms; first mention of "*Zoanthus* zone"	"in abundance"	Intertidal, 1 to 4 fathoms	Unknown	Dominance	Duerden (1898)
2. Ocho Rios+Discovery Bay, Jamaica	Atlantic	*Zoanthus sociatus*, *Zoanthus solanderi*	Natural	Intertidal "*Zoanthus* zone"	"much"; cover extensive areas	Intertidal	Unknown	Dominance	Goreau (1959), Kinzie (1973), Karlson (1980, 1981, 1983)
3. Kaneohe Bay, Oahu, USA	Pacific	*Zoanthus pacificus*, *Palythoa vestitus*	Anthropogenic	Freshwater+terrigenous input, sewage pollution, replacement of scleractinian corals	"extensive beds"	Intertidal	Unknown	Barrens	Cooke (1976), Smith et al. (1981)
4. Galeta, Panama	Pacific	*Zoanthus sociatus*, *Zoanthus solanderi, Palythoa variabilis, Palythoa caribaeorum*	Natural	Intertidal "*Zoanthus* zone"	"abundant"	Intertidal to forereef	Unknown	Dominance	Sebens (1977, 1982)
5. Sao Sebastio, Brazil	Atlantic	*Zoanthus sociatus*, *Palythoa variabilis, Palythoa caribaeorum*	Natural	Intertidal "*Zoanthus* zone"	"large expanses"	Intertidal	Unknown	Dominance	Sebens (1977)
6. Isla Raton, Venezuela	Atlantic	*Palythoa caribaeorum*, *Zoanthus sociatus*	Natural	Intertidal zone	33.91%, 19.81%, respectively	Intertidal	Unknown	Dominance	Bastidas & Bone (1996)
7. Sakurajima, Kagoshima, Japan	Pacific	*Zoanthus sansibaricus*	Natural	Unknown, possibly related to volcanic ashfall or increasing water temperatures	Up to 65%	Subtidal to 10 m	Unknown	Dominance	Ono et al. (2003), Ono et al. (2007), Ono et al. (2010)

(*Continued*)

Table 3 (*Continued*) Overview of zoantharian dominance reports and information on location, ocean, genera/species involved, general and detailed causes, coverage details, depths, possible effects, category (dominance/barrens/phase shift), and relevant references

Location	Ocean	Genus/species	General Causes	Possible causes, notes	Maximum coverage, area	Depths	Possible effects	Category	Reference(s)
8. Southwestern Puerto Rico	Atlantic	*Zoanthus sociatus*	Anthropogenic	Correlation with fecal pollution indicators	"dominance"	Unknown, but appears shallow (<5 m) from figures	Reef degradation	Barrens	Hernández-Delgado et al. (2008)
9. Abrolhos Bank, Brazil	Atlantic	*Palythoa caribaeorum*	Anthropogenic	Sedimentation and/or turbidity due to dredging in two places and nitrification in another two more close to shore (n=4 sites)	Up to 55.9%	Subtidal 1–5 m	Possible reduction in Scleractinia	Dominance	Castro et al. (2012); also Costa et al. (2002); Segal & Castro (2011)
10. Pirangi, Brazil	Atlantic	*Palythoa caribaeorum*, *Zoanthus sociatus*	Natural	Intertidal "*Zoanthus* zone"	32% and 49%	Intertidal	Unknown	Dominance	Azevedo et al. (2011)
11. Arraial do Cabo, Brazil	Atlantic	*Palythoa caribaeorum*	Anthropogenic	Collection of ornamental organisms for aquarists	Up to 30%	Subtidal 3–9 m	Reduction of hidrocorals *Millepora alcicornis*	Barrens	Rogers et al. (2014)
12. Trinidad & Tobago, West Indies	Atlantic	*Palythoa caribaeorum*, *Zoanthus sociatus*	Anthropogenic	Opportunistic manifestation of coral loss and intertidal exposure? Close to wastewater source	Up to >20%, almost 70%	Unknown, but close to shore	Reduction of biodiversity, reef health, services	Barrens	Lapointe et al. (2010), Belford & Phillip (2012)
13. Okinawa, Japan	Pacific	*Palythoa tuberculosa*	Anthropogenic	Environmental factor unknown, possibly decreased water quality?	25%, higher in patches	Intertidal	Unknown	Barrens	Yang et al. (2013)

(*Continued*)

Table 3 (*Continued*) Overview of zoantharian dominance reports and information on location, ocean, genera/species involved, general and detailed causes, coverage details, depths, possible effects, category (dominance/barrens/phase shift), and relevant references

Location	Ocean	Genus/species	General Causes	Possible causes, notes	Maximum coverage, area	Depths	Possible effects	Category	Reference(s)
14. Todos os Santos Bay, Brazil	Atlantic	*Palythoa* cf. *variabilis*	Anthropogenic	Increased competitive advantage of *Palythoa* over scleractinians? Environmental factor unknown, possibly decreased water quality?	Up to 70%	2.5–7 m	Reduction in coral cover, reef structural complexity, fish richness	Phase shift	Cruz et al. (2014, 2015a, 2015b, 2016)
15. Kahului, Maui	Pacific	"Zoanthids"	Anthropogenic	Sewage effluent	50%–90%; area of 0.31 km^2	<3 m	Low benthic diversity	Barrens	Amato et al. (2016)
16. Pulau Redang, Malaysia	Pacific	*Zoanthus*	Anthropogenic and natural	Increased cover after coral death from monsoon event. Opportunistic manifestation of coral loss; decreased water quality	Up to 72%	3–5 m	Low live coral coverage; non-diverse coral assemblages	Barrens	Wee et al. (2017); Lachs et al. (2019)
17. Maio Island, Cabo Verde Islands	Atlantic	*Zoanthus sociatus*, *Zoanthus solanderi*	Anthropogenic	Unknown, terrigenous runoff (water quality)?	Area = 4 ha; unknown %	1.5 m	Unknown	Dominance	López et al. (2018)
18. Canary Islands	Atlantic	*Palythoa* spp., *Zoanthus* spp.	Anthropogenic and natural	Rising SSTs, opening of spaces from grazing	41.6%, 91.5%, respectively	Intertidal (tide pools)	Increase in species richness	Dominance	González-Delgado et al. (2018); Lopez et al. (2020)
19. Jeju Island, South Korea	Pacific	*Palythoa* sp.	Anthropogenic	Rising SSTs, possible wastewater from aquaculture	Dominant	1–5 m	Loss of commercial species of macroalgae	Barrens	Reimer & Choi (Unpublished)

Note: Supplementary Material 2 shows simplified categories for analyses (Kruskal–Wallis, Wilcoxon pairwise, chi-squared tests).

competitive with other benthic species when in direct contact (Suchanek & Green 1981, Cruz et al. 2016). Both *Zoanthus* and *Palythoa* spp. have been reported to be quite flexible in their associations with different Symbiodiniaceae types (Burnett 2002, Reimer et al. 2006, Noda et al. 2017), have adaptable photobiology (Leal et al. 2016, Rosa et al. 2016), and are plastic mixotrophs (Rosa et al. 2016, 2018, Santos et al. 2021). In addition, while data are sparse, it appears *Zoanthus* and *Palythoa* spp. have annual broadcast spawning events in summer, with external fertilization and planktonic larvae (Yamazato et al. 1973, Cooke 1976, Ryland 1997, Ono et al. 2005, Hirose et al. 2011). These larvae can apparently drift for very long periods (up to 170 days) (Ryland et al. 2000, Polak et al. 2011), helping to explain the wide distributions of some species across ocean basins. Settlement on artificial objects has also been reported, suggesting dispersal by drifting is also possible (Santos & Reimer 2018).

Combined, these observations demonstrate the resilient and flexible nature of species in these genera. Indeed, *Palythoa caribaeorum*, a common Caribbean species, is known to bleach comparatively early during episodes of high sea surface temperatures (SSTs), yet experiences low mortality during such events (Jiménez 2001, López et al. 2020b). All of these characters demonstrate that *Zoanthus* and *Palythoa* spp. have numerous traits that may allow them to quickly take advantage of changing or disturbed environments.

Ecological roles of Zoanthus *and* Palythoa *in SHS ecosystems*

In healthy SHS ecosystems, *Zoanthus* and *Palythoa* spp. often form small colonies of up to several centimetres in areas between other benthic species, and they are but one component of a diverse ecosystem. Zooxanthellate zoantharians' ecological roles in SHS ecosystems have not been well examined (Ong et al. 2013), but based on their colonial forms, symbioses with Symbiodiniaceae, and primarily subtropical and tropical distributions, they can be assumed to have similar roles to their more well-known zooxanthellate scleractinian and octocoral anthozoan cousins. However, in areas with low benthic coverage of other organisms, zoantharians are often dominant, as they are one of the fastest growing anthozoans (Moore & Scheuer 1971). In such areas, colonies can reach tens of metres in size on occasion (e.g. Figure 2). Both *Zoanthus* and *Palythoa* spp. use energy from their Symbiodiniaceae and also consume plankton (Trench 1974, Fabricius & Metzner 2004), and are in turn food sources for other animals (Stampar et al. 2007, Francini-Filho & de Moura 2010), but few studies have examined their trophic designations and functions in detail (but see Santos et al. 2021).

Literature review

To make a general comparison of the relative amount of research that has been conducted on phase shifts among major taxonomic groups, we searched the Web of Science's core collection on May 30, 2020, using each common names or derivatives for each taxon (i.e. "anemone", "macroalgae", "corallimor*", "sponge", "cyanobacteria", "zoanthid", or "coral reef") paired with "phase shift" (Supplementary Material 1). We then focused our search on papers discussing comparatively high abundances of zoantharians (benthic coverages of >25%, = a dominant group *c.f.* Bruno et al. 2009) on shallow water coral reefs and coral communities, widening our search to include historical literature published before 1994, when the Web of Science core collection begins, as well as including other non-Web of Science sources. Although robust data were scarce in the historical literature, these studies were included in our review in order to gain a better perspective on the natural conditions of coral reefs before anthropogenic stressor impacts became more evident. Thus, historical papers were added to our dataset based on the Google Scholar searches (terms as given for Web of Science search in Supplementary Table 1; full list of papers in Table 3) and the combined authors' knowledge of historical literature. For each paper, we examined (1) location, (2) depth(s), (3) what species/genera were reported as common, (4) if there was a different previous dominant condition reported and if so what, (5) information on possible causes and if these were natural or anthropogenic, (6) maximum coverage area or coverage percentage (when available), and (7) reported effects of high zoantharian coverage. We considered reports as phase shifts when there was evidence of (i) the replacement of dominant groups with an increase of zoantharian coverage and a corresponding decrease in the previously dominant group (Done 1992); and (ii) permanence of Zoantharia dominance for a period of at least five years (Norstrom et al. 2009).

We then classified these records into one of three conditions: (1) **dominance**, when there was not enough information about a previous condition to allow confirmation if there was a change in dominance; (2) **barrens**, when there was evidence of benthic change, but there had not been enough time to confirm persistence, namely, the maintenance of dominance for five years or more (c.f. Norström et al. 2009); and (3) **phase shift**, when there was evidence of a community change and at least five years of zoantharian dominance. Thus, we have included in this review papers focused not only on phase shifts, but also on zoantharian barrens and dominance. While we cannot be sure whether cases of barrens or dominance are truly phase shifts or not, due to the sparse amount of data available, focusing only on proven zoantharian phase shifts would reduce the scope and context of this review.

Patterns of zoantharian dominance, barrens, and phase shifts over time

A list of Zoantharia papers examined and their relevant information, comprising 34 reports from 19 locations, is provided in Table 3. We added one unpublished report of a zoantharian barren from Jeju Island, South Korea, into the dataset. To examine the development and patterns of high zoantharian coverage reported in the literature throughout the years, we compared natural and anthropogenic causes pointing to increases in zoantharian coverage by using documented details in each report (=independent variables) including ocean (Pacific/Atlantic Ocean), genera of dominant zoantharian(s) (*Zoanthus*, *Palythoa*), general and detailed causes of increases in coverage, coverage (as %), depth, possible effect(s) of high zoantharian coverage, and categories of high zoantharian coverage (=Dominance, Barrens, Phase Shift, see Table 1) (Table 3, Supplementary Material 2), with the most recent year of reported high zoantharian coverage as the dependent variable. To achieve this, Kruskal–Wallis tests among the years with other the reported details were conducted using R V4.0.0 and RStudio graphical interface V1.3.959 (R Core Team 2020, RStudio Team 2020). Post hoc tests (Wilcoxon pairwise test with Holm's correction) were conducted for documented details that showed significant differences between years, to identify any pairwise differences within each group. Chi-squared (X^2) tests were conducted to test the dependencies between the reported details of the high zoantharian coverage. Post hoc tests on significant dependencies were conducted by comparing standardized residual (stdres) of the relationship with distribution of the adjusted alpha value (qnorm [Bonferroni's correction]).

Modeling areas vulnerable to zoantharian outbreaks

Although the data available for accurately projecting distribution models are scarce (van Proosdij et al. 2016), we wanted to examine potential vulnerable zones where new zoantharian outbreaks might occur. In order to do so, maximum sea surface temperature (SST^{max}) and maximum nitrate variables were selected for projecting areas where zoantharians might proliferate, as according to previous literature, outbreaks of zoantharians are related to temperature increases (e.g. González-Delgado et al. 2018, López et al. 2020b) and eutrophic waters (e.g. Cooke 1976, Smith et al. 1981, Hernández-Delgado et al. 2008) (see also Table 3).

Environmental raster layers were downloaded from Bio-ORACLE at 0.008° resolution (=1 km^2) (Tyberghein et al. 2012, Assis et al. 2018) and restricted to a depth of 50 m to avoid oceanic areas. Layers were also cropped to areas where SST is higher than 18°C as this is the lowest temperature tolerated by *Zoanthus* and *Palythoa* larvae (Ryland et al. 2000). The relationships between these environmental variables and the occurrence of zoantharian barrens were analyzed by using maximum entropy modelling (MaxEnt) through the R package ENMtools (Warren et al. 2019). The MaxEnt model predicted likely areas suitable for zoantharian barrens based on the environmental characteristics of the sites where they were found. The model's prediction reliability is subject to the environmental space (i.e. the ranges of the various predictor variables) represented in building the model or, in other words, whether the observations represent the full environmental range or space one wishes to predict into. Most species distribution models are based on the absence–presence data, but given the lack of systematic records, the zoantharian barrens reported here lack absence; i.e., locations where they are absent have not been confirmed. Thus, given these limited observations we have for zoantharian barrens, it is likely that we do not cover the full range of environmental space in which barrens may occur now and in the future. However, having our observations reasonably well spread out across the world we believe that our MaxEnt model should perform adequately. MaxEnt models solve the absence-only problem by considering the probability of maximum entropy (Phillips et al. 2006, Elith et al. 2011). Models were performed by bootstrapping, using 70% of the points as randomly selected for training and 30% for validating.

Inferences from literature and our analyses

Global and temporal spread of zoantharian barrens

From our literature search, we selected 34 scientific papers focused on *Zoanthus* and *Palythoa*, and supplemented these with previously unreported data from one location (Table 3). These reports start in the late 19th century and continue to the present day. Overall, these data represent 19 locations with high levels of zooxanthellate zoantharian coverage on coral reefs, rocky shores, and macroalgal beds, spanning both the Atlantic and Indo-Pacific Oceans (Figure 1). Of these 19 locations, 10 were classified as dominance, where we cannot confirm the previous state or dominant taxa, eight as barrens, where we confirmed a change from another benthic community, and one confirmed phase shift in Todos os Santos Bay, Brazil, with a change that has persisted for more than five years from the previous scleractinian-dominated community (Cruz et al. 2014). We suspect several more of the barrens are in fact phase shifts (e.g. Oahu, Maui, Jeju, Okinawa), but data are lacking to confirm this.

Differences between historical and recent zoantharian barrens

The records of high zoantharian abundance areas have shifted from intertidal to subtidal outbreaks. From the literature search and statistical analyses, we noted significant differences between year of the report with the cause(s) (Kruskal–Wallis: $X^2 = 9.914$, $df = 2$, $p = 0.007$) and depth (Kruskal–Wallis: $X^2 = 5.954$, $df = 1$, $p = 0.015$) of increased zoantharian abundances (and zoantharian zones). Specifically, earlier reports between 1898 and 2010 ($n = 7$) reported zoantharian dominance mostly in intertidal zones that were caused by natural disturbances (Wilcoxon pairwise [Holm's correction]: $p = 0.033$). Only in later research (2005–2017, $n = 10$) did studies start to identify anthropogenic stressors as a potential cause of zoantharian outbreaks, which were predominantly recorded at subtidal depths. There were two records, in 2016 and 2017, that noted both natural and anthropogenic causes of high zoantharian abundance.

In the literature, natural causes of zoantharian dominance were linked to observed "*Zoanthus* zones", while zoantharian barrens and phase shifts were attributed to anthropogenic pollution. There was a significant dependency between the general causes (natural or anthropogenic) and detailed causes of high zoantharian coverage (X^2: $X^2 = 16.602$, $df = 6$, $p = 0.011$). This was due to naturally occurring high zoantharian coverage being significantly tied to the "*Zoanthus* zone", while pollution (=decreased water quality) was identified as the main detailed anthropogenic cause of increased zoantharian coverage. Furthermore, zoantharian dominance was assumed to be due to natural causes, while anthropogenic disturbances were noted to create zoantharian barrens and phase shifts (X^2: $X^2 = 10.735$, $df = 4$, $p = 0.030$). The possible effects of zoantharian barrens were described in more detail when anthropogenic causes were involved while, on the other hand, the effects of naturally occurring zoantharian dominance in ecosystems were generally not described (X^2: $X^2 = 14.667$, $df = 6$, $p = 0.023$).

The depth at which zoantharian coverage was documented was related to the causes given in the same report (X^2: $X^2 = 8.75$, $df = 3$, $p = 0.033$). Furthermore, there was a significant dependency between possible effects of increased zoantharian coverage with depth (X^2: $X^2 = 12.582$, $df = 3$, $p = 0.006$); increases at subtidal sites were noted to cause reductions in biodiversity, while intertidal events were generally not described well.

We could confirm only a single clear case of a zoantharian phase shift—at Todos os Santo Bay, Brazil—from our literature dataset and analyses (Cruz et al. 2015a, 2015b, 2016). This low number of confirmed zoantharian phase shifts is also reflected by the absence of time series data. In the few studies where information over time is present, the periods are commonly too short (e.g. <5 years following Bruno et al. (2009)) to allow the confirmation of persistence of new zoantharian barrens. Thus, the absence of monitoring data is a limiting factor to better understand this problem and, by extension, its cause(s). Information from the volcanic coastline of Sakurajima, Kagoshima, southern Japan, suggests that *Zoanthus* spp. barrens can persist for periods of up to 40 years (Ono et al. 2002, 2007, 2010) and are still present as of 2019 (JD Reimer, observations from September 2019). However, little information exists on what was at this site before zoantharians (before 1980; Ono et al. 2002). Monitoring data from 2003 until 2011 in Todos os Santo Bay, Brazil (Cruz et al. 2015a,b, 2016) show zoantharian persistence for several years. *Zoanthus* spp. barrens at some sites around Okinawa have subsequently disappeared due to the disease outbreaks after a few years of existence (JD Reimer, unpublished data). However, these sites represent only a few locations, and in the future, closely monitoring such locations at regular intervals should help confirm the persistence of zoantharian phase shifts and barrens.

Possible causes of zoantharian barrens: natural and anthropogenic

Determining the cause of ecological events in marine systems is challenging (Chen & Dai 2004, Norström et al. 2009, Dubois et al. 2019, Todd et al. 2019), and clearly, the issue of zoantharian barrens and phase shifts is no exception. The question of whether zoantharian barrens are a natural occurrence or a response to anthropogenic stressors is difficult to definitively answer from the information currently available.

Of the original studies at 19 locations with high levels of zoantharian dominance, nine of them were considered to be natural in occurrence, while 12 were at least partially due to anthropogenically linked impacts (note the total equals 21 as two locations were due to both natural and anthropogenic factors; Table 3). Evidence that zoantharian barrens may be natural comes from the reports from the 1890s and 1950s in Jamaica, well before most anthropogenically linked coral reef degradation problems were reported (but see Dajka et al. 2020). Specifically, in the case of Goreau (1959), a large "*Zoanthus* zone" was reported along the generally pristine coral reef coast of northern Jamaica (also Goreau & Goreau 1973). From such reports, we believe that zoantharian barrens can generate naturally under suitable conditions, such as intermediate disturbance levels caused by storms or predation (Karlson 1980, 1983), which likely favour *Zoanthus* and *Palythoa* species over scleractinian corals and many other benthos.

Anthropogenic causes of zoantharian outbreaks are more difficult to discern clearly. While three papers and unpublished data from Jeju Island, Korea, offered strong evidence of zoantharian outbreaks due to close proximity to a clear disturbance (e.g. Cooke 1976, Smith et al. 1981, Amato et al. 2016), other studies offered only preliminary suggestions (e.g. Yang et al. 2013, Cruz et al. 2014, López et al. 2018), while some made only vague or no mention of causes (e.g. Ono et al. 2003, 2007) (Table 3). It is notable that for most purported anthropogenically generated zoantharian communities, reduced water quality was often mentioned (10/12 cases, Table 3). A zoantharian outbreak could be triggered by a direct effect such as increase of nutrients and consequently their autotrophic or heterotrophic feeding, as well as by an indirect opportunistic manifestation as the presence of free substrate space left by a die-off of other organisms. Other implicated anthropogenically linked causes include rising SSTs (*n* = 1 case; González-Delgado et al. 2018, López et al. 2020b), which can bleach scleractinian corals and thus create new areas for zoantharian settlement and expansion, ashfall, and other terrigenous inputs (*n* = 2 cases; Ono et al. 2002, López et al. 2018), and opening of substrate space due to increased aquarium trade collection of ornamentals (*n* = 1 case; Rogers et al. 2014) or due to grazing (*n* = 1 case; González-Delgado et al. 2018, López et al. 2020b). It may be that, in some circumstances, both natural and anthropogenic influences contribute to the formation of zoantharian phase shifts and barrens.

Zoantharian species were among the first coral reef organisms to be formally described from the Caribbean (Ellis 1768), and the presence of large intertidal to subtidal mats is easily noticeable to observers (Figure 2). Indeed, there are historical literature reports of the dominance of zoantharians in the intertidal zone at various locations across the Caribbean (e.g. Duerden 1898, Goreau 1959, Sebens 1977), and these may be naturally occurring phenomena. On the other hand, more recent literature (from the 1990s onwards) has described zoantharian barrens, and one confirmed phase shift in subtidal areas. However, there are probably less data from subtidal areas before the advent of scientific SCUBA diving in the 1950s to 1970s, and this represents a possible source of "observer bias" in our dataset.

Characteristics of zoantharian barrens and phase shifts

From the summary of these reports (Table 3), some generalizations on the characteristics of zoantharian dominance, barrens, and phase shifts can be made. All of these reports have very high benthic coverage of zoantharians, usually above 25% (Norström et al. 2009). Naturally occurring zoantharian-dominant areas occur in intertidal or very shallow subtidal waters (López et al. 2020b; this study), often with chronic or regular natural disturbance, such as intertidal desiccation (Sebens 1982, Rosa et al. 2018), storms (Karlson 1980, 1983, Acosta et al. 2001), or predation (Karlson 1983), that potentially keeps other benthos such as scleractinian corals and macroalgae from establishing and expanding. Anthropogenically generated zoantharian phase shifts and barrens are slightly different than naturally occurring ones, being slightly deeper, reported from depths of 1 to 8 m (Table 3), and appear to be most likely generated by reduced water quality, with sedimentation, increased turbidity, and wastewater implicated as causes (e.g. Cooke 1976, Hernández-Delgado et al. 2008, Castro et al. 2012, Lachs et al. 2019, see also Table 3). The mechanisms for the generation of barrens remain to be examined; it is not known whether zoantharians benefit from increased food availability (Reimer 1971, Fabricius & Metzner 2004), or they are competitively superior to zooxanthellate scleractinian corals under such conditions (Leal et al. 2016), or if the mechanism is a combination of both factors, which the available literature seems to indicate.

New zoantharian outbreaks?

Where can we expect zoantharian phase shifts and barrens to appear in the future? Certainly, with increasing levels of anthropogenic degradation predicted for coastal areas globally (Costa et al. 2014, Hughes et al. 2018, Abelson et al. 2016) combined with ongoing climate change and tropicalization of temperate and subtropical zones (López et al. 2019), we can expect an increase in their occurrence. According to the maximum entropy model, higher temperatures and a decrease in water quality could lead to subtropical and temperate latitudes as vulnerable zones to new zoantharians barrens (Figure 3). Our projected maps of habitat suitability where zoantharian barrens may be reported in the future show comparatively high probabilities along much of the North, Central, and South America's Atlantic coast, in parts of western Africa, and the Mediterranean and Europe in the Atlantic region, and around Australia, southern New Guinea, Pakistan, the western Yellow Sea, and southern mainland Japan in the Indo-Pacific (Figure 3). Although our model performance has to be taken with caution because of the low number of zoantharian outbreaks reported and their widespread distribution (van Proosdij et al. 2016), the results reflect those previously reported by Cruz et al. (2018), who suggested that zoantharian phase shifts in the Southeast Atlantic were more likely in subtropical and temperate coasts near urbanized areas with artificial coastlines and dredging, and the results we found here on a global scale (Cruz et al. 2018) (Figure 3). Importantly, in the same work, a negative correlation was reported with zoantharian abundance and increases in SST of more than 1°C (Cruz et al. 2018). These results could help explain the trend observed in our data of intertidal tropical zoantharian barrens reported in historical literature, while some more recent works report on subtidal phase shifts and barrens in temperate zones (Reimer et al. 2018, López et al. 2019), where although SSTs are increasing, they are still below levels expected to cause serious bleaching and mortality (usually approximately >30°C; Hibino et al. 2013). Also of potential importance are unsubstantiated observations that *Zoanthus* and *Palythoa* spp. abundances in the intertidal zones of tropical areas may be decreasing, based on the comparisons of collection information and numbers of historical and modern museum specimens from the Dutch Caribbean (Montenegro et al. 2020). Note that the individual papers we examined here did not specifically test for the causes of barrens and phase shifts, and our analyses are therefore testing, in effect, what the researchers of these past papers postulated. However, the scientific consensus of these papers is that there has been a shift from naturally occurring intertidal zoantharian dominance to anthropogenically induced subtidal barrens and phase shifts. If this is the case, given increasing levels of anthropogenic impacts on marine ecosystems (e.g. Williams et al. 2019) and rapid climate change (Ripple et al. 2019), we predict more zoantharian barrens in coming years.

One aspect of climate change that remains to be largely examined with regard to zoantharians is ocean acidification. Although it is generally believed that under ocean acidification, non-calcifying organisms such as zoantharians, sea anemones, and corallimorpharians will increase in numbers compared to calcifying taxa such as scleractinian and other reef-building corals (Done 1992, Hoegh-Guldberg et al. 2007), results from the few studies on zoantharians and ocean acidification thus far are conflicting. While one aquaria-based study testing low pH suggested impaired growth and reduced photosynthesis of endosymbiotic Symbiodiniaceae in two different *Palythoa* spp. (López et al. 2020a), another aquaria study showed differing positive and negative results for *Zoanthus* and *Palythoa* species, respectively (Graham & Sanders 2016). In contrast to these aquaria experiments, two species of *Palythoa* have been reported as abundant at a naturally acidified volcanic reef in southern Japan (Inoue et al. 2013, Reimer et al. 2021). Combined, these studies' results raise questions about the sensitivity to ocean acidification in different zoantharian species and their Symbiodiniaceae (Graham & Sanders 2016), as well as about the effects of different lengths of low pH exposure. Clearly, like so many other facets of zoantharian ecology, this topic needs more research before conclusions can be reached.

Effects of zoantharian barrens and phase shifts

The outcomes of zoantharian dominance, barrens and phase shifts include lowered benthic diversity (Cruz et al. 2015a), lowered fish diversity (Cruz et al. 2015b), a reduction in the three-dimensional structure of the reef (Cruz et al. 2015b), and a loss of commercially important species such as macroalgae (López et al. 2020b). Thus, anthropogenically related zoantharian outbreaks can cause potential reductions in a range of ecosystem services. We believe that reports and records of zoantharian

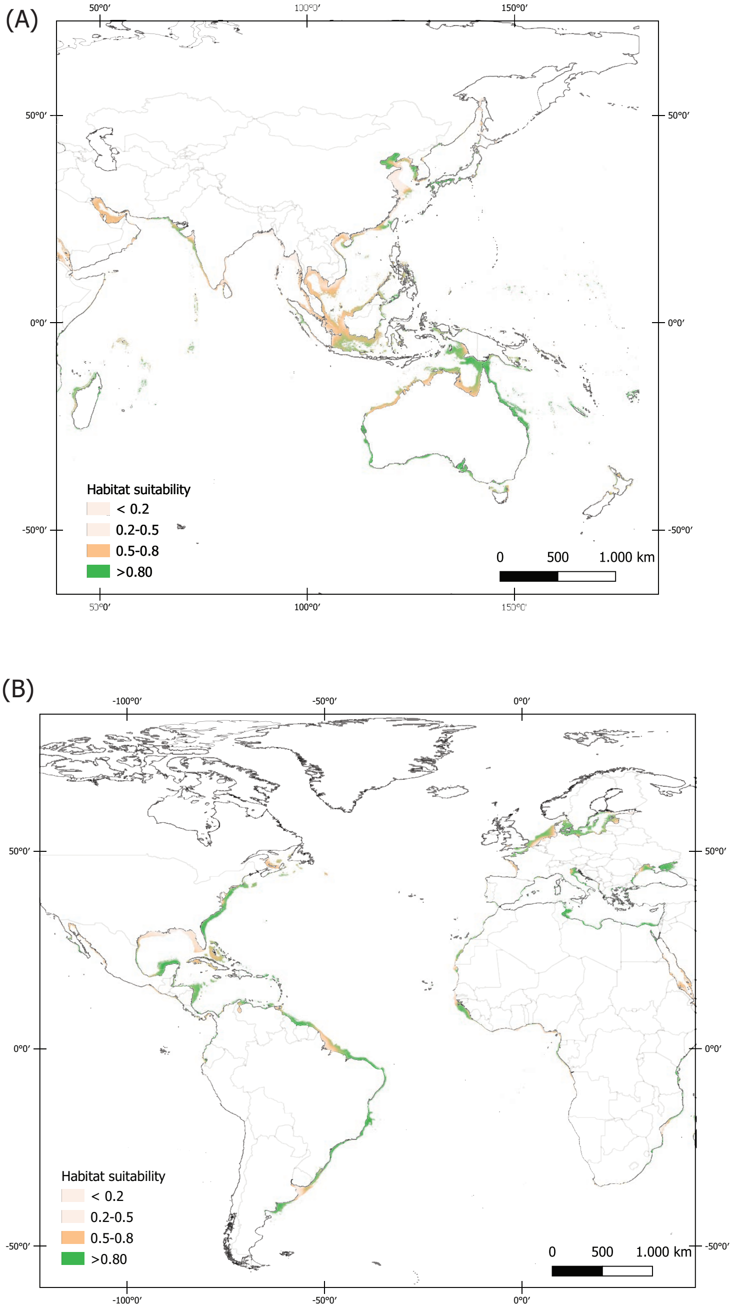

Figure 3 Projected maps of habitat suitability where new zoantharian barrens may occur, according to the maximum entropy model for (A) the Indo-Pacific region, and the (B) the Atlantic Ocean and the Americas.

barren outbreaks are also still generally under-reported in the literature. An anthozoan that resembles a hard scleractinian coral could easily go unnoticed by researchers who are not cnidarian experts, and it is not uncommon to find studies that have combined all anthozoans into a group called “corals” (Medeiros et al. 2010, Krajewski & Floeter 2011). Thus, the few studies that have reported on zoantharian dominance, barrens, and phase shifts could represent only a fraction of a widespread and under-reported phenomenon. Indeed, during the course of writing this review, the first author received images of zoantharian barrens not yet reported in the scientific literature from India and Cambodia (Ruzbeh Tehmurasp Mirza and Prof. Geeta Padate, Maharaja Sayajirao University of Baroda; Amick Haïssoune, Marine Conservation Cambodia, both personal communication).

All phase shifts could potentially be an alternative stable state (Dudgeon et al. 2010, Cruz et al. 2014), i.e. the state an ecosystem reaches after having its resilience broken from its previous state (Scheffer et al. 2001, Dudgeon et al. 2010). These phase shifts can be characterized by the existence of two or more ecosystem stable states in a similar range of environmental conditions, which have different tipping points to move to the other state (hysteresis; Scheffer et al. 2001). If high zoantharian coverage is an alternative stable state, the phenomenon becomes a greater environmental issue as after crossing the tipping point, such a community may not recover, even with interventions. Hence, it is important to pay attention to zoantharian coverage, and we recommend including zoantharian monitoring in international monitoring protocols (e.g. as in AGRRA protocol, Lang et al. 2010; AIMS protocol, Jonker et al. 2008).

Aside from *Zoanthus* and *Palythoa*, other anthozoans outbreaks have been reported on coral reefs, including corallimorpharians (Loya 2004, Work et al. 2008, Crane et al. 2016, Carter et al. 2019) and sea anemones (Chen & Dai 2004, Tkachenko et al. 2007). Additionally, many regions have noted a shift from scleractinian coral to octocoral dominance (Fox et al. 2003, Fabricius & De’ath 2004, Edmunds & Lasker 2019), and although it has been difficult to confirm, these shifts have also been linked to decreases in overall water quality (Norström et al. 2009). Whether all of these non-scleractinian anthozoan outbreaks are the opportunistic manifestation of lowered coral coverage (Loya 2004), or from outcomes of direct competition (Cruz et al. 2016), or via other mechanisms, remains to be studied, and such research is critically needed in this era of increasing coral reef ecosystem degradation.

Based on this review, we propose two possible functional models for *Zoanthus* and *Palythoa* outbreak occurrences, one each for coral reef and macroalgae-dominated hard substrate ecosystems (Figure 4). On coral reefs, under stress, many scleractinian corals bleach and subsequently die more quickly than zoantharians (Jiménez 2001, López et al. 2020b), leaving free benthic space for zoantharians to occupy, based on their fast growth (Wee et al. 2017). Alternately, some disturbance (natural or anthropogenic) could trigger zoantharians to increase rapidly, which then displace scleractinian corals via competition, depending on their relative competitiveness compared to other benthic anthozoans (Suchanek & Green 1981, Cruz et al. 2016). In macroalgae-dominated shores (González-Delgado et al. 2018, Reimer et al. 2018), an outbreak of sea urchins or another event could remove macroalgae, leaving free space for zoantharians to spread. Alternately, some other disturbance could trigger zoantharians to increase in abundance, subsequently displacing macroalgae via competition.

Recommendations for future research

It is anticipated that this review will spur increased awareness of zoantharian dominance, barrens, and phase shifts among marine researchers and managers. As we predict increases in *Zoanthus* and *Palythoa* spp. abundances in marginal coral reefs and communities, particularly in areas with decreasing water quality and in subtropical and temperate areas experiencing increases in SST, as well as in locations experiencing decreases in other benthic taxa, it would be prudent for local marine ecosystem managers to familiarize themselves with these taxa. Long-term studies examining the accuracy of our proposed functional models of zoantharian outbreaks would allow a better understanding of the mechanisms causing outbreaks, opening potential avenues for preventative

measure research. Aside from macroalgae, most of the taxa listed in Table 2, including Zoantharia, have been understudied and largely ignored in the scientific literature, and even basic research on the progress of outbreaks and phase shifts and their persistence, along with fundamental ecological and physiological observations, is needed if we are to make headway on better understanding such phenomena. Given that the outcomes of zoantharian dominance, barrens, and phase shifts span a wide range of reduced ecosystem services, this research can be considered of critical importance.

Conclusions

In summary, the current literature review and analyses of zoantharian dominance, barrens, and phase shifts show that

1. Zoantharian dominance and barrens have been reported across the globe in tropical and subtropical shallow water systems, although the reported information related to their causes, effects, and longevity remains scarce.
2. While some of these zoantharian-dominant sites are naturally occurring, the literature suggests that an increasing number of anthropogenically induced barrens are present, particularly from 2006 onwards. Currently, only one zoantharian phase shift has been conclusively shown, from Todos os Santos Bay, Brazil.
3. Preliminary statistical analyses show anthropogenically linked zoantharian barrens are subtidal, likely to be linked to decreases in water quality or increased pollution (e.g. increases in sedimentation and/or turbidity), and can reduce ecosystem services, while naturally occurring zoantharian dominance is more likely to be intertidal. Thus, the appearance of subtidal zoantharian barrens can potentially act as an indicator for reduced water quality or other disturbances, and coral reef managers should be aware of possible environmental conditions indicated by their new appearance at a given location.
4. In the future, we expect increased occurrences of zoantharian barrens in urbanized and other regions experiencing decreased water quality, particularly in subtropical and temperate regions that will be newly available potential habitat for subtropical and tropical species.
5. Increased monitoring efforts and analyses of generated data will greatly better our understanding of zoantharian dominance, barrens, and phase shifts. To this end, field workers and marine managers should be aware of zoantharian species, and be vigilant in reporting new outbreaks and barrens.

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SPECIES' DISTRIBUTION AND EVOLUTIONARY HISTORY INFLUENCE THE RESPONSES OF MARINE COPEPODS TO CLIMATE CHANGE: A GLOBAL META-ANALYSIS

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Abstract Ocean acidification (OA) and ocean warming (OW) are predicted to drive changes to the distribution of species and the structure of biological communities globally. Differences in life-history, physical traits, and the phenotypic response of organisms will, however, mean that the effects of OA and OW will differ among species. Geographical differences in environmental characteristics across habitats will also influence the effects of OA and OW, thereby driving inter-population differences in phenotypic response as determined by local adaptations. While is it accepted that the response of species will vary globally, predicting the trends in response of species remains highly uncertain. We undertook a meta-analysis of key biological traits of 47 marine copepod species from 88 studies to identify the intrinsic and extrinsic factors influencing the effects of OA and OW on copepod population demographics. Data from OA and OW were analysed independently due to insufficient two-stressor studies. We found that the large disparity in the response of species to OA and OW is largely defined by their environmental history. Additionally, the response of copepod species to OW is related to their evolutionary history which has less influence on their response to OA. Therefore, our study identified that the response of copepods to OA is driven by a combination of biotic and abiotic factors in their habitats. Under OA alone, copepods from less variable environments may be more susceptible, but the effects of OA will only be strongly negative at extreme low pH (<7). On the other hand, the response to OW is deeply tied to their phylogeny, whereby closely related species share similar costs and trade-offs. However, the effects of near-future OW (+2 to 4°C) seem mainly positive unless these temperatures exceed a species' thermal limit. Finally, our analysis revealed that OW has a greater influence on key copepod traits than OA. Overall, this study shows that attempting to draw global patterns in the response of species to climate change from a single species or habitat without consideration of environmental and evolutionary history could lead to inaccurate and misleading predictions with respect to the future of biological communities.

Keywords: Inter-species variation; phenotypic plasticity; local adaptation; environmental history; phylogenetic signal; ocean warming; ocean acidification

Introduction

Ocean acidification (OA) and ocean warming (OW), major components of anthropogenic climate change, are predicted to be important drivers of genetic, phenotypic and biodiversity change at a global scale, altering the functioning of marine communities and ecosystems (Parmesan 2006, Hoegh-Guldberg & Bruno 2010, Doney et al. 2012, Russell et al. 2012; Nadeau et al. 2017, Pecl et al. 2017). The ecological effects of OA and OW are expected to vary among different species depending on intrinsic characteristics of marine organisms such as their physiological tolerance

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(Pörtner & Knust 2007, Hofmann & Todgham 2010, Sorte et al. 2011; Minuti et al. 2021), their life stages (Dupont et al. 2010, Byrne & Przeslawski 2013), and their capacity for plastic responses and rapid adaptation (Hofmann & Todgham 2010, Reusch 2014, Leung et al. 2019, 2020). Moreover, the effects of OA and OW are also expected to vary across temporal and spatial scales due to extrinsic factors such as the rate of environmental change (Hoffmann & Sgrò 2011, Silbiger & Sorte 2018), the degree of environmental variability (Eriander et al. 2016) and the differences in environmental conditions among regions and habitats (Boyd et al. 2015). For instance, populations inhabiting highly variable environments, characterized by high natural environmental variability in sea surface temperature (SST), pH and pCO_2 (e.g. upwelling regions; Sobarzo et al. 2007, Letelier et al. 2009, Kapsenberg & Hofmann 2016, Chavez et al. 2018), can display greater resilience or plasticity to climate change compared to those inhabiting more stable systems (Berg et al. 2010, Donelson et al. 2018). Nevertheless, these habitat-related responses are not consistent across different regions and taxa (e.g. Cornwall et al. 2020), challenging our capacity to make more accurate predictions of the effects of climate change on populations, communities and ecosystems. In order to address this problem, it is necessary to assess the potential sources and causes that influence the documented heterogeneity in the phenotypic responses of marine organisms to OA and OW.

One of the main issues with estimating the effect of climate change on species is that most empirical studies consider species as a single unit where individuals from all populations respond equally to environmental pressures (Valladares et al. 2014). However, populations across the geographical distribution of a species can experience vastly different environmental conditions that influence differences in local adaptation, phenotypic plasticity and the capacity for phenotypic/genetic responses to OA and OW (Boyd et al. 2015, Gaitán-Espitia et al. 2017a,b, Leung et al. 2021). In coastal systems, for instance, chemical and physical processes differ across geographical regions but also across ecosystems in close proximity (Gunderson et al. 2016, Fassbender et al. 2018, Silbiger & Sorte 2018). Therefore, coastal zones are influenced by local suites of environmental parameters which can change biological outcomes. For example, in areas where upwelling events are prevalent, ecosystems are naturally exposed to high variation in carbon dioxide concentration, oxygen concentration, pH and temperature (Sobarzo et al. 2007, Letelier et al. 2009, Kapsenberg & Hofmann 2016, Reum et al. 2016, Chavez et al. 2018). Conversely, in areas of extensive estuarine discharge, fluctuations in salinity, pH and turbidity are common (Sarma et al. 2012, Aguilera et al. 2013, Shen et al. 2013, Asp et al. 2018). As a result, species from these different habitats may respond differently to climate change because their tolerances and sensitivities have been differentially shaped by natural selection (Vargas et al. 2017, Gaitán-Espitia et al. 2017a).

Heterogeneity in phenotypic responses to OA and OW can also originate from sources of intrinsic biological characteristics such as body size (Daufresne et al. 2009, Garzke et al. 2015) and the evolutionary history of the species (Davis et al. 2010, Buckley & Kingsolver 2012). Body size is an important determinant of fitness, physiology and performance in many organisms (Roff 2002). It has been documented that intra- and inter-species variation in this important trait can influence the species' and communities' responses to environmental stress and climate change (Daufresne et al. 2009, Garzke et al. 2015, Rice et al. 2015). However, this variation, as well as variation in other phenotypic traits and responses to climate change, is highly dependent on the evolutionary history of species because closely related species share more similar characteristics than distantly related species (i.e. species are not statistically independent) (Felsenstein 1985). Thus, comparative assessments of the phenotypic responses of species to OA and OW in a taxonomically resolved framework are important (Buckley & Kingsolver 2012) whereby the exclusion of phylogenetic distribution can potentially hide phylogenetic signals inducing bias in our interpretations of the species' and communities' susceptibility to climate change.

Here, we use copepods as model taxon to explore potential intrinsic and extrinsic causes of heterogeneity in biological responses of marine organisms to climate change. Copepods occupy various niches in multiple marine habitats, including coastal, estuarine, oceanic and intertidal habitats (McGinty et al. 2018). As a result, these crustaceans are exposed to a vast array of environments, including fluctuations in salinity, oxygen concentration, temperature and pH level. Some oceanic copepod species, for example, undergo deep diel migrations and are exposed to large variations in temperature and pH on a daily basis (Lewis et al. 2013, Svetlichny et al. 2000). On the other hand, coastal and estuarine species can be exposed to upwelling or high freshwater discharge that drastically change their environmental pH, temperature, oxygen concentrations or salinity (Escribano & Hidalgo 2000, Aguilera et al. 2013, 2016). Copepod species can also inhabit extreme environments such as intertidal rockpools, characterised by extremely large diel and seasonal changes in pH and temperature linked to variation in sunlight exposure, primary production and respiration (Powlik 1999, McAllen & Brennan 2009, Willett 2010). The responses of different species of copepods to their abiotic conditions are as varied as the environments themselves (Edmands & Harrison 2003, Brun et al. 2016, Horne et al. 2016, Pereira et al. 2017). While life-history theory predicts that different traits evolve in different environments, concurrently, phylogenetic history may restrict natural selection by dictating the range of phenotypes that selection can act upon (Hairston & Bohonak 1998). Therefore, closely related taxa may share similar traits and trade-offs when exposed to similar variation in their abiotic environment.

Since different environments and phylogenetic histories can influence the biological traits of copepods, the effect of climate change on traits can also be expected to vary across habitats and taxa. In fact, short-term exposure to OA causes varied effects on the biological traits of different copepod species (Zhang et al. 2011, Lewis et al. 2013, McConville et al. 2013, Wang et al. 2018), different populations (Thor et al. 2018) and copepods from different habitats, such as between coastal (Cripps et al. 2014), estuarine (Aguilera et al. 2016, Hemraj et al. 2017) and oceanic habitats (Mayor et al. 2007, Weydmann et al. 2012). Similarly, OW can cause varied effects among species (Chinnery & Williams 2004), populations (Scheffler et al. 2019) and habitats (Han et al. 2018). In addition to short-term variation, long-term increases in pCO_2 and temperature are expected to have trans- or multigenerational effects through selection (Thor & Dupont 2015). In contrast to predictions, however, persistent benefits to fitness across generations are not consistently observed (Byrne et al. 2020). Thus, the effects of OA and OW on copepods are not generic, and estimating their effects on different species across global oceans is highly ambiguous. Therefore, to understand the potential intrinsic and extrinsic causes of heterogeneity in biological responses of marine organisms to projected climate change, we undertook a global meta-analysis and review of the studies of OA and OW on biological traits of copepods (Figure 1).

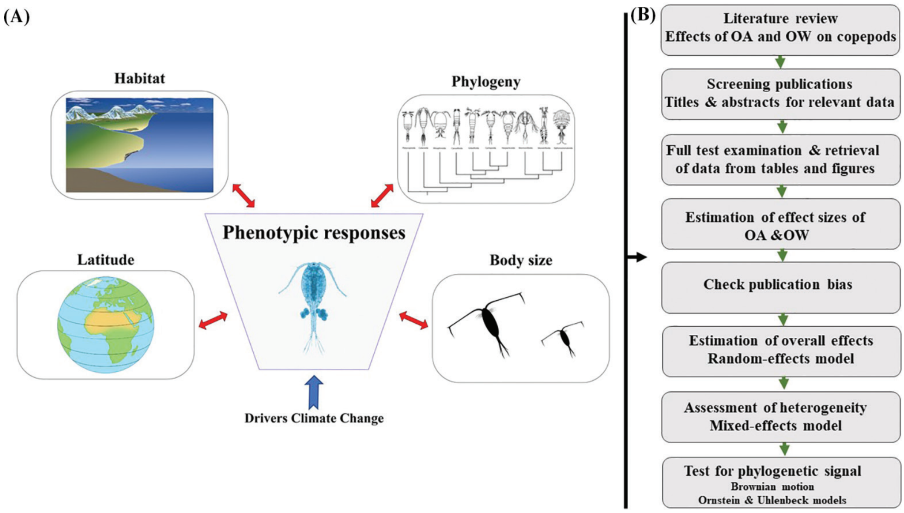

Figure 1 (A) Graphical hypothesis displaying the possible factors that influence the response of copepods and (B) workflow used in the meta-analysis of the effects of ocean acidification and ocean warming on copepod biological traits.

Data from OA and OW were analysed independently due to insufficient two-stressor studies (Vehmaa et al. 2012, 2013, Hildebrandt et al. 2014, Preziosi et al. 2017, Garzke et al. 2020).

First, we investigated the variation in the effects of OA and OW on copepod fecundity (egg production and hatching success) and adult survival across latitudes, marine habitats (estuarine, intertidal, coastal and oceanic), and among taxonomic groups. We used reproduction and adult survival since these are part of the fundamental activities that define fitness in organisms (Litchman et al. 2013). Second, we investigated the influence of the number of eggs produced on the hatching success under OA and OW to identify the extent of investment in reproductive output of different species and how these may drive their fitness under climate change. Finally, we investigated the influence of metabolic scaling across copepod species in defining possible metabolic costs as a trade-off for surviving in acidified or warmer oceans. We, therefore, provide a more comprehensive understanding of the causes of heterogeneity in response to OA and OW observed in copepods.

Methods

Data selection and suitability criteria

Meta-analyses were carried out following the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) and the CEE (Collaboration for Environmental Evidence) guidelines. We undertook a comprehensive search for peer-reviewed papers explicitly investigating the effects of OA and OW on copepods. Searches were carried out on ScienceDirect, PubMed, Microsoft Academic and ISI Web of Science using the following search strings: TS = [("copepod") AND ("climate change" OR "ocean acidification" OR "hypercapnia" OR "pH")], as well as TS = [("copepod") AND ("global warming" OR "ocean warming" OR "temperature")]. Searches included papers published between January 1990 and March 2020, as most climate change studies that manipulated climate change conditions in regard to IPCC AR1 predictions (the first assessment and model of future CO_2 concentrations or temperature increase which are used as baseline conditions to test for organismal response to future climate change) and subsequent updates (IPCC 1990, 2007) were published post-1990. However, we also included experimental studies that investigated the effect of temperature increments on copepod biological response outside of the climate change context, irrelevant of the year, as these experiments were comparable (i.e. account for temperature increments which are within estimates of future ocean warming under climate change) and provided a more comprehensive dataset for investigating the influence of ocean warming on copepods. Our full search yielded 27,273 potential papers. Papers were screened to only include studies that undertook controlled manipulative experiments on trait responses at specific treatment conditions (e.g. response at pH 8.1, 7.7. 7.2 and 6.9; or response at temperature 20°C, 15°C and 10°C) or undertook measurements of different biological responses directly on organisms across naturally occurring pH or temperature gradients (e.g. comparing traits of a copepod species that naturally has populations occurring in coastal waters and low-pH estuarine waters in close proximity). In addition, we further screened papers to include only those that investigated the influence of OA and OW on fecundity, survival/mortality, respiration/metabolic rates and feeding rates since these are the only traits analysed in this study. Finally, we only included studies that reported data on adults of a particular species fed *ad libitum* to avoid confounding factors such as life-cycle stage or different food availability. After this manual screening and removal of duplicates, out of 116 papers that investigated the response of copepods to OA or OW, 88 papers remained from which biological response data of interest could be collected (see supplementary materials for the list of papers). In the instance where a study reported multiple independent variables, only data from "ambient" conditions and the variable of interest were used in our analysis. For example, if a study reported biological response data at "ambient" conditions, "low-pH", "low-food", and "low-pH × low-food", only "ambient" and "low-pH" data were used. In the instance where organisms were sampled along environmental gradients, such as a pH gradient, data were collected from each pH value to the closest one decimal point (e.g. 8.1, 8.0, 7.9. and 7.8) or as grouped within the original paper (e.g. in Aguilera et al. 2020; $\mathrm{pH} > 8$ considered as high pH, pH 7.8–7.9 considered as low pH group one and $\mathrm{pH} < 7.8$ considered as low pH group two). This was done to account for as much data and variation as possible. Additionally, when repeated measurements were undertaken on the same individuals over time (e.g. egg production rate estimated on day 2, day 4 and day 6; at temperature 0°C or 4°C), an average of the measurements was used at each variable level (mean of days 2, 4 and 6 at temperature 0°C and mean of days 2, 4 and 6 at temperature 4°C represented as egg produced per female per day) to ensure we captured the overall response of these individuals rather than individual or diel variations. Alternatively, if cumulative measurements were reported (e.g. percentage eggs hatched from clutch 1 on days 1, 3, and 5), only the final measurements were used as that denoted the final maximum in that treatment. Several studies included data from multiple species, locations and independent variable levels (e.g. pH 7.8, 7.5, and 7.2). In these cases, all variable levels, species and locations were included in the analysis as independent measurements if they met the suitability criteria above; each species from each separate population was analysed at each variable level. This approach ensured that we captured the broad range of response in our analysis.

Finally, to be included in the analysis, studies that met the suitability criteria had to either provide a full dataset as supplementary or the data had to be reported as mean or median, a measure of variance (standard deviation, standard error, 95 % confidence interval or range), and sample size (N). Raw data were obtained by searching for supplementary datasets on the journal websites, the Ocean Acidification International Coordination Centre through GOA-ON (http://portal.goa-on.org/) or PANGAEA (https://www.pangaea.de/). For studies that did not provide datasets, the means, variances and sample sizes were extracted from tables in the paper or from graphical displays using PlotDigitizer™ for windows (http://plotdigitizer.sourceforge.net/).

Data analysis

The effect size of biological responses between controls and treatments were calculated using the means, standard deviations and sample sizes following Hedges et al. (1999). By using effect sizes in our analyses rather than real measured values, we estimated the change in traits based on different pH or temperature levels directly, therefore, limiting (but not eliminating) the possible effects of confounding factors (e.g. seasons) in our analyses. We selected log response ratio (LnRR) to estimate the effect size because of the capacity to detect true effects and robustness to small sample sizes (Lajeunesse & Forbes 2003). For each biological response, LnRR values were calculated using the following equation:

$$\mathrm{LnRR} = \ln\left(\mathrm{Mean}_T\right) - \left(\mathrm{Mean}_C\right)$$

where Mean_T is the mean of treatment, and Mean_C is the mean of control. In some studies, variances were reported as standard error (SE) or as median and ranges. When standard errors were reported, standard deviations (SD) were calculated using the following equation:

$$\mathrm{SD} = \mathrm{SE} \times \sqrt{N}$$

where SE is the standard error, and N is the sample size. When median and ranges were reported, means and standard deviation were calculated as per Hozo et al. (2005) with the following equations:

$$\mathrm{Mean} = (\mathrm{a} + 2m + b)/4$$

where a is the lower range, b is the upper range, and m is the median,

$$\mathrm{SD} = \left(1/12\right)\left\{\left(a - \ 2m + b\right)^2/4 + \left(b - a\right)^2\right\}$$

for $N < 15$, where, a is the lower range, b is the upper range, and m is the median and

$$\mathrm{SD} = \mathrm{Range}/4$$

for $N > 15$. Finally, when 95% confidence intervals were reported, standard deviation was calculated using the following equation from Higgins et al. (2019):

$$\mathrm{SD} = \sqrt{N}\ \ (\text{upper limit} - \text{lower limit})/3.92$$

Prior to formal meta-analysis, we calculated a Rosenberg fail-safe number to test for publication bias. Publication bias may be caused if studies finding non-significant effects are not published (Rosenberg 2005) and are therefore not included in analysis, and thus may influence results and interpretation. The fail-safe number calculates the number of studies with non-significant effects (effect size of zero) that would be required to change the results of the meta-analysis from significant to non-significant (Rosenberg 2005). The Rosenberg fail-safe numbers calculated were larger than $5n + 10$, where n is the number of studies included in our analysis (Rosenberg 2005); therefore, our analyses are generally robust, and publication bias was unlikely to affect our results. Following the publication bias test, we undertook the meta-analyses using weighted random effects models (restricted maximum likelihood) that utilise inverse-variance weighting to account for variation within and between studies (Wallace et al. 2017), therefore accounting for random sampling variation within each experiment and variation among studies in estimated effect size (Harvey et al. 2013, Hancock et al. 2020). The weighted random effects model provides wider confidence intervals when there is heterogeneity, thus statistical significance is more conservative. The model calculates the true variation in effect size by the between-study variance (using the ln-transformed response ratios, LnRR), with each study weighted by the inverse sum of the individual study variance (Hancock et al. 2020). This includes a heterogeneity test (Q) that compares the variation in study outcomes between studies and indicates the percentage variation between studies due to heterogeneity (i.e. differences in outcomes between different studies; also denoted as I^2) rather than chance (Wallace et al. 2017). To test for differences between pre-defined groups and perform explanatory analyses for variation in effect sizes, we performed meta-regressions using mixed-effects models (Harvey et al. 2013) using pH, temperature, latitude from where organisms were sampled, habitat from which organisms were sampled, species body size (prosome length), genus and species as explanatory variables. We grouped different species based on their egg production rates (low, medium and high egg production rates (< 10, 10–20, and >20 eggs female^{-1}day^{-1}, respectively) and analysed the effects that OA and OW have on their hatching success. We grouped the egg production rates at ambient conditions (control conditions used within studies) for adult females only for each species from different papers and used the mean egg production rate for each species to categorize them within different groups (low, medium, high). All data were converted to the number of eggs female^{-1}day^{-1} to standardize egg production data for analysis (e.g. if three adult females produced 120 eggs at day 5 of an experiment, the egg production rate used was calculated as $((120/5)/3) = 8$ eggs female^{-1}day^{-1}). In addition to egg production, we analysed the effects of OA and OW on the hatching success of species based on their spawning mode (broadcast or sac spawners). To test for the influence of metabolic scaling on the metabolic costs of copepods under novel environmental conditions, we analysed the effect size of OA and OW on the metabolism (energy expenditure) and feeding rates (energy intake) of copepods in relation to the species body size (average prosome length). Finally, to test for the effect of evolutionary history on traits, and because we analysed biological responses per species rather than overall response per study, we used phylogenetic analyses throughout the study to reflect evolutionary history whereby closely related species share a common evolutionary history more than distantly related species. We tested for the percentage heterogeneity attributed to phylogeny (phylogenetic heterogeneity) in biological response using both Pagel's lambda (Brownian motion model) and Martins and Hansen's alpha (Ornstein and Uhlenbeck model) as measure for phylogenetic signal. Phylogenetic signal is a statistical measure of the degree to which evolutionary history has driven trait distribution. Phylogenetic relationships were analysed in MEGA (version 10.1.7), using maximum-likelihood phylogenetic trees, based on the best model estimation and accounting for branch lengths and rates of molecular evolution. Molecular data (cytochrome oxidase I) were obtained from NCBI taxonomy database. Calculation of effect sizes, meta-analysis, meta-regressions and analysis of phylogenetic heterogeneity were performed on OpenMEE (Wallace et al. 2017), which is an open-source software specifically designed for meta-analysis in ecology and evolutionary biology, and based on the "metafor" and "ape" packages for R. To ensure the sensitivity of our analyses, we reran analyses by removing the studies showing larger effect sizes (Harvey et al. 2013). In addition, to verify the robustness of the analyses, we used an effect-size correction technique (RR^{Δ}) as outlined in Lajeunesse (2015) and re-analysed the data. No differences in results were found when RR^{Δ} was used compared to lnRR, therefore confirming the robustness of the analyses.

Results

The 88 papers that passed our suitability criteria assessed the effect of OA and OW on the egg production hatching success, survival, metabolism and feeding rates of 47 species of copepod. Overall, 585 effect sizes were calculated using data from these studies. The majority of the studies were undertaken in the northern hemisphere, investigating the effects of OA and OW primarily on coastal copepod species in temperate regions (Figure 2). Overall, OA and OW had opposing effects on copepod fecundity and survival (Tables 1 and 2). When considering all studies, OA decreased both fecundity and survival while OW generally increased these traits (Figure 3). However, there was high heterogeneity in the effects of both OA and OW, confirming variation in the response of different species and studies.

Fine-scale analysis revealed that the effect of OA on copepod fecundity (Figure 4) was more marked at lower pH. Nonetheless, this relationship seems to be driven by extreme low pH ($pH < 7.0$; Table 1), because the relationship was neither significant at $pH > 7.7$ (estimated end of century OA) nor at $pH > 7.0$ (Table 1). Moreover, OA did not have significant overall effect on the fecundity of copepods independent of their different habitats, latitudes or body sizes (Table 1). Although similar findings were documented for survival (Table 1; Figure 5), our results revealed an interesting trend in which copepods living at higher temperatures (lower latitudes) tend to be less affected by OA than copepods from cooler environments at higher latitudes (Mean effect size for $\text{latitude} > 50° = -0.324$, $\text{latitude} < 50° = -0.107$; Table 1). Higher metabolic rates (mean effect size: 0.145) but decreased feeding rates (men effect size −0.255) in response to OA (Table 3) suggested an energetic mismatch where energy demands increased but energy acquisition was reduced, as seen in Thor et al. (2018). However, these effects were independent of habitat, latitudes and especially body size suggesting a lack of influence of metabolic scaling as observed by the lack of significant relationship between body size and the effect size of OW on metabolism (Table 3). The assessment of other potential sources of heterogeneity in the phenotypic responses of copepods to OA suggests that the species identity and evolutionary history are important factors. For instance, hatching success based on the egg production rate is differentially affected by OA depending on species' specific characteristics. Species with higher egg production rates (>20 eggs $\text{female}^{-1}\text{day}^{-1}$) endured greater reduction in hatching success (mean effect size: −0.686, −0.142 and −0.11 for high, medium and low egg production, respectively) under OA (Table 4; Figure 6), while no differences were found between broadcast and sac spawners (Table 4). Contrary to fecundity, the effects of OA on survival varied

Table 1 Weighted random effect models, meta-regressions and phylogenetic regressions of copepod egg production, hatching and survival as a function of ocean acidification

Statistical model	Egg production					Hatching					Survival				
Full model (Weighed random effect model)	δ	CI_{low}	CI_{high}	P		δ	CI_{low}	CI_{high}	$\boldsymbol{P}$		δ	CI_{low}	CI_{high}	$\boldsymbol{P}$	
Ocean acidification	–0.408	–0.538	–0.278	< 0.001		–0.298	–0.428	–0.168	< 0.001		–0.241	–0.346	–0.136	<0.001	
	d.f	Q	P		I^2	d.f	Q	P		I^2	d.f	Q	P		I^2
	73	812.197	< 0.001	↓	92.967	72	6360.785	<0.001	↓	99.724	18	1705.848	<0.001	↓	98.628
Meta-regression															
pH	1	6.61	0.01	–		1	8.312	0.004	–		1	1.148	0.284		
pH > 7.7	1	0.0154	0.901			1	0.193	0.516			1	0.136	0.712		
pH > 7	1	1.222	0.269			1	3.744	0.053			1	1.704	0.192		
Temperature	1	4.146	0.042	–		1	6.797	0.009	–		1	6.015	0.014	–	
Latitude	1	0.307	0.58			1	0.012	0.914			1	7.075	0.008	+	
Prosome length	1	0.883	0.347			1	1.679	0.195			1	1.336	0.248		
Habitat	2	2.276	0.32			3	3.136	0.371			2	0.802	0.67		
Genus	6	0.009	0.173			5	5.221	0.389			3	12.531	0.006	**	
Species	18	38.78	0.003	**		13	21.188	0.069			7	13.248	0.066		
Phylogenetic regression															
Pagel's $\lambda = 1$	σ^2 between study = 0.2561 σ^2 phylogeny = 0.0497 *Percentage variance due to phylogeny = 16.25*					σ^2 between study = 0.2988 σ^2 phylogeny = 0.0337 *Percentage variance due to phylogeny = 10.13*					σ^2 between study = 0.0336 σ^2 phylogeny = 0.0173 *Percentage variance due to phylogeny = 33.99*				
Martins and Hansen's $\alpha = 1$	σ^2 between study = 0.2241 σ^2 phylogeny = 0.0569 *Percentage variance due to phylogeny = 20.25*					σ^2 between study = 0.2886 σ^2 phylogeny = 0.033 *Percentage variance due to phylogeny = 10.26*					σ^2 between study = 0.0349 σ^2 phylogeny = 0.0147 *Percentage variance due to phylogeny = 29.64*				

Abbreviations: δ, overall effect size; CI, 95% confidence interval; P, p-value, d.f, degrees of freedom; Q, regression coefficient; σ_2, variance.

Note: Arrows indicate the overall effect of OA (increase or decrease) on copepod traits. The direction of significant relationships between variables is indicated as positive or negative signs. * denotes a statistically significant result (* $p<0.05$, ** $p<0.01$, *** $p<0.001$).

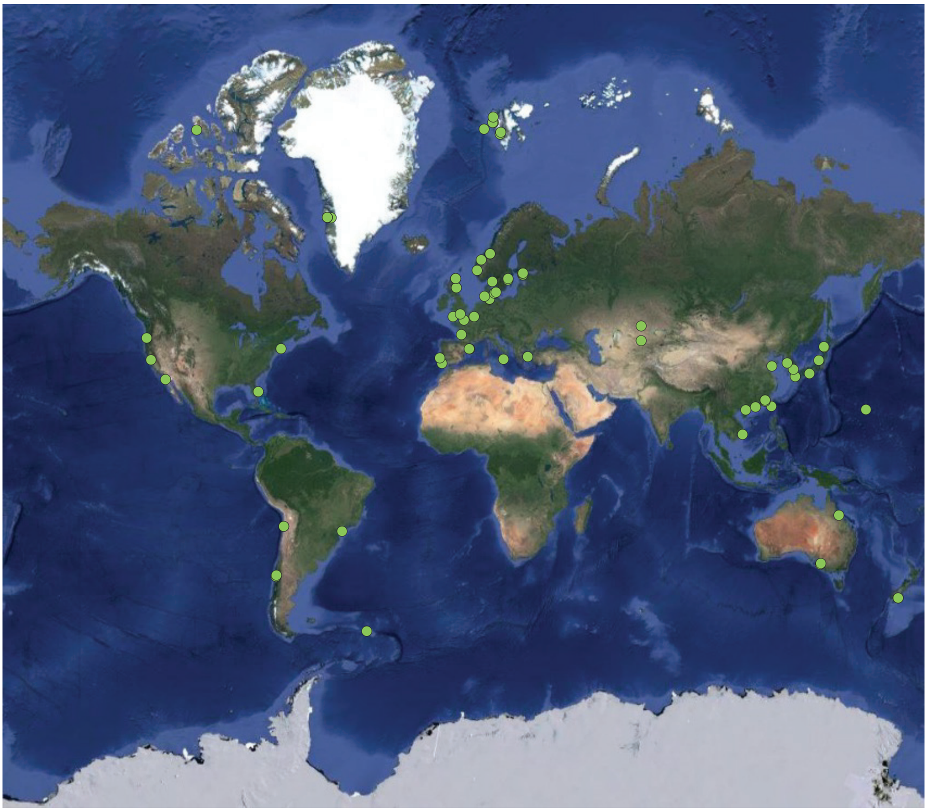

Figure 2 Map of the distribution of copepod populations from studies used for the meta-analysis. The map was constructed using QGIS, and coordinate layers were made from coordinates extracted from individual papers or estimated using Google Maps based on place names when no specific coordinates were reported in the paper.

among different genera (Table 1). For this trait, the oceanic genus *Oithona* was more negatively affected by OA than other groups (Figure 5). There was partial phylogenetic influence on the effect of OA on egg production, hatching and survival. Phylogeny explained 18%, 10% and 32% (average estimated from Pagel's lambda and Martins and Hansen's alpha) of heterogeneity in the effect of OA on egg production, hatching and survival, respectively (Table 1). When the phylogenetic influence was removed from the models, the overall effect of OA on fecundity and survival remained negative, suggesting that other biotic or abiotic factors are also influencing the phenotypic responses of copepods to OA.

OW generally increased fecundity in copepods (Table 2, Figure 7). However, the increase followed a hormesis shape (biphasic, involving an increase followed by a decrease over a temperature gradient; supplementary Figure 3). There were no distinct overall differences in the effect of OW on fecundity among different habitats, but egg production in oceanic species increased significantly more than that in estuarine species ($p=0.034$). In contrast, hatching success of coastal species increased compared to that of oceanic species (+22.7 % and −9.5 % on average, respectively; Table 4). OW increased hatching success in species with higher natural egg production (>20 eggs female^{-1}day^{-1}) compared to those with medium and low egg production rates (mean effect size: 0.763, −0.112, 0.154 for high, medium and low egg production, respectively; Table 4), while no differences were found in hatching success between broadcast and sac spawners (Table 4). As for survival (Figure 8), no differences between habitats were observed (Table 2); however, within coastal

Table 2 Weighted random effect models, meta-regressions and phylogenetic regressions of copepod egg production, hatching and survival as a function of ocean warming

Statistical model	Egg production					Hatching					Survival				
Full model (weighed random effect model)	δ	CI_{low}	CI_{high}	P		δ	CI_{low}	CI_{high}	P		δ	CI_{low}	CI_{high}	***P***	
Ocean warming	0.587	0.443	0.731	<0.001		0.309	0.106	0.511	0.003		–0.063	–0.192	0.066	0.338	
	d.f	*Q*	*P*		I^2	d.f	*Q*	*P*		I^2	d.f	*Q*	*P*		I^2
	120	25871.94	< 0.001	↑	99.243	66	330434.6	< 0.001	↑	99.973	55	1431.391	<0.001	↑	99.773
Meta-regression															
Temperature	1	0.216	0.642			1	2.011	0.156			1	8.888	0.003	+	
Latitude	1	0.726	0.394			1	1.577	0.209			1	0.004	0.948		
Prosome length	1	3.212	0.073			1	4	0.04	–		1	0	0.649		
Habitat	2	4.739	0.094			2	10.29	0.006	**		3	6.593	0.086		
Genus	10	52.457	< 0.001	***		6	20.319	0.002	**		5	71.073	<0.001	***	
Species	18	68.887	< 0.001	***		16	35.605	0.003	**		14	113.289	<0.001	***	
Phylogenetic regression															
Pagel's $\lambda = 1$	σ^2 between study = 0.4816					σ^2 between study = 0.5865					σ^2 between study = 0.0499				
	σ^2 phylogeny = 1.1834					σ^2 phylogeny = 0.1077					σ^2 phylogeny = 0.418				
	Percentage variance due to phylogeny = 71.08					*Percentage variance due to phylogeny = 15.51*					*Percentage variance due to phylogeny = 89.34*				
Martins and Hansen's $\alpha = 1$	σ^2 between study = 0.4623					σ^2 between study = 0.5847					σ^2 between study = 0.0519				
	σ^2 phylogeny = 0.5645					σ^2 phylogeny = 0.0841					σ^2 phylogeny = 0.2485				
	Percentage variance due to phylogeny = 54.98					*Percentage variance due to phylogeny = 12.57*					*Percentage variance due to phylogeny = 82.72*				

Abbreviations: δ, overall effect size; CI, 95% confidence interval; *P*, *p*-value; d.f, degrees of freedom; *Q*, regression coefficient; σ_2, variance.

Note: Arrows indicate the overall effect of OW (increase or decrease) on copepod traits. The direction of significant relationships between variables are indicated as positive or negative signs. * denotes a statistically significant result (* $p<0.05$, ** $p<0.01$, *** $p<0.001$).

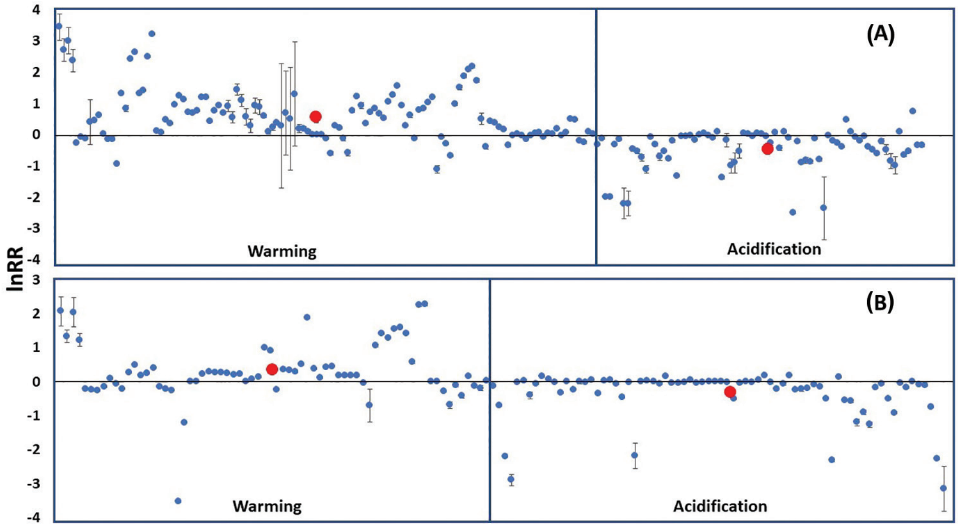

Figure 3 Response of copepod (A) egg production and (B) hatching success to ocean acidification and warming displayed as mean response ratio with 95% confidence intervals. Each blue dot is an effect size calculated for a single study. Red dots represent the overall effect size of warming or acidification.

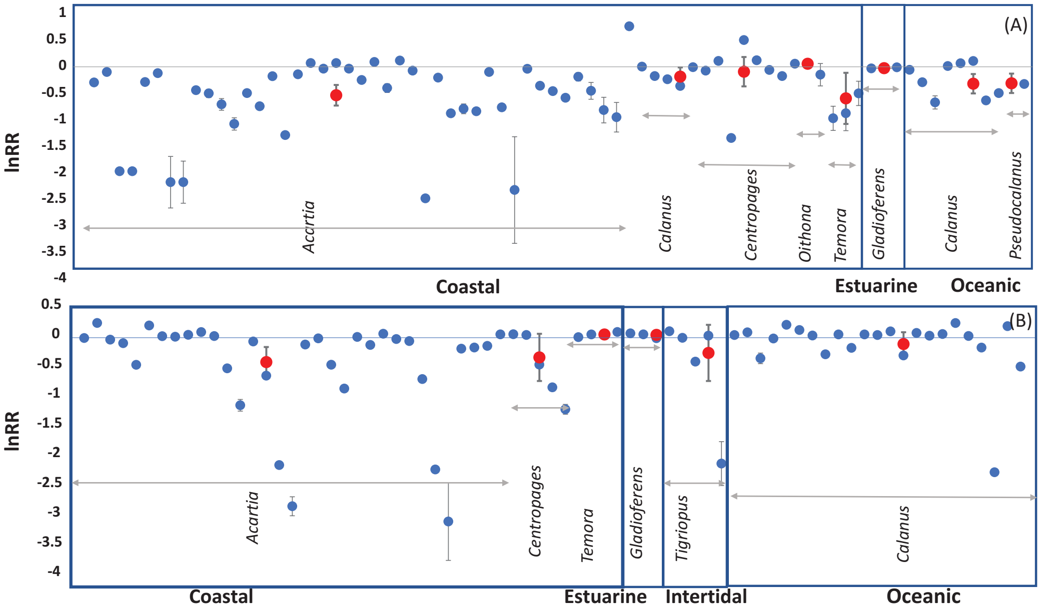

Figure 4 The effect of acidification on (A) egg production and (B) hatching success of different genera of copepods. Mean response ratio with 95% confidence intervals is grouped by copepod genus and habitat based on known areas occupied by the species. Arrows indicate the different effect sizes for each genus. Each blue dot is an effect size calculated for a single study. Red dots represent the overall effect size for the genus.

habitats OW significantly increased the survival of *Acartia* spp., while other coastal copepods had weaker response ($p<0.05$). Latitudinal distribution had no influence on the effect of OW on fecundity or survival (Table 2). On the other hand, the hatching success of smaller copepods (<2 mm prosome length) increased compared to that of larger copepods (>2 mm prosome length) under OW

Table 3 Weighted random effect models and meta-regressions of copepod metabolic and feeding rates as a function of ocean acidification and warming

Statistical model	Metabolic rate				Feeding rate			
Full model (Weighed random effect model)	δ	CI_{low}	CI_{high}	P	δ	CI_{low}	CI_{high}	P
Ocean acidification	0.145	0.064	0.227	<0.001 ↑	−0.255	−0.457	−0.054	0.013 ↓
Meta-regressions	**d.f**	**Q**	**P**		**d.f**	**Q**	**P**	
Body size	1	1.75	0.186		1	2.017	0.156	
Habitat	2	0.356	0.837		3	6.775	0.079	
Latitude	1	0.151	697		1	1.528	0.216	
Genus	5	0.742	0.981		5	2.211	0.819	
Species	7	3.563	0.894		7	2.221	0.947	
Temperature	1	0.326	0.568		1	0.572	0.449	
pH	1	0.645	0.422		1	2.269	0.132	
Ocean warming	0.666	0.447	0.885	<0.001 ↑	0.155	−0.2	0.51	0.392
Body size	1	0.344	0.558					
Habitat	2	62.273	<0.001		1	0.43	0.512	
Latitude	1	0.486	0.486		1	1.439	0.23	
Genus	8	59.971	<0.001	***	5	3.076	0.668	
Species	10	70.012	<0.001	***	5	3.076	0.688	
Temperature	1	0.058	0.81		1	0.754	0.385	

Abbreviations: δ, overall effect size; CI, 95% confidence interval; *P*, *p*-value; d.f, degrees of freedom; *Q*, regression coefficient.

Note: Arrows indicate the overall effect of OA or OW (increase or decrease) on copepod traits. * denotes a statistically significant result (* p<0.05, ** p<0.01, *** p<0.001).

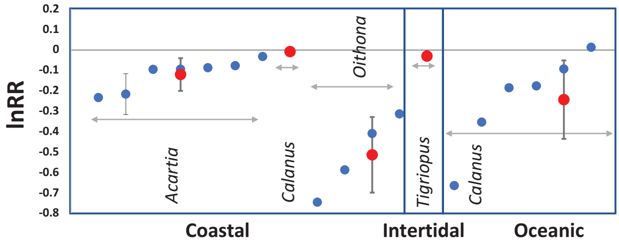

Figure 5 Copepod survival as a function of acidification. Mean response ratio and 95% confidence intervals are grouped by copepod genus and habitat based on known areas occupied by the species. Each blue dot is an effect size calculated for a single study, and red dots represent the overall effect size for the genus.

(mean effect size: 0.533 and –0.140, respectively), while metabolic rates of species inhabiting coastal regions increased more than that of oceanic and intertidal species (mean effect size: 0.855, 0.557 and –0.483, respectively; Table 3). There were strong differences among the responses of different genera and species, and strong phylogenetic signals were observed (Table 2). Phylogenetic distribution contributed to 63%, 14% and 86% (average estimated from Pagel's lambda and Martins and Hansen's alpha) of variance in the effect of OW on egg production, hatching and survival, respectively. When the phylogenetic influence was removed from the models, the overall effect of OW on fecundity and survival changed from positive to neutral, indicating that closely related species tend to respond similarly to OW.

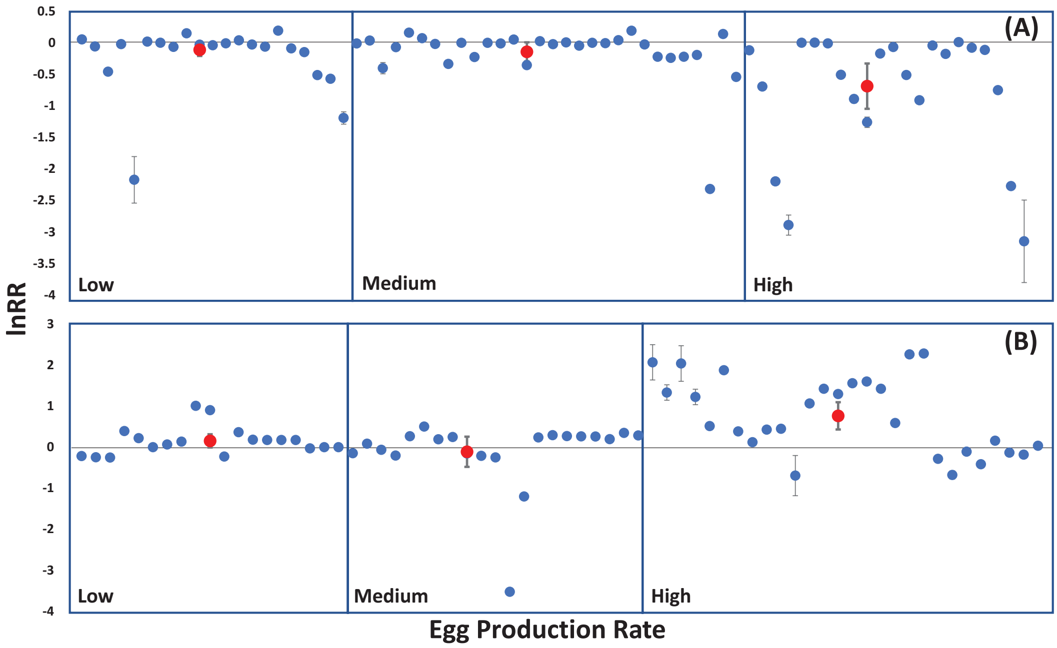

Figure 6 Copepod hatching success as a function of acidification (A) and warming (B). Mean response ratio and 95% confidence intervals are grouped by average egg production rates (eggs female^{-1}day^{-1}) of the species (< 10, 10–20, and >20 eggs female^{-1}day^{-1}, respectively). Each blue dot is an effect size calculated for a single study, and red dots represent the overall effect size at different egg production rates.

Discussion

Substantial changes in the pH and temperature of the oceans are among the primary threats predicted to affect marine life at a global scale. Empirical evidence suggests that marine organisms will likely undergo rapid phenotypic changes (e.g. increasing metabolic rates, decreasing body size) in response to OA and OW (Kroeker et al. 2013). Although these changes potentially involve important functional and genetic trade-offs (Gaitán-Espitia et al. 2017a), they provide a mechanism to ameliorate the negative effects of OW and OA on fitness, increasing either their survival or the survival of their progeny. As a consequence, phenotypic changes and the associated trade-offs driven by OA and OW are expected to influence dynamics in natural populations and communities, with profound ecosystem-level effects. Here, we show that OA and OW can drive varied phenotypic responses that are conditioned to some extent by the habitat, life-history traits and the phylogeny of a species. Therefore, we elucidate the importance of incorporating environmental and evolutionary histories into predictions of how species will respond to OA and OW.

Our study focusses on traits including reproductive output, survival and energy intake to identify the effects of OA and OW copepods. While we undertook an in-depth analysis using these traits, our study may be limited by some factors: (1) we did not include all traits under “life history” and “physiology”; therefore, our study does not encompass all copepod traits that have been analysed under OA and OW; (2) our study focusses on adult copepods and did not analyse the effects of OA and OW on development and different nauplii and copepodite stages; and (3) we did not include genetic analyses in the meta-analysis. Although our study may lack analysis of some traits, considering meta-analyses may generalize overall effects, we believe we have undertaken thorough analyses to identify the effects of OA and OW as single stressors on the copepod traits included in our study.

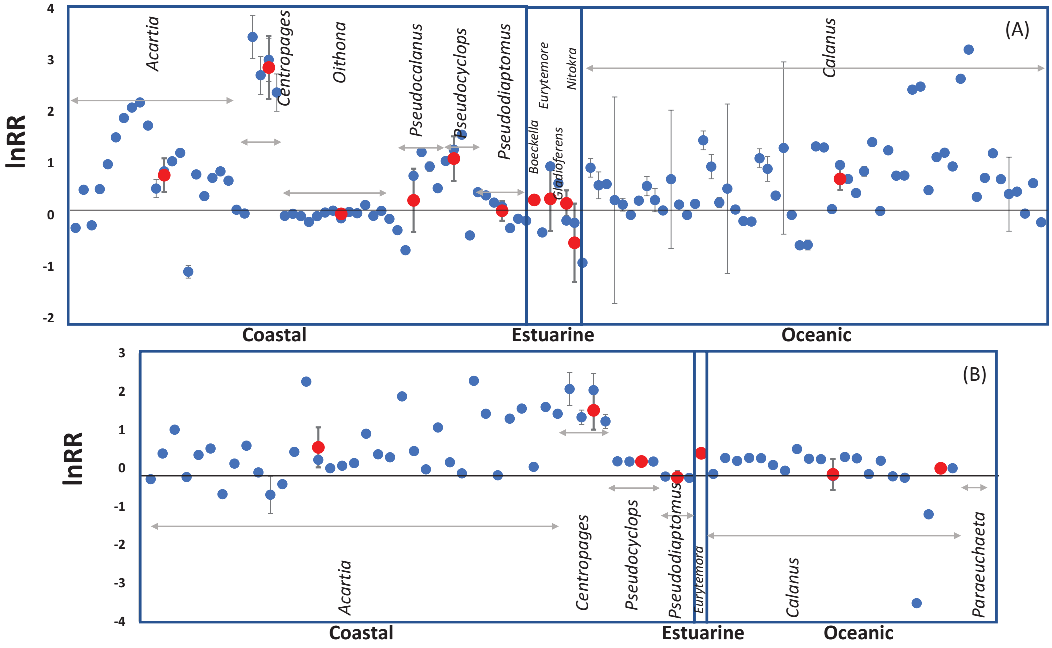

Figure 7 Copepod (A) egg production and (B) hatching as a function of warming. Mean response ratio and 95% confidence intervals are grouped by copepod genus and habitat based on known areas occupied by the species. Arrows indicate the different effect sizes for each genus. Each blue dot is an effect size calculated for a single study. Red dots represent the overall effect size for the genus.

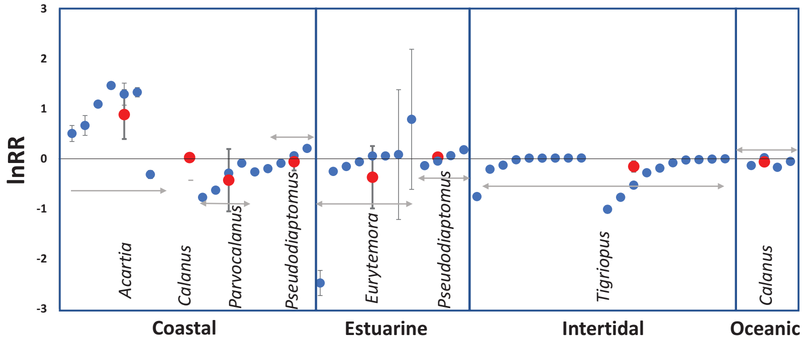

Figure 8 Copepod survival as a function of warming. Mean response ratio and 95% confidence intervals are grouped by copepod genus and habitat based on known areas occupied by the species. Each blue dot is an effect size calculated for a single study. Red dots represent the overall effect size for the genus.

OA and OW as drivers of phenotypic change in copepods

Heterogeneity in phenotypic responses of marine organisms to OA and OW can be influenced by intrinsic features of the species such as reproductive performance, maternal effects and fecundity (He et al. 2016). While several studies have evaluated the role of maternal effects in the performance of copepods across different environments (Jónasdóttir & Kiørboe 1996, Lacoste et al. 2001, Auel 2004, Ianora et al. 2004, Rodríguez-Graña et al. 2010, He et al. 2016, 2020) and experimental conditions (Thor & Dupont 2015, Preziosi et al. 2017), few have directly tested maternal effects in the climate change context (Vehmaa et al. 2012, Cripps et al. 2014, Thor et al. 2018). Maternal

Table 4 Weighted random effect models and meta-regressions comparing the hatching success as a function of egg production rates (low, medium and high) of copepods exposed to ocean acidification and warming

Statistical model	Ocean acidification					Ocean warming				
Weighed random effect model per egg production category	δ	CI_{low}	CI_{high}	P		δ	CI_{low}	CI_{high}	P	
Low	–0.11	–0.207	–0.013	0.027	*	0.154	–0.008	0.315	0.062	
Medium	–0.142	–0.293	0.009	0.066		–0.112	–0.48	0.257	0.552	
High	–0.686	–1.046	–0.326	<0.001	***	0.763	0.433	1.092	<0.001	***
Meta-regression	**d.f**	*Q*	*P*			**d.f**	*Q*	*P*		
Egg production category	2	11.615	0.003	**		2	16.836	<0.001	***	
Spawning mode	1	0.224	0.636			1	1.45	0.229		
pH										
	1	3.085	0.079							
Temperature										
						1	3.0842	0.05		

Abbreviations: δ, overall effect size; CI, 95% confidence interval; *P*, *p*-value; d.f, degrees of freedom; *Q*, regression coefficient. * denotes a statistically significant result (* $p<0.05$, ** $p<0.01$, *** $p<0.001$).

investment is defined by the balance in energy and resource allocated to either offspring numbers or offspring quality, whereby offspring production by mothers in generally inversely correlated to per offspring investment (Marshall et al. 2006). In invertebrates such as copepods, optimum reproductive investment often involves trade-offs between egg size or quality, and the number of eggs produced which can change depending on factors including food availability, predator avoidance or environmental conditions (Poulin 1995, Bjærke et al. 2016, He et al. 2016).

Here, we evaluated the extent to which fecundity, physiology, performance and fitness (e.g. reproductive effort, survival) are influenced by OA and OW. We found that OA decreases fecundity and survival in the majority of copepod species, a response that is aligned to the negative effects documented for physiological traits. It is well known that OA affects organismal physiology by deviating ion equilibrium, thus influencing changes in intracellular acid–base balance (Pörtner 2008, Melzner et al. 2009) and affecting various cellular processes, including enzyme activity, metabolism and protein synthesis. As a result, functioning of different tissues is altered, and energy homeostasis is affected, which can lead to trade-offs between fitness-related traits and maintaining vital functions (Pörtner 2008, Hofmann & Togdham 2010). Thus, the overall phenotypic effects of OA are conditioned by the ability of different organisms to regulate their cellular acid–base equilibrium and manage energy homeostasis. For copepods, the reduction in fecundity and survival caused by OA may be linked to a change in antioxidant enzyme activity and protein synthesis (Lee et al. 2019, Zhang et al. 2016). Despite this mechanistic understanding of the effects of OA on physiology, survival and fecundity, it is important to highlight that the level (e.g. small vs. large change in pH) and duration of exposure can contribute to the level of phenotypic responses documented (Pörtner 2008). For instance, we found no significant overall effect of OA on copepods at pH over 7.7 (estimated end of century OA) and even at pH over 7. This confirms the findings of Runge et al. (2016). Thus, acute exposure at more extreme OA levels (lower pH) can substantially affect physiology and survival, whereas minor changes in pH can fall within a species' tolerance windows. However, exposure to minor OA over prolonged periods (weeks or months) may have adverse biological and population-level effects (Pörtner 2008). While it is not known exactly why copepods show such resistance to OA, studies suggest that their ability to regulate their physiology under OA may provide higher adaptability (Engström-Öst et al. 2019, 2020)

In contrast to OA, OW causes a significant increase in most of the physiological processes such as metabolism, protein synthesis and enzyme activity (Brown et al. 2004). These, in turn, regulate systemic processes and, therefore, influence variations in biological traits (Pörtner & Farrell 2008). For example, temperature-induced change in metabolic rates can ultimately control life-history traits, behaviour and phenology (Brown & Sibly 2006, Sponaugle et al. 2006, O'Connor et al. 2009). Our observation of increased egg production and hatching success under warming conditions is aligned with the predicted increase in biological activity due to rising temperature (Brown et al. 2004). In our analysis, positive effect sizes are likely derivative of increased physiological rates which lead to higher fecundity with increased temperature. This increase in copepod fecundity across a large temperature gradient has previously been demonstrated (Bunker & Hirst 2004, Peck et al. 2015). On the other hand, negative effect sizes may denote the response of organisms beyond their thermal tolerance limits, whereby fecundity is severely impacted. This indicates that, under warming conditions alone, copepod fecundity will likely increase until temperatures surpass species- or population-specific tolerance limits. Therefore, like in other ectotherms, raising ocean temperatures that fall within the thermal tolerance window of marine copepods are likely to cause an increase in fecundity under climate change. Simplistic predictions on the effects of OW and OA which take a narrow view of characteristics must, however, be viewed with caution. For example, it is well established that intrinsic characteristics of marine organisms such as body size, life-history stage and evolutionary history can differentially influence responses to climate change (Pörtner & Knust 2007, Dupont et al., 2010, Hofmann & Todgham 2010, Sorte et al. 2011; Byrne and Przeslawski 2013, Reusch 2014). Similarly, extrinsic factors such as the level and duration of exposure to environmental stress (Ishimatsu et al. 2008), the rate of environmental change (Hoffmann & Sgrò 2011, Silbiger & Sorte 2018), the degree of environmental variability (Eriander et al. 2016) and the differences in environmental conditions between regions and habitats (Boyd et al. 2015) can also play an important role in determining the phenotypic responses of marine organisms to OA and OW.

Do local habitat characteristics influence phenotypic responses to OA and OW?

Coastal and oceanic landscapes are characterised by mosaics of environmental conditions that influence the biology, ecology and evolution of marine organisms (Pittman 2017). While there is some evidence of responses of copepods to both OA and OW, our results revealed that this is not a general rule for all species. Significant heterogeneity in phenotypic responses have been documented within the same habitats. This phenotypic variability might be explained by the differences in the level of environmental variation experienced in the same type of habitat in different geographic regions (Vargas et al. 2017). The particular seascape characteristics (e.g. coastal/submarine ridges; river discharges, fjords) of each habitat is therefore an important factor influencing within- and among-habitats differences in phenotypic responses of copepods. For example, the egg production of *Acartia tonsa* is less affected by OA in populations from coastal waters in proximity to an estuarine system with highly variable pH compared to populations residing further from the estuarine system where pH tends to be more stable (Aguilera at al. 2013). Similarly, different populations of *Calanus glacialis* from Kongsfjord, Billefjord and Disko Bay respond differently to pH changes whereby those from Disko Bay may be pre-conditioned to natural pH variation in their environment (Thor et al. 2018). Finally, comparison of heat tolerance in populations of intertidal copepods revealed inter-population variation, indicating that the genetic basis for selection was different among populations (Kelly et al. 2012; 2013). Such differences among populations suggest that environmental history plays an important role in influencing local adaptation and the phenotypic responses of copepods to OA and OW (Berg et al. 2010, Vargas et al. 2017, Donelson et al. 2018). For copepods, however, inter-population discrepancies in response to OA and OW based on environmental history remain understudied.

Another potential confounding factor in the overall phenotypic responses of marine organisms to climate change is the latitudinal distribution of populations and species (e.g. Gaitán-Espitia 2017a,b). Latitudinal gradients are characterised by clines in SST, aragonite saturation and CO_2 solubility that have important implications in biological characteristics of marine organisms and their susceptibility to climate change (Fabry et al. 2009, Leong et al. 2018). In fact, phenotypic traits of copepods are known to vary across latitudes (Brun et al. 2016). For example, latitudinal variation in diapause egg production (Marcus 1984), growth rates (Lonsdale & Levinton 1985), body size (Brun et al. 2016) and thermal tolerance (Pereira et al. 2017) has been documented for diverse copepod taxa. These are associated with the different thermal regimens experienced by species and populations across latitudes. Despite this biological trend, here we found that phenotypic effects of increasing SST due to OW are not influenced by latitudinal distribution. This finding could be driven by the limited number of studies exploring the effects of OW on tropical species compared to studies on temperate species. Similarly, to OW, the effects of OA on biological traits, with the exception of survival, were independent of latitude. Higher survival in copepods at lower latitudes under OA conditions may be an indirect result of the influence of higher temperatures on physiological rates, performance and fitness. However, there are some thresholds for these beneficial effects because stressful conditions induced by the interaction of OA and OW have marked negative effects on marine organisms (Harvey et al. 2013, Kroeker et al. 2013).

Is body size a good predictor of copepod's susceptibility to OA and OW?

It is well established that body mass is a key determinant of physiological rates (Kolokotrones et al. 2010, Carey and Sigwart 2014), evidenced by a scaling relationship in which these rates change parallel with body mass changes (Gillooly et al. 2001, Kolokotrones et al. 2010). This scaling relationship is temperature dependent (Gillooly et al 2001), and thus, physiological changes induced by OW and OA are expected to be conditioned by body mass or size. It is often observed that metabolic costs (difference in metabolic rate) are lower in large than small organisms for the same activity or across similar changes in environmental parameters (Carey & Sigwart 2014, Carey et al. 2016). Because of this, body mass is usually incorporated as a predictor of species and community responses to environmental stress and climate change (Mccain & King 2014, Lefort et al. 2015). Copepods generally conform size variation across temperature and latitudinal clines (Evans et al. 2020), as well as to metabolic scaling whereby metabolic rates and energy acquisition increase with body mass (Ikeda et al. 2001, Saiz & Calbet 2007). However, in our analysis we did not find evidence of the influence of body size on the heterogeneity of phenotypic responses of biological traits to OA and OW in copepods. One potential explanation of this finding is the range of body size that characterise the studied copepods (prosome length ranging 0.31–4.55 mm) may affect the resolution of the influence of this trait on physiological responses to environmental stress and climate change, therefore rendering precise comparison of physiological costs difficult. Moreover, our study showed that phylogenetic relationships are influential on trait response to OW. Therefore, investigating metabolic scaling within populations of the same species or of closely related species may provide more accurate estimation of the effects of OA and OW on the relationship between body size and metabolic rates. In addition to body size influencing the effects of OA and OW, body size itself can be affected by OA and OW. For example, OW can cause reductions in copepod prosome size in larval and adult stages (Garzke et al. 2015) while a combination of OA and OW can have antagonistic effects on copepod body size (Garzke et al. 2016). Moreover, moulting through nauplii and copepodite stages are positively dependent on temperature, while the intermoult somatic growth is more dependent on other factors such as food concentration (Peterson 2001). Such variation in size may result from compensation mechanisms to limit other physiological costs from environmental change, thus regulating changes in physiological rates and energy demands.

Do phylogenetic relationships matter for the assessment of phenotypic responses to OA and OW?

The evolutionary history of organisms defines variation in phenotypic traits and responses to climate change because closely related species share similar characteristics compared to distantly related species (Felsenstein 1985). Thus, comparative assessments of the phylogenetic signals in the phenotypic responses of copepods to OA and OW can provide insights and predictive tools to infer how different species will respond to future climate change. One important finding of our study is that phylogenetic relationships partially influenced the response of copepods to OA, but more substantial influences were found for OW. For example, egg production of *Acartia steuri* and *A. tonsa* was significantly affected by OA, followed by *Centropages typicus*. While *Acartia steuri* and *A. tonsa* are very closely related species, *Centropages typicus* is not closely related to the latter two, yet also showed more drastic effects of OA. Therefore, although there is some phylogenetic signal explaining the heterogeneity of responses to OA, it seems that the major physiological costs are broadly shared among species independent, to some extent, of the evolutionary history. As for OW, the genera *Acartia* and *Centropages* demonstrated larger positive response to OW, while the hatching success of the *Pseudocyclops* and *Calanus* changed the least. On the other hand, *Pseudodiaptomus* copepods responded negatively to OW. The differences in response among species and genera are likely due non-independence in the evolution of physiological tolerances and sensitivities to changes in environmental temperature (i.e. closely related species have evolved similar thermal tolerances compared to distantly related species). For example, in the genus *Calanus*, copepods undertake deep diel migrations and therefore are exposed to great variations in temperature and pH (Svetlichny et al. 2000, Maps et al. 2011), while *Acartia* species do not undertake such deep diel migrations (Kouassi et al. 2001, Holliland et al. 2012). Moreover, direct comparison of two species with different modes of life (migrator vs. non-migrator; *Calanus* spp. vs. *Oithona similis*, respectively) within the same habitat showed that species may have different sensitivities to OA based on their exposure (Lewis et al. 2013). These behavioural traits are the result of the interactions between evolutionary and ecological processes that have shaped the feeding strategies and population dynamics of different species along the water column (Lampert 1989, Ohman 1990, Hays 2003).

Overall, here we highlight that the phenotypic cost to OA is partially influenced by the evolutionary history but more importantly by the environmental history. The low phylogenetic signal yet high heterogeneity suggests that the majority of physiological costs are shared among species independent of their phylogenetic relationship and largely explained by other biotic/abiotic factors. On the other hand, the phenotypic response to OW is linked to thermal tolerance which is widely documented to have a deep relationship with the evolutionary history of the species (Kellermann et al. 2012, Grigg & Buckley 2013, Comte & Olden 2017). These findings suggest that more accurate predictions of the response to OA and OW may be obtained by integrating the influence of both the evolutionary and environmental history of the species.

Conclusions

Fine-scale analysis of the response of copepods to climate change revealed that the effects of OA and OW differ drastically. While OA has a negative influence on most biological traits, the effects of OW tend align with predicted hormesis trend in biological activity with temperature increase. Under future OA levels only, unless copepods develop adaptive responses, they will likely experience decreases in biological traits, thus affecting their population demographics. Such changes in populations will also lead to negative community- and ecosystem-wide effects. On the other hand, under ocean warming conditions alone, it seems that copepod biological traits will likely increase until temperatures surpass the different tolerance limits of different species. Interestingly, habitat, latitude and body size were only partially influential on the effects of OA and OW on copepods. On the other hand, the phylogenetic relationship partially influenced the response of copepods to OA but more substantially the effects of OW. While OA and OW independently have contrasting effects on copepod biological traits, their future effects will occur concurrently and, therefore, interact. While we analysed the effects of OA and OW independently, other studies suggest that their combined effects on copepod traits can be additive, antagonistic or synergistic, therefore, highly complex with varying interactions between species and the level of change in pH or temperature within the habitats (e.g. Vehmaa et al. 2012, 2013, Hildebrandt et al. 2014, Preziosi et al. 2017, Garzke et al. 2020). Therefore, our findings point to the importance of species- and population-specific environmental history, mode of life and evolutionary history in defining the overall effects of OA and OW on copepod biological traits. More importantly, these findings reveal that assuming general trends in the response of copepods to climate change based on few traits and single habitat or species could be extremely misguiding.

Finally, while we analysed the effects of OA and OW on phenotypic responses, genetic adaptations will perpetually play a major role in copepod response to these conditions. However, relatively fewer studies have fully examined the changes in genetic pathway leading to adaptations in copepods. Some of the genetic mechanisms that have been found to be involved in the response of copepod to OA include upregulation of genetic pathways to increase ribosomal function, ion transport, oxidative phosphorylation, DNA repair, redox regulation, protein folding and proteolysis (De Wit et al. 2016, Bailey et al. 2017). As for the response to OW, major pathways that are upregulated include cellular and metabolic processes, catalytic activities, genetic information processing, ubiquitination and proteolysis (Schoville et al. 2012, Ramos et al. 2015, Semmouri et al. 2019). While these studies point out some of the genetic pathways involved in responding to OA and OW, there is still a significant lack of understanding on how these will be involved in defining genetic adaptations in different species and populations of copepods.

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THE NATURE AND ECOLOGICAL SIGNIFICANCE OF EPIFAUNAL COMMUNITIES WITHIN MARINE ECOSYSTEMS

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Abstract As the rate of global change increases, the structure and functioning of marine ecosystems, including the food webs that underpin them, will radically alter. Forecasting the consequences of these changes requires a sound understanding of the fundamental components of marine food webs: their community composition, baseline biomass and productivity. Epifauna, a term restricted here to small invertebrates (both mobile and sessile) that inhabit living and non-living surfaces within marine ecosystems, are a ubiquitous and pivotal component of marine food webs, supporting the flow of energy through marine ecosystems and providing a critical trophic link between benthic primary producers and higher-order consumers. Yet, despite their importance, epifauna are rarely studied compared to the more visible and gregarious components of marine ecosystems. They are also typically neglected in management strategies for the protection of marine habitats. In addition, the plethora of alternative terms used within this research field (macrobenthos, cryptofauna, epibiont, mesograzer) can be a barrier to understanding and assimilating existing research knowledge. This review provides an assessment of epifaunal communities studied within tropical, subtropical and temperate marine ecosystems globally. We first review alternative terms used to describe marine epifaunal communities, with the aim of offering a consensus-based definition of epifauna as an aid for unifying different research areas. We then review the primary literature on epifauna, including the scarce information on tropical marine habitats. We outline how a detailed understanding of epifaunal communities within individual habitats is needed to predict how benthic food webs will alter under global change. While epifauna can persist under degraded habitat conditions, changes to taxonomic composition can fundamentally affect secondary productivity, and impact higher-order consumers through changes in prey size-spectra and foraging habitats. Finally, we issue a “call-to-arms” for increased focus on the study of epifauna, given their potential to underpin critical aspects of marine ecosystem functioning. We highlight the potential for eDNA sampling, other new technologies, and monitoring by citizen scientists to facilitate the use of epifaunal community metrics, including incorporation into marine ecosystem planning.

Keywords: Climate Change; Epibiota; Epifauna; Ecosystem Functioning; Marine Food Web; Mobile Invertebrates; Sessile Invertebrates

Introduction

Marine ecosystems are facing severe disruption through habitat and biodiversity loss caused by human activities, including interactions with climate (Ives & Carpenter 2007, Wernberg et al. 2013, Tuya et al. 2016, Miloslavich et al. 2018, Smale et al. 2019). The fundamental knowledge required

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to best support and manage ecosystems includes accurate information on trophic flows – the processes by which energy is transferred through the food web. Yet detailed examination of several critical trophic flows has been neglected in literature on marine ecosystem functioning (Bellwood et al. 2004, Mouillot et al. 2014, Brandl et al. 2016, although see Nagelkerken et al. 2020 for an exception). The biomass and secondary productivity of the direct consumers of primary production represent important metrics of ecosystem health and can be used to evaluate various aspects of ecosystem dynamics, the impacts of environmental change, and relationships between biodiversity and ecosystem functioning (Taylor 1998a, Burkepile & Hay 2008, Dolbeth et al. 2012).

In many marine ecosystems, these critical secondary consumers are dominated by epifaunal communities (Edgar 1994, Taylor 1998a, Cowles et al. 2009). Epifauna is a collective term given to the small, mobile or sessile invertebrates, here defined as <10 mm in body length, which are common to all marine habitats, especially within the living canopy of other organisms such as macroalgae, corals and seagrasses (Edgar & Klumpp 2003, Witman et al. 2004, Fraser et al. 2020a). Their extreme abundances and rapid turnover rates mean that they play a key role in supporting the flow of energy through marine ecosystems (Newcombe & Taylor 2010, Wenger et al. 2018, Fulton et al. 2019). As an essential element in the marine food web, epifauna are therefore a critical trophic link between benthic primary producers and higher-order consumers such as carnivorous invertebrates and fish species, many of which are the targets of fisheries. Epifauna have high levels of secondary production that can represent up to 75% of the total annual secondary production within a habitat – sufficient to support large populations of macroinvertebrates and fishes that consume them (Edgar & Aoki 1993, Taylor 1998a, Kramer et al. 2015). Yet despite their ubiquity and their importance in underpinning marine food webs and ecosystem functioning, epifauna are a relatively poorly studied component of marine habitats (Gan et al. 2019, Chen et al. 2020, Fraser et al. 2020a). Three main reasons account for this: (1) their inconspicuousness compared to vertebrate and invertebrate macro- and mega-fauna (i.e. individuals >10 mm long); (2) the difficulty of quantitatively sampling epifaunal communities within structurally diverse habitats, and associated processing challenges related to their tiny body size and cryptic behaviour (Edgar 1990b, Taylor 1998a, Kramer et al. 2012); (3) the difficulty of providing high taxonomic resolution when quantifying and describing the constituent organisms within epifaunal samples, due to a lack of taxonomic specialists (Edgar 1990b, Edgar 1994, Taylor 1998a, Cowles et al. 2009). As a result, our understanding of the ecological importance of epifaunal communities in marine ecosystems is far from complete. As potentially one of the largest contributors to production of higher-order consumers, we are therefore unable to accurately estimate the bottom-up consequences of changes in primary productivity for overall structure and function of many marine ecosystems. Moreover, to our knowledge, the nature and role of epifaunal communities in marine ecosystems has not been systematically mapped in the past 20 years.

Here we summarize investigations of marine epifaunal communities to date. We begin with a seemingly trivial question: what are epifauna? Answering this question, however, proves to be a non-trivial task due to a Pandora's box of definitional issues and challenges. In order to resolve these challenges, we argue that rationalisation of nomenclature is needed within the field, and that researchers should provide key details of the organisms studied to facilitate future comparative analyses. We set out some minimum definitional criteria that would aid in this regard. Based on a systematic mapping of the literature, we then summarise geographic and habitat trends among investigations of epifaunal communities (as opposed to studies on single species of epifauna) to date and highlight major gaps in our understanding. We then present some of the existing knowledge of temporal and spatial fluctuations in epifaunal community structure, with a focus on tropical ecosystems, and discuss the potential responses of epifaunal communities to disturbance events, including those associated with anthropogenically driven climate change. Finally, our review issues a "call-to-arms" for an increased focus within the scientific community on the ecology of epifaunal communities: their composition, size-structure, productivity, population dynamics, and interactions with other biota and environmental stressors, given their critical contribution to the integrity of trophic flows under conditions of global change.

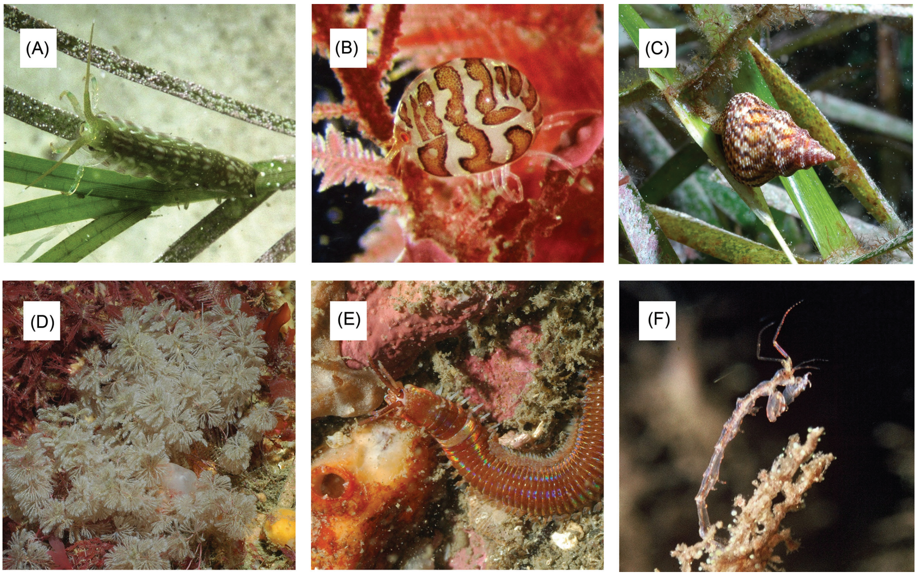

Figure 1 Representative taxa commonly found within samples of marine epifauna. (A) Isopod (*Euidotea* sp.). (B) Amphipod (*Cyproidea* sp.). (C) Gastropod (*Prothalotia lehmanni*). (D) Bryozoan. (E) Polychaete (*Eunice* sp.). (F) Caprellid amphipod (*Caprella* sp.).

What are epifauna – a taxonomic definition?

On one level, defining marine epifauna as a list of taxonomic components that are typically studied – orders, classes, subclasses, and genera of organisms – is straightforward (Figure 1). Nevertheless, the taxonomic range within epifaunal communities is bewildering. Mobile epifauna contain groups of Arthropoda, especially Crustacea (e.g. isopods, amphipods, tanaidaceans, cumaceans and other peracarids, as well as copepods, ostracods and small decapods), Mollusca (chiefly gastropods, bivalves and chitons), and also Polychaeta, Echinodermata (ophiuroids, echinoids, asteroids, crinoids, holothurioids), Platyhelminthes, Nematoda, Nemertea and Foraminifera. Sessile epifauna contain groups within the Arthropoda (e.g. barnacles), Polychaeta (e.g. serpulids), Cnidaria, Porifera, Tunicata and Bryozoa. The purpose of this review is not to present the taxonomic details or listings of all organisms classified as marine epifauna, rather our focus is at the collective level of the community and its functional role.

Community-level nomenclature challenges

Moving on from a taxonomic view of epifauna, challenges arise when defining the community at the collective level. The term "epifauna" is perhaps best defined by etymology: "epi" from the Ancient Greek "on top of", and "fauna" from the Late Latin for "collection of animal life present in a particular place or time". The Oxford English Dictionary thus defines epifauna as, "animals living on the surface of the seabed or a riverbed, or attached to submerged objects or aquatic animals or plants". Marine benthic communities essentially divide into two categories based on whether those organisms are found "on" (epifauna) or "within" (infauna and endofauna) substrates. Infauna live buried in seafloor sediments or riverbeds, while endofauna bore into solid structures such as coral reefs or the skeletons of marine organisms (Figure 2A).

As uncontroversial as this definition of epifauna might seem, challenges nevertheless arise when undertaking a review of the topic, due to the use of alternative terminology to refer either to the same or similar groups of organisms within marine ecosystems. For example, many studies limit their

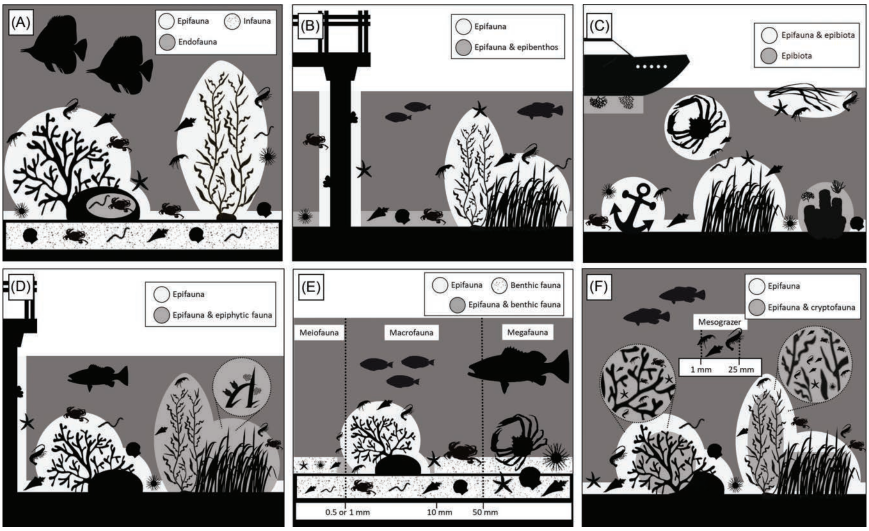

Figure 2 Conceptual representation of the relationship between terms used interchangeably within the literature to refer to epifaunal organisms and highlighting of the distinctions between such terms under a strict definitional approach. (A) The distinction between marine epifauna and infauna (including endofauna). (B) The relationship between epifauna and epibenthos. (C) The relationship between epifauna and epibiota. (D) The relationship between epifauna and epiphytic fauna. (E) The relationship between epifauna and macrofauna/macrobenthos. (F) The distinction between epifauna, cryptofauna and mesograzers.

classification of epifauna to mobile taxa only (Edgar 1990a, Martin-Smith 1993, Viejo & Åberg 2003, Arponen & Boström 2012, Bedini et al. 2014, Tano et al. 2016, Wee et al. 2019, Fraser et al. 2020a), whereas others include sessile organisms such as sea anemones, bryozoans and ascidians in their definition of epifauna (Shin 1981; Fowler & Laffoley 1993, Bradshaw et al. 2003, Hepburn et al. 2006, Demers et al. 2016, Kaiser et al. 2018). For reasons of historical legacy (the fact that most of the early studies of epifauna were based in temperate, deep sea habitats), some will think only of sessile, primarily planktivorous, invertebrates when using the term epifauna. Most researchers limit their classification of epifauna to invertebrate communities, but some include vertebrates such as small (<10 cm), benthic-dwelling fishes (Viejo 1999, Hovel et al. 2002). Others use the term in its broadest sense to refer to any organism living on the surface of another, for example Buckle & Harris (1980) used the term "epifauna" to refer to the community of fleas living on a red fox (*Vulpes* vulpes). At the same time, some authors that studied epifauna may have also studied small plants/algae (i.e. not just fauna) and may have used the broader term "epibiota" to include both small animals and plants/algae living on top of substrata (Johnston et al. 2011, Marzinelli et al. 2011, 2012, Clark et al. 2015). A search of the literature relating just to "epifauna" may therefore miss some such studies.

By contrast, depending on the sampling method used or the particular research question asked, some investigators do not use the term at all, even though their study organisms fall under the classification of epifauna (Baden 1990, Irving et al. 2007, Stella et al. 2011, Kramer et al. 2012, Ellis et al. 2013, Kramer et al. 2014, Kramer et al. 2015, Kramer et al. 2017, Nakamoto et al. 2018). Alternative terms fall into one of two categories: (1) terms that might be considered close synonyms in that they represent some form of overlap with the term epifauna (e.g. epibenthic fauna, epibenthos, epibiota) (Table 1) and (2) terms that, strictly speaking, have a different meaning to "epifauna", in terms of either the size of organism they refer to, the broader class of organisms included, or the differential habitat niche that they reference (e.g. macrobenthos, cryptofauna) (Table 1). This diversity of terms has little parallel with the floral equivalent term "epiphyte", which is widely used for organisms growing on seagrasses or macroalgae.

Table 1 Summary of synonyms and alternative terms used within the scientific literature to refer to epifaunal organisms within marine ecosystems, including a commonly accepted definition of the term within the marine context, and examples used in the literature

Nomenclature	Definition and relationship to the term "epifauna"	Examples
Epifauna nomenclature		
Epibenthic fauna/epibenthos/ epibenthic assemblage/ epibenthic invertebrate/ epibenthic community/ epibenthic macrofauna	Epibenthic fauna are those organisms that live on or just above the bottom substrate in a body of water. Although "epibenthic" is often used interchangeably with "epifauna", epibenthos should be considered a smaller subset of epifauna, as it refers only to animals on the bottom substrate (or benthos), as opposed to animals on any type of surface (upright and benthic) within a given habitat (Figure 2B)	Howard (1985), Kaiser et al. (1994), Edgar & Shaw (1995), Prena et al. (1999), Cocito et al. (2000), Cohen et al. (2000), Ellis et al. (2000), Jennings et al. (2001a), Zühlke et al. (2001), Callaway et al. (2002a,b), Koch & Wolff (2002), Stachowicz et al. (2002), Colloca et al. (2003), Polte et al. (2005a,b), Hosack et al. (2006), Walker et al. (2007), Nagelkerken et al. (2008), Neumann et al. (2008, 2017), Wilkie et al. (2012), Brandt et al. (2013), Gribben et al. (2013), Michaelis et al. (2019a,b), González-García et al. (2020), Proudfoot et al. (2020)
Epibionts/epibiota/epibiotic invertebrate/epibiotic organism/ epibiotic community	Strictly speaking, an epibiont refers to an organism living on the surface of another *living* organism, although there can be different interpretations in common usage (see text above). For example, many studies may use the broader term "epibiota" to include both small animals and plants/seaweeds living on top of substrata (live or inert) The term "epibiota" therefore could refer to epifauna when animal groups are included but in this case should exclude phytal communities (Figure 2C)	Daniel & Robertson (1990), Hopkinson et al. (1991), Nalesso et al. (1995), Connell & Anderson (1999), Glasby (1998, 1999a–c, 2000), Bradshaw et al. (2003), Wernberg et al. (2004), Schmidt & Scheibling (2006), Harries et al. (2007), Summerhayes et al. (2009), Johnston et al. (2011), Marzinelli et al. (2011, 2012), Byers et al. (2012), Gribben et al. (2013), Blake et al. (2014), Clark et al. (2015), Cúrdia et al. (2015), Arnold et al. (2016), Gribben et al. (2017), Kniesz et al. (2018), Powell et al. (2019), Ledbetter & Hovel (2020)
Epiphytic fauna/epiphytic organism/epiphytic macrofauna/epiphytic community/epiphytal fauna/ epiphytal arthropod assemblage	Epiphytes in marine systems – as distinct from terrestrial epiphytes – are species of algae, bacteria, fungi, sponges, bryozoans, ascidians, protozoa, crustaceans, molluscs and any other *sessile* organism that grow on the surfaces of marine macrophytes. The term should therefore be considered a smaller subset of epifauna (i.e. referring just to the subset of non-mobile epifauna that are found on living surfaces, although common usage can sometimes extend to mobile organisms within these classifications living on plant surfaces) (Figure 2D)	Cancino et al. (1987), Anderson et al. (1991), Russo (1991), Nakaoka et al. (2001), Schmidt & Scheibling (2006), Hirst (2007), Popadić et al. (2013), Chen et al. (2015), Belattmania et al. (2018a,b), Jacobucci et al. (2019)

(*Continued*)

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Nomenclature	Definition and relationship to the term "epifauna"	Examples
Related terms		
Macrobenthos/macrobenthic invertebrate/macrobenthic community/macrobenthic fauna	Organisms living on, in or near the benthic substrate that are greater than 1 mm in size (in some classification systems > 0.5 mm). Macrobenthos are therefore defined by their size *and* habitat. As in the case of "epibenthos", macrobenthic organisms are essentially a subset of epifauna that excludes animals living on macrophytes or artificial structures, although infauna are also sometimes included (Figure 2E)	McDonald (1983), Lana & Guiss (1991), Migné & Davoult (1995), Kühne & Rachor (1996), Wright et al. (1997), Flynn et al. (1998), Gage et al. (2000), Thrush et al. (2001), Smith & Rule (2002), Pagliosa & Lana (2005), Jing et al. (2007), McKinnon et al. (2009), Tang & Kristensen (2010), Sokołowski et al. (2015), Zharikov & Lysenko (2016), Hossain (2019)
Macrofauna/macroepifauna/macro-epibenthic fauna	Macrofauna are classified as organisms that are 1–50 mm in size. (>0.5 mm in some classifications). The term "macrofauna" makes no presumption of location of the animal and can refer to infaunal organisms, e.g. those living within marine sediments (Figure 2E), unless specified as macro-epibenthic	Webb & Parsons (1991), Jean & Hilly (1994), Ellis et al. (1996), Russo (1997), Bologna & Heck (1999), Hovel et al. (2002), Tanaka & Leite (2003), O'Brien et al. (2006), Garcia et al. (2008), Kon et al. (2011), Leopardas et al. (2014), Ge et al. (2020)
Benthic community/benthic faunal assemblage/benthic macrofauna/benthic invertebrate/benthic organism	Community of organisms that live on, in or near the seabed (the benthic zone). These are typically invertebrates and will include mobile and sessile organisms, and can include organisms > 50 mm, for example sea anemones, sponges, corals, sea stars, sea urchins. Therefore, likely to include a much larger set of organisms than just "epifauna", unless the study refers to a specific size range within the benthic faunal assemblage that would exclude animals not considered to be epifauna (e.g. large sea stars) (Figure 2E)	Howard (1985), Edgar (1990b), Aller & Stupakoff (1996), Aller (1997), Collie et al. (1997), Engel & Kvitek (1998), Jewett et al. (1999), Dumbauld et al. (2001), Jennings et al. (2001b), Sfriso et al. (2001), Edgar & Barrett (2002), Witman et al. (2004, 2008), Osman & Whitlatch (2004), Kon et al. (2010), Pagliosa et al. (2012), Broszeit et al. (2013), Riera et al. (2013), Leopardas et al. (2014), Lambert et al. (2017), Henseler et al. (2019), Yeager et al. (2019), Noble-James et al. (2020)
Mesograzer/mesoherbivore/epifaunal mesograzer	The term "mesograzer" is chiefly used to describe small benthic herbivorous invertebrates that live and feed on their macrophytal hosts (e.g. macroalgae, seagrasses). They are generally less than 25 mm in length, and can include juveniles of some larger species. The term "mesograzer" therefore refers to just a single trophic component of epifauna (the herbivorous component) and tends to include a larger size range of organisms than might typically be thought of under a strict definition of epifauna (Figure 2F)	Viejo & Arrontes (1992), Schaffelke et al. (1995), Hay (1997), Ruesink (2000), Taylor et al. (2003), Dick et al. (2005), Jaschinski & Sommer (2008), Best & Stachowicz (2012), Berthelsen & Taylor (2014), Martínez-Crego et al. (2015), Campbell et al. (2018)

(*Continued*)

Table 1 (*Continued*) Summary of synonyms and alternative terms used within the scientific literature to refer to epifaunal organisms within marine ecosystems, including a commonly accepted definition of the term within the marine context, and examples used in the literature

Nomenclature	Definition and relationship to the term "epifauna"	Examples
Phytal fauna	"Phytal" from the term coined by Remane (1933) to denote a third main habitat in the marine environment as distinct from benthic and pelagic. Phytal refers to areas with major vegetation as well as sessile animal growths (e.g. hydroids, corals and bryozoans). Phytal fauna typically refers to motile animals living on macrophytes. Can include organisms belonging to meiofaunal size classes (nematodes, copepods, ostracods and mites), but excludes sessile organisms (e.g. bryozoans, foraminiferans, sponges, sedentary polychaetes, bivalve molluscs and brachiopods). This term has tended to fall out of common usage	Moore (1981), Edgar (1983), Zander et al. (2015)
Cryptobenthos/cryptofauna/cryptic epifauna/cryptic invertebrate	The term "cryptofauna" strictly refers to animals concealed within a microhabitat or within intra- and inter-skeletal voids formed by framework structures, although the term is also commonly used to refer to cryptobenthic fishes such as gobies and blennies that inhabit branches of corals. Cryptofauna would therefore be considered distinct from epifauna by virtue of their different microhabitat usage (Figure 2F)	Fishelson & Haran (1986), Todd & Turner (1986), Baden (1990), Enochs (2012), Kramer et al. (2012)
Fouling community/fouling organism	Fouling communities are assemblages of fauna and flora found on artificial substrates, commonly comprised of sessile organisms such as ascidians, bryozoans, sponges and barnacles. They can have negative economic impacts (e.g. block fishing nets and cages, damage boats and buoys, increase hydrodynamic volume and hydrodynamic friction of a vessel which leads to more fuel consumption). This term tends to include a range of organisms in terms of both size (can be megafauna) and taxonomy (can be algae) than "epifauna"	Walker et al. (2007), Osman et al. (2010), Johnston et al. (2011), Karlson & Osman (2012), Marzinelli et al. (2012), Fernandez-Gonzalez & Sanchez-Jerez (2017), Carmen & Grunden (2019)

The use of multiple terms for epifaunal communities has been a persistent feature of the field from its inception and continues to challenge researchers when attempting to synthesize the literature (Table 1). A summary of the alternative descriptions of epifauna within the field highlights the absence of any strong temporal trends in usage of particular terms, other than potentially a decline in the use of "epiphytic", as the teaching of Latin in schools decreases and scholars lose their childhood links to Latin nomenclature. In most cases, although the terms are indeed linked to the definition of epifauna, they are not strict synonyms and instead represent either a smaller subset of the epifaunal community (e.g. for terms excluding fauna on vertical living surfaces) or a larger group of organisms that include algae and/or animals that typically would not be considered epifauna (e.g. spider crabs, sponges and sea-stars greater in size than 50 mm) (Table 1). In addition, we note that terminology provided here is not exhaustive and excludes terms that appear relatively infrequently (e.g. "suprabenthos", Cartes et al. 2002; "macroscopic epifauna", Saarinen et al. 2018; "meio-epifaunal community", Raes & Vanreusel 2005; "macrozoobenthic fauna", de Jong et al. 2015; "zoobenthic community", Davidson 2005), or that represent organisms that are generally not considered part of the epifaunal community, as in the case of "megabenthos" (Diaz et al. 2004, Kenchington et al. 2007), "megabenthic" (Ramos 1999), or "mega-epifauna" (Du Preez et al. 2016), where the epithet "mega" would typically only be applied to organisms greater than 50 mm.

A primary challenge therefore in synthesising the existing literature on marine epifaunal communities and in carrying out a review of the topic is a lack of consensus in the application of the term "epifauna". What size class of organisms is included? Is the term restricted to invertebrate classes or does it include small vertebrates? Is the epifaunal community composed only of sessile organisms, or mobile organisms, or both? In many cases, the use of one particular term over another relates to the methods used to obtain samples for the study and the level of precision afforded by those methods. The most commonly used quantitative sampling methods for epifauna are: underwater visual survey, towed gear sampling, vacuum or suction sampling, core sampling, full-enclosure sampling, and light traps (Table 2). For example, sampling by towed gears will usually result in the collection of all benthic fauna, including megafauna, as well as some infaunal samples. A researcher using this sampling method is unlikely to be able to distinguish between cryptofauna and epifauna and it is arguable as to whether the distinction between the two is even important, depending on the research question. However, even in those cases where the study aims do not require a distinction to be made (e.g. in cases where habitat or trophic specificity is unimportant), it is important that nomenclature be used consistently. To this end, we advocate for the careful and precise application of terminology at the community level, based on the lexicon presented in Table 1. Where distinctions between particular parts of the community are important, for example where it is critical to exclude animals living on macrophytes or artificial structures, or to distinguish between the epifaunal community as a whole and those animals living just on benthic surfaces within a particular habitat (the epibenthos or macrobenthos), then the different terms must persist. However, where such distinctions are unimportant, use of the broader term "epifauna" could lend cohesion. For example, although not a redundant distinction, viewed from the perspective of community function, how important is it to distinguish between sessile (epiphytal fauna) and motile epifauna? Undoubtedly there will still be the need, on occasion, to differentiate between the two, making it unlikely that terms can drop out of use completely. However, consideration should certainly be given to elimination of redundant terms: those cases where alternative terms have the same definitional meaning (e.g. benthic community/benthic faunal assemblage/benthic macrofauna). This kind of rationalisation would have the benefit of making the literature more accessible to those new to the field and of facilitating future comparative analyses. At the same time, provision of clear hypotheses, descriptions of sampling methods used, and sufficient detail with respect to key traits of the organisms included in sampling will aid in future comparative studies and meta-analyses to be conducted on the literature within this field.

Table 2 Summary of techniques most commonly used for collecting quantitative samples of epifauna

Sampling method	Description	Examples
Underwater visual survey	This underwater observation is usually applied for epifauna, macrobenthic fauna (e.g. sponges, sea stars, scallops) or megafauna which can be detected by eye. *In situ* photos and/or videos of epifauna are taken by SCUBA divers or ROVs (remotely operated vehicle)	Collie et al. (2000a), Kollmann & Stachowitsch (2001), Valente (2006), Hughes (2014), Zharikov & Lysenko (2016), Michaelis et al. (2019a,b), Lopez-Garrido et al. (2020)
Towed gear sampling	This method usually involves collections of macrofauna on the benthic substrata with coarse mesh size (e.g. >10 mm), conducted by towed gears such as dredge sleds, research vessels or fishing vessels	Jean & Hilly (1994), Kaiser et al. (1994), Prena et al. (1999), Hamazaki et al. (2005), Kenchington et al. (2006), Lange & Griffiths (2014), Piras et al. (2016)
Vacuum/suction sampling	This sampling is conducted by using an underwater vacuum or suction sampler. Epifauna are directly taken from the sediments or structurally simple habitats such as turf algae and EAM (epilithic algal matrix). A fine filter (e.g. 0.05 mm mesh size) is attached to retain particles for further processing	Taylor et al. (1995), Taylor (1998a,b), Roberts & Poore (2006), Cowles et al. (2009), Kramer et al. (2012), Berthelsen & Taylor (2014), Fraser et al. (2020a)
Core sampling	Cores are used for collecting the fine, soft bottom sediments (e.g. <0.5 mm particle size) with associated epifauna. After extraction from the core, epifauna are usually sorted by sieves that fractionise these core samples by mesh size	Webb & Parsons (1991), Parker et al. (2001), Thrush et al. (2001), Commito et al. (2008), Norkko et al. (2010), Smeulders et al. (2014), Rosli et al. (2016)
Enclosure sampling	This sampling method is chiefly for harvesting epifauna from marine macrophytes (e.g. macroalgae, seagrasses). It involves using bags to fully enclose the whole plant before detaching the plant from the benthic substrata. Bags are then immediately sealed to prevent epifauna from escaping from macrophytal canopies. Harvested plants with associated epifauna are size-fractionated by using a series of nested sieves with different mesh size (proposed by Edgar 1990b)	Baden (1990), Edgar & Aoki (1993), Jernakoff & Nielsen (1998), Gartner et al. (2010), Tuya et al. (2014), Tano et al. (2016), Chen et al. (2020)
Light trap	This is an emerging technique in the sampling of benthic fauna including epifauna, although it has been more typically used for sampling of plankton, fish larvae and pelagic fauna. It involves using light sources to attract organisms with minimal damage of habitats and specimens	Holmes & O'Connor, (1988), Cohen & Oakley (2017), Costello et al. (2017), McLeod & Costello (2017)

Methods for systematic mapping of the term epifauna within primary literature

In order to map the use of the term "epifauna" and the contexts in which the term has been applied and defined, we conducted a search of the peer-reviewed scientific literature using ISI Web of Science. All research articles (in English only) published between 1953 and July 2020 including the terms "epifauna" or "epifaunal" in their research titles, abstracts, keywords and/or keyword plus, were included to establish a broad initial search. This initial search yielded a total of 2632 potential papers. We then refined the results using the Web of Science "categories" function in order to exclude studies from terrestrial and freshwater habitats, or those with a non-biological focus. Specifically, we excluded studies listed under the following categories: geology, limnology, engineering, paleontology, biotechnology and microbiology. This process resulted in a total of 1780 studies. We also excluded studies conducted in polar (Arctic and Antarctic) marine ecosystems to focus on tropical, subtropical and temperate zones that share more similar habitat conditions, environmental factors and economic/fishery value. For inclusion in the final database, we then applied the following criteria to each paper: (1) studies that used the term epifauna on three or fewer occasions in the main text, or where the term epifauna was used only in the Discussion were excluded as not having sufficient focus on the biological or ecological role of epifauna; (2) studies where the term epifauna was used less than 10 times were screened to confirm that the aims of the study did indeed relate to the ecology of this group; (3) papers where the title and/or abstract revealed that the study did not lie within the relevant scope of this review (i.e. epifaunal communities) for example where the study focused on a single species within the epifaunal community. In order to confirm no omission of significant studies in the field and to ensure we had encompassed the synonyms and related terms detailed in Table 1, we conducted a second scan with cross-checks using the search strings “macrobenth*”, “macrofaun*” and “cryoptofaun*” in combination with “epi*” (with the exception of “mesograzer”, unless the authors also used the term epifauna in their abstract or keywords). From this cross-check and refinement process we identified 993 studies of the biology and ecology of marine epifaunal communities (Appendix A). All searches and study assessments were done by a single observer (Y-Y.C). At the end of the screening process, this observer re-assessed the first 20% of studies in order to check for consistency in the application of the refinement criteria (1–3 above) over the assessment period. Of these re-assessed studies, only one was differently categorized in the repeat exercise.

For each study within our final database, we recorded the following details: (1) date of publication; (2) the geographic region in which the study was performed, with regions categorized by latitude (tropical: 0°± 23.5°; subtropical: 23.5°–35°; temperate: 35°–66.5° excluding studies within the Antarctic Polar Front; Arctic and Antarctic studies are therefore not included in this review); (3) nomenclature used to describe epifauna, with synonyms (if presented); (4) the size range of animals classed as epifauna within the study; and (5) the habitat(s) in which the study was conducted (Appendix B).

Development of the field and trends in the literature on marine epifauna

The field of marine epifaunal biology and ecology research grew at a steady pace in the 1970s and 1980s, predominantly via the work of researchers such as Moore and Seed (e.g. Seed & Boaden 1977, Moore 1981, and review by Seed & O’Connor 1981b). Moore’s initial work focused on epifaunal organisms occupying kelp holdfasts, where a major contribution highlighted habitat niche partitioning among epifaunal communities: showing that the organisms found on kelp holdfasts were predominantly of different trophic status to those on leaves and fronds (Moore 1972, 1977, 1981, McKenzie & Moore 1981). Later, Buchanan & Moore (1986) were among the first to investigate the effects of temperature on macrofaunal communities as part of a long-term monitoring program, showing that species diversity declined following cold winters for macrofaunal communities along the UK Northumberland coast. In the 1980s, the focus on epifaunal communities associated with macroalgal kelp continued with the work of Seed, whose contributions included documenting the epifauna found on kelp fronds from coastal intertidal habitats in the UK including Northern Ireland (Seed 1976, Seed & Harris, 1980, Seed et al. 1981) and Wales (Wood & Seed 1980, Seed & O’Connor 1981a, Oswald & Seed 1986). Much of this early work on epifauna was directed towards understanding community structure, the role of classical ecological processes (i.e. competition, predation) in shaping communities and recovery from disturbance events (e.g. Dauvin & Gentil 1990).

Epifaunal communities were found to possess a large component of species with rapid recolonisation rates (Edgar 1992, Martin-Smith 1994), including "demersal zooplankton" species that swim at night (Alldredge & King 1977, 1980, Hammer 1981).

A major broadening of studies of marine epifauna occurred in the 1980s and 1990s, with extended focus on temperate macroalgal habitats (Edgar 1983, Edgar & Moore 1986), seagrass (Heck & Whetstone 1977, Orth & Van Montfrans 1984, Orth et al. 1984, Edgar 1990a, Edgar & Robertson 1992, Heck et al. 1995) and standardized artificial marine habitats (Edgar 1991a,b) (Figure 3). This expansion was also marked by a fundamental shift in the focus of research on epifaunal communities, from descriptive studies interested in patterns to manipulative studies involving processes, particularly caging studies for assessing effects of predation (Heck & Orth 1980, Heck & Thoman 1981, Howard 1982, Van Montfrans et al. 1982, Robertson & Lucas 1983, Robertson & Lenanton 1984, Leber 1985), investigations of the critical functional role played by epifaunal grazers in reducing epiphyte loads on seagrasses and macroalgae (Howard 1982, Duffy 1990, Duffy & Hay 2000, Duffy & Harvilicz 2001, Duffy et al. 2001) and interactions involving algal chemical defences, epifauna and predatory fishes (Duffy & Hay 1990, 1991, 1994, Duffy & Paul 1992).

While most investigations to 2000 continued to contrast roles of predation, resource limitation and abiotic drivers, new empirical methods based on metabolic theory also allowed the productivity of marine epifaunal communities to be estimated (Robertson 1979, Banse & Mosher 1980, Edgar 1990b). This provided an altered perspective on epifauna, from use as a model system for understanding classic ecological principles to recognition of their value as a critical component of marine ecosystem processes (nutrient cycling and productivity flows) (Edgar 1992, 1993, 1994). Epifaunal communities of varying composition had varying abilities to support biomass of higher-order consumers, meaning that the ability of different habitats to support different levels of fish production could be linked back to the epifaunal communities they harboured (Edgar & Shaw 1995). One unexpected finding was that secondary production of shallow-water epifauna is extremely consistent and predictable worldwide (Edgar 1993, Edgar & Aoki 1993).

Despite these publications highlighting the importance of marine epifaunal communities in food webs and energy flows, and important subsequent contributions (Taylor 1998a,b, Taylor & Rees 1998, Glasby 1999a,b, 2000, 2001, Metcalfe & Glasby 2008), the increase in published studies within the field of epifauna lagged behind the overall growth in scientific literature in the new century. By 2010, the field fell well behind general growth in scientific publications; less than 200 papers were published on the topic of epifauna in the second half of the decade, compared to an expected number of 346 (Figure 3A). In the last five years, based on our search criteria (studies using the terms "epifauna" or "epifaunal" in their research titles, abstracts, keywords and/or keyword plus), only 215 studies have been published on the topic of marine epifauna, compared to an expectation of 748 (Figure 3A). The understudied nature of the field is clearly evident when research on marine epifauna is contrasted with publication rates in related fields such as the study of infauna, plankton and coral reefs, where a total of 603 (infauna), 3634 (plankton) and 8394 (corals) studies have been published in the last five years (Figure 3B).

A notable finding when conducting this review was that many authors provided no taxonomic definition of what constituted the epifauna category of animal (e.g. whether vertebrates were included), or biological or ecological traits of the animals (mobile only or inclusive of sessile organisms), or size range. In the extreme, this resulted in some cases where animals larger than 100 mm were classified as epifauna (e.g. Viejo 1999, Meyer et al. 2016). Of the 993 studies within our database, only 78 provided a definition of the size range of animals classified as epifauna within that study. Nearly 50% (485) provided no detail of the size of animals classified as epifauna within the study or recorded as part of the epifaunal community (Figure 4).

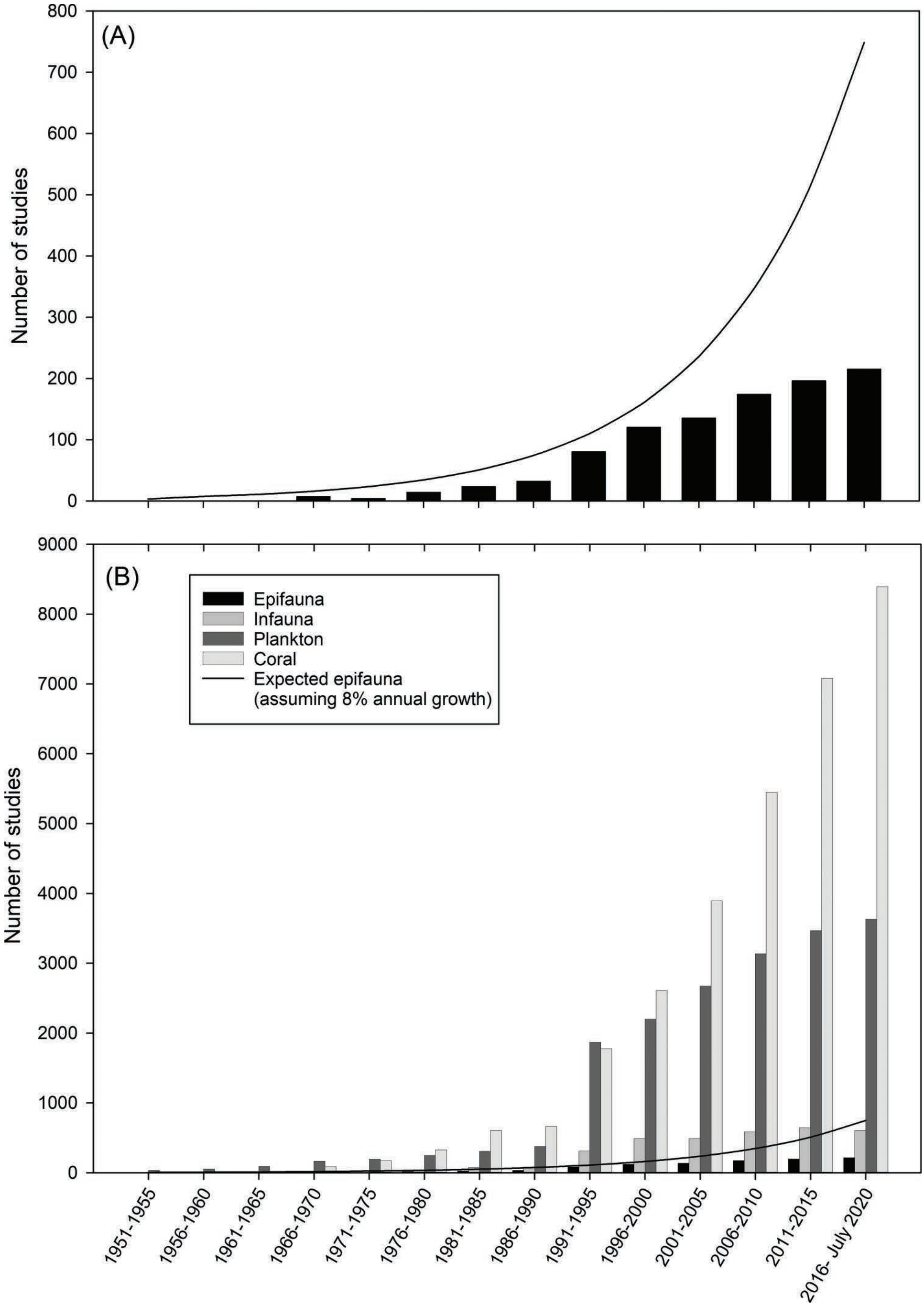

Figure 3 (A) Number of research articles on marine epifauna published within each half decade spanning the period (1950–2020) (grey bars), and expected growth across all scientific publications (black line) estimated by Bornmann & Mutz (2015) to be 8% p.a. (B) Growth in the published research on epifauna relative to related fields of "infauna", "plankton" and "corals". Results for epifauna research articles are based on a literature search conducted in the ISI Web of Science database in July 2020 using the terms "epifauna" and "epifaunal".

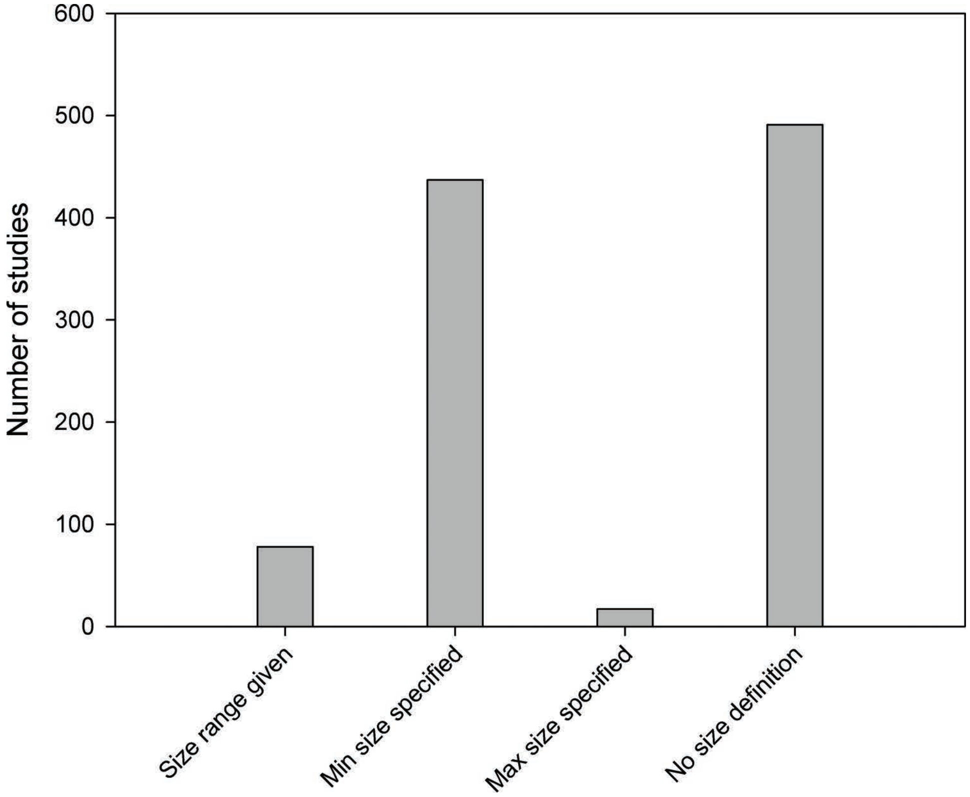

Figure 4 Number of studies within the published literature on marine epifauna that define epifaunal organisms according to their size within the publication text. Studies were assigned to one of the following four categories: (1) size range of animals defined; (2) only minimum size specified; (3) only maximum size specified; and (4) no size definition of epifauna given. Results are based on a literature search conducted in the ISI Web of Science database in July 2020 using the terms "epifauna" and "epifaunal".

Towards a unified framework for the study of epifauna within marine ecosystems

Based on the lexicon presented in Table 1, better precision is clearly needed when defining what is meant by an epifaunal community within a particular context, and when epifauna might be considered distinct from some of the terms that have previously been used synonymously. To resolve these issues, we suggest that researchers provide within their written methods section, at a minimum: (1) habitat sampled (e.g. seagrass bed, macroalgal meadow); (2) habitat niche, i.e. the precise nature or location of surfaces sampled (e.g. seagrass leaf blades, macroalgal thalli and leaves); (3) method of sampling; (4) organism size range; and (5) organism mobility. Non-essential, but potentially useful extra definitional elements could cover relevant biological and ecological traits of the target community such as taxonomic classes included; whether specific trophic levels are included or excluded; whether both living and artificial surfaces are included.

A majority of studies consider epifauna to refer only to invertebrates. However, excluding two animal classes (Osteichthyes and Chondrichthyes) has little phylogenetic or ecological validity. For example, small vertebrates such as gobiesocid clingfishes living attached to the surfaces of macrophytes exist within epifaunal communities and have overlap in functional roles with small shrimps and crabs. We therefore suggest that arbitrary taxonomic exclusions are not applied to "epifauna". Nevertheless, inclusion of larger cryptobenthic fishes such as gobies and blennies would be inconsistent with most views of epifauna, and a defined size range is needed. Recognition that epifaunal organisms are constrained within a defined size range would allow a distinct separation from the totality of marine macrobenthos and also be helpful in establishing the identity of the functional group of epifauna as a distinct entity. A summary of the size range of organisms considered "epifauna" for those studies within the scientific literature where a size range, a maximum size, or a minimum size are defined in the publication text indicates that most authors consider epifauna to be organisms between 0.5 and 10 mm in size (Figure 5).

Overall, within the "macrofauna", we therefore define epifaunal communities through general consensus as those animals, 0.5–10 mm in size (most usually, but not always invertebrates) found living on the surface of sediment, turf algae, marine macrophytal canopies, marine macrophytal rafts, other biogenic habitats and artificial structures. They usually, but not always, range freely over surfaces; sessile organisms such as bryozoans, ascidians and barnacles also fall within the definition when attached to surfaces and in the 0.5–10 mm size range (Figure 6). In terms of habitat niche, we consider that all surfaces (living and artificial) within marine habitats should be considered as hosting epifaunal communities. Artificial surfaces are explicitly included because their associated communities contribute in a similar way as natural surfaces to nutrient cycling, energy transfer and other ecosystem processes. Epifauna must live at the interface between microhabitat surfaces and water, excluding cryptofaunal organisms living within the intra- and inter-skeletal voids formed by framework structures (Figure 6).

Epifaunal communities may be composed of individuals belonging to multiple trophic levels, including herbivores, carnivores, detritivores and filter-feeders. Likewise, epifaunal communities which fall in the 0.5–10 mm size range can comprise assemblages with no distinction between different ontogenetic developmental stages such as adults, juveniles or larvae, since they are functionally serving the same role within that community. For example, juveniles of the bivalve scallop *Chlamys* (Pectinidae) may be found in seagrass meadows, where they attach to the leaves until they pass on

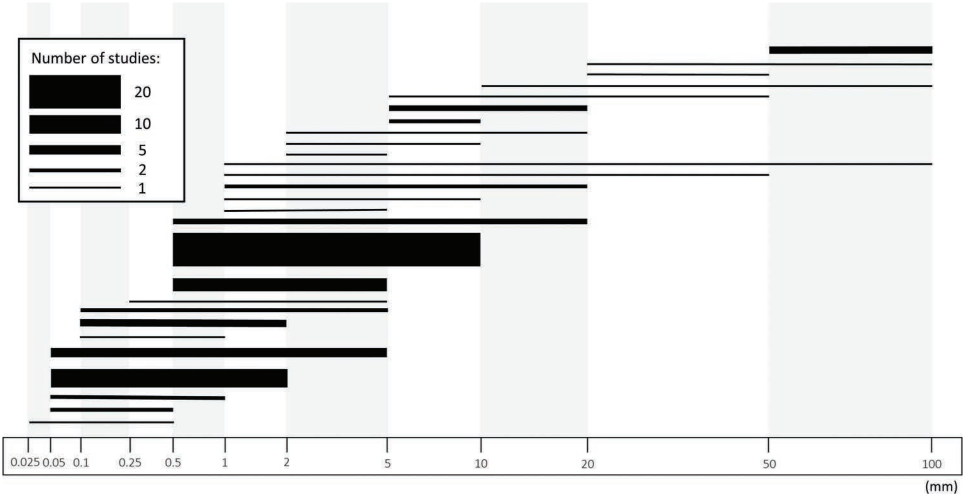

Figure 5 Summary of the size range of organisms considered as "epifauna" within the published scientific literature based on a search conducted in the ISI Web of Science database in July 2020 using the terms "epifauna" and "epifaunal". Data are presented only for those studies where a size range is defined in the publication text. Thickness of the bar for each size range represents the number of studies using that particular definition. Note that size (mm) on the *x*-axis is presented on an ordinal scale.

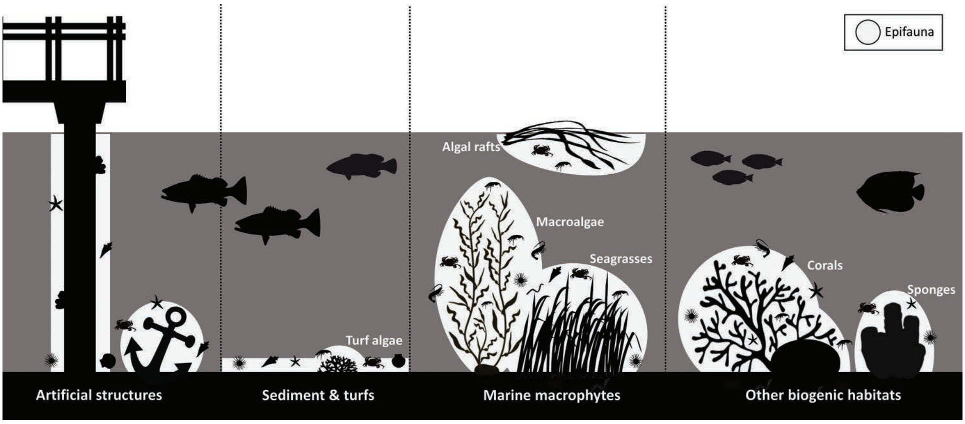

Figure 6 Schematic representation of the consensus view of marine epifaunal communities. The diagram shows the predominant living and non-living substrata on which epifauna are typically found within marine ecosystems.

to larger free-swimming stages. These juveniles would be classified as epifauna under our proposed consensus definition, given that they are functionally part of the surface-dwelling community.

Based on the lexicon presented in Table 1, the epifaunal community of a particular marine habitat is thus defined as

$$\text{epifauna} = \sum_{k=0.5\,\text{mm}}^{10\,\text{mm}} (\text{epibenthic fauna} + \text{epiphytic fauna}) - (\text{cryptofauna} + \text{infauna})$$

where a particular marine habitat contains no surfaces other than the benthos (i.e. no macrophytes or vertical structures) then the definition of epifauna above essentially collapses to that of “epibenthos” or “macrobenthos”, with the important distinction that epifauna fall within the size range of 0.5–10 mm, and are thus a smaller subset than the epibenthic/macrobenthic community, which could be taken to include organisms > 10 mm, for example sea anemones, sponges, corals, sea stars, and sea urchins.

The role of epifauna in marine ecosystem processes

Having established the scope of this review, we next address the question: why care about epifaunal communities? The answer primarily relates to the key roles of epifauna in marine ecosystem processes. Epifauna, by virtue of their ubiquity and abundance, are important contributors to two marine ecosystem processes: (1) they function as mediators between nutrients in the water column and microbes in the benthos, contributing to the biogeochemical cycling of carbon and nitrogen, and (2) they function in the transfer of energy along the marine food web via their role as secondary producers, connecting primary producers to higher-order consumers such as carnivorous invertebrates and invertivorous fishes (Edgar 1994, Taylor 1998a, Cowles et al. 2009, Newcombe & Taylor 2010, Wenger et al. 2018).

Epifauna as mediators within marine ecosystems

Depending on habitat, epifauna can contribute greatly to cycling of carbon, nitrogen and other nutrients between the water column and microbes in the benthos. Epifauna interact with microbes through multiple processes, including ecosystem engineering, grazing and symbiosis. Stief (2013) reviews how these interactions contribute to nitrogen retention, nitrogen removal, and ammonium and nitrous oxide emissions. The effects of ecosystem engineering occur predominantly through the influence of infauna on nitrogen cycling in marine sediments, rather than epifauna (see review by Herbert 1999). However, sessile epifauna can play a role in terms of providing an enlarged surface area for microbial colonisation, thereby increasing nitrogen recycling (Hepburn et al. 2012, Stief 2013). The ingestion of free-living and particle-attached bacteria by epifauna can, however, result in a decline in metabolic activity of grazing-sensitive bacteria and reduced nitrification activity. Nevertheless, epifaunal grazing on the microbes themselves is thought to have only small or neutral effects on nitrogen cycling overall (Stief 2013). Epifaunal processing of macrophytic detritus, on the other hand, contributes to the microbial-macrofaunal shredder loop (part of the microbial loop, *sensu* Azam et al. 1983, Fenchel 2008). Epifaunal grazers, such as amphipods in the genera *Gammarus* and *Allorchestes*, “shred” leaves and other particulate organic matter, breaking down macrophyte debris into finer fractions (Robertson & Lucas 1983, Robertson & Lenanton 1984). This process facilitates the remineralisation of nitrogen by microbes, making it available faster. For systems where phytoplankton and macrophytes are the dominant primary producers, this rapid regeneration of nitrogen can enhance primary production and ultimately increase the overall productivity of the ecosystem in terms of the biomass that can be supported (Taylor & Rees 1998, Hepburn et al. 2012, Stief 2013).

Epifauna as secondary producers: Quantifying the contribution to energy transfer within marine ecosystems

Epifauna also have a role as secondary producers in their own right. Secondary production by epifauna facilitates the flow of energy through the ecosystem from primary producers to higher-order consumers. Epifaunal secondary production is therefore one of the most important ecological parameters needed to understand population dynamics, trophic flow and environmental variability. Classical methods for estimating the secondary production of epifauna have been applied to individual species or to populations based on their change in body mass over time. Population production is then primarily a function of three major factors: (1) the metabolic rate–body size relationship of individuals, (2) the distribution of body sizes and (3) ambient temperature. However, even if these factors could be directly ascertained, getting an estimate of total production in this way is generally impractical because measurement of sizes of all individuals and determination of a body size–production relationship for each species is logistically challenging. Estimates of epifaunal secondary production at the community level are therefore relatively rare because of methodological and sampling difficulties.

Several empirical methods have been proposed to circumvent these challenges (reviewed in Dolbeth et al. 2012). These empirical models are chiefly based on multiple regression equations for production or the P/B ratio (P: secondary production, B: biomass) and include population characteristics (e.g. population biomass, metabolic rate, life span) as predictors and environmental parameters (e.g. water temperature, depth) as coefficients (Robertson 1979, Schwinghamer et al. 1986, Edgar 1990b, Brey 1990, 1999, 2001, Tumbiolo & Downing 1994, Cusson & Bourget 2005).

Biomass determinations are necessary for secondary production assessments, and ash-free dry weight (AFDW) provides arguably the best predictor for invertebrate biomass given that it minimizes issues dealing with heavy calcareous shells and gelatinous tissues. However, measuring AFDW requires the incineration of dried samples at high temperature (commonly 520°C), which can require long periods of time, significant research effort and the destruction of the sample. Several empirical models utilize conversion factors to convert wet weight (WW) or dry weight (DW) to AFDW (Ricciardi & Bourget 1998, Brey et al. 2010). Brey et al. (2010) build a global data bank of conversion factors in aquatic organisms. It covers ratios between body mass (i.e. WW, DW, AFDW), body composition (i.e. protein, carbohydrate, lipid), macro-elements (i.e. C, P, N) and energy content, making it much easier to estimate biomass and production of marine fauna.

Edgar's sieve method (1990b), Brey's general model (1990, 2001) and global data bank (2010) are some of the most commonly adopted models for quantifying secondary production and energy content. Edgar's sieve method entails pouring samples through a series of nested sieves with decreasing mesh size (8.0, 5.6, 4.0, 2.8, 2.0, 1.4, 1.0, 0.7 and 0.5 mm) and counting the number of individuals belonging to major morphological groups on each sieve (crustaceans, molluscs, polychaetes, platyhelminthes and caprellid amphipods). The latter are separated due to a propensity for their thin appendages to become entangled over coarser sieves, leading to potential overestimation of biomass. Total mean biomass (AFDW) of different functional groups retained by different-sized sieves can then be predicted based on known mean AFDW values of each sieve size. Associated allometric equations make it possible to estimate the productivity of epifauna at the assemblage level by predicting epifaunal secondary productivity as a function of body mass and water temperature. Error involved in predicting the productivity of individual species using this method can be high, but tends to cancel out in assemblage-level estimates (Edgar 1990b). This method has been widely adopted by subsequent investigators assessing benthic faunal secondary production in both temperate and tropical regions due to its tractability.

The nature and significance of epifaunal communities within marine habitats

In reviewing the published literature on epifauna, we found a strong Northern Hemisphere bias, with 73% of studies concentrating on marine habitats within the Northern Hemisphere (Figure 7). Of these Northern Hemisphere studies, 534 out of 778 (69%) focused on temperate marine habitats. Across both hemispheres, only 189 (17%) of published studies of marine epifauna considered tropical habitats (Figure 7). The neglect of tropical studies is not surprising: epifauna tend to be less abundant and conspicuous within tropical marine ecosystems, making them a much less "visible"

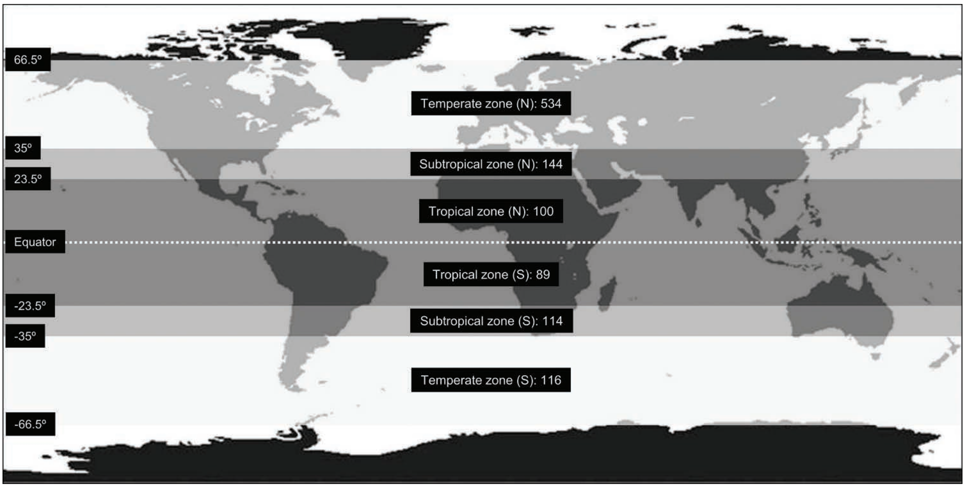

Figure 7 Number of studies within the published literature on marine epifaunal communities conducted within each latitudinal zone (tropical: 0°± 23.5°; subtropical: 23.5°–35°; temperate: 35°–66.5°) excluding polar (Arctic and Antarctic) zones. Numbers are based on a search conducted in ISI Web of Science database, up to and including July 2020, using the terms "epifauna" and "epifaunal". Note that the numbers here sum to 1097 (greater than the 993 studies listed in Appendix B) as some studies extend across more than one latitudinal zone.

component of the system. However, given that these tropical ecosystems account for almost half of the world's fish catches and that epifauna are a critical link in the food chain supporting such fisheries, the relative paucity of studies of epifauna within tropical marine habitats is a noteworthy gap in the existing literature. We advocate for a research emphasis on epifaunal communities within tropical habitats.

At the local scale, the nature of a community whose etymology relates to habitat surfaces necessarily links the community to that particular habitat. Thus, epifaunal communities in seagrass habitats, for example, are bound by definition to the nature and structure of seagrass canopies. Variation of epifaunal communities will be underpinned by variation in habitat type and quality across different locations. Recent evidence demonstrating that habitat is the most important correlate of variation in epifaunal assemblage has come from the work of Fraser et al. (2020a), who showed that reef-associated epifaunal assemblages varied significantly across 21 benthic microhabitat types sampled from temperate to tropical latitudes (28.6° latitudinal span), with much less variation according to latitude. Similarly, assemblage size distributions were much more affected by microhabitat type than latitude (Fraser et al. 2020b). In this section, we focus attention on the current status of knowledge of epifaunal communities in temperate and tropical latitudes across the two best studied habitats: seagrass meadows and macroalgal beds.

Seagrass meadows

Seagrasses are marine flowering plants that create key shallow-water habitats across all parts of the globe except Antarctica. Their dense canopies and associated deposition of organic matter in sediments provide food and shelter for a large community of organisms, including commercially important invertebrates and fishes. By forming extensive meadows connected with a mosaic of adjacent habitats, seagrasses are among the most productive marine ecosystems that supply ecosystem goods (e.g. maintenance of fisheries, supporting food security) and services (e.g. erosion control, coastal protection) to humanity.

Latitudinal differences in seagrass habitat structure exist, with temperate seagrass meadows typically monospecific (plus some macroalgae), while tropical meadows display greater habitat heterogeneity, with seagrass interspersed with corals, sponges and calcareous green algae (Virnstein et al. 1984, Duffy 2006). Seagrass habitats harbour abundant epifaunal invertebrates (Edgar 1990c, Nakamura & Sano 2005, Moore & Hovel 2010), such as gammarid amphipods and gastropods, which provide trophic pathways connecting seagrass primary production to larger invertebrates and carnivorous fishes. Epifaunal community composition and production is therefore an important metric for managers with responsibility for these habitats (Duffy 2006, Wong 2018).

Epifauna in seagrass beds have been more extensively studied than in coral, mangrove and algal turf habitats (Figure 8). In particular, the diversity and community structure of mobile and sessile epifauna within Neptune grass (*Posidonia* spp., dominant in the Mediterranean Sea), eelgrass (*Zostera* spp., globally widespread) and turtlegrass (*Thalassia* spp., chiefly distributed in Indo-Pacific and West Atlantic) meadows are relatively well documented (Virnstein et al. 1984, Knowles & Bell 1998, Sánchez-Jerez et al. 1999, Wong & Dowd 2015, Demers et al. 2016, McDonald et al. 2016, Tano et al. 2016, Boyé et al. 2017). Numerous published studies focus on plant–animal interactions and energy flows within seagrass meadows (Jernakoff & Nielsen 1998, Lepoint et al. 1999, Lewis & Anderson 2012, Hammerschlag-Peyer et al. 2013). Overall, seagrass systems are much less studied in the tropics (although see Ansari et al. 1991, Klumpp et al. 1992, Prieto et al. 2003, Unsworth et al. 2007, Leopardas & Nakaoka 2014, Tano et al. 2016, Cavalcante et al. 2019) than temperate latitudes (Hootsmans & Vermaat 1985, Edgar & Shaw 1995, Heck et al. 1995, Nakamura & Sano 2005, Polte et al. 2005a,b, Spivak et al. 2009, Gullström et al. 2012, Wong & Dowd 2015, Lefcheck & Duffy 2015, Lefcheck et al. 2016, Boyé et al. 2017, Wong 2018) or subtropical zones (Edgar 1990c, Connolly 1995, Lemmens et al. 1996, Jernakoff & Nielsen 1998, Alfaro 2006, Micheli et al. 2008,

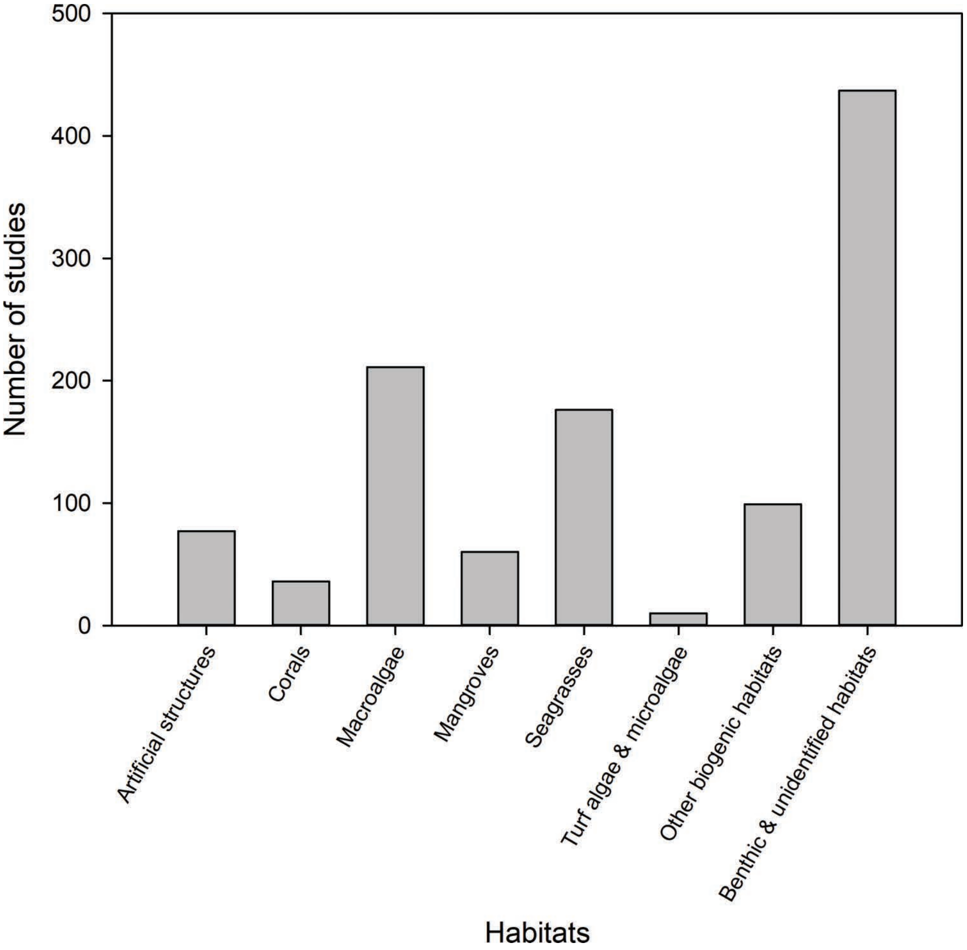

Figure 8 Number of studies conducted on epifaunal communities within particular marine habitats. Values are based on a search conducted in ISI Web of Science database in July 2020 using the terms "epifauna" and "epifaunal".

Lewis & Anderson 2012, Hammerschlag-Peyer et al. 2013, McDonald et al. 2016, Douglass et al. 2018, Ledbetter & Hovel 2020). Limited tropical evidence does, however, suggest that latitudinal influences are likely less significant than differences between epifaunal communities at the level of microhabitat structure (Fraser et al. 2020a).

The abundance, biomass and secondary production of epifaunal invertebrates is high in seagrass meadows and among canopy-forming macroalgae relative to marine habitats, including corals, mangroves and bare sediments, across tropical, subtropical and temperate zones (Edgar 1990c, Ansari et al. 1991, Heck et al. 1995, Connolly 1997, Nakamura & Sano 2005, Polte et al. 2005a,b, Alfaro 2006, Bologna 2006, Wong 2018). Tropical seagrass ecosystems tend to include a large component of sessile invertebrates such as sponges and ascidians (Duffy 2006). In general, epifaunal abundance, biomass and diversity are positively associated with seagrass canopy size in terms of above-ground biomass, rhizome density, percent cover (Connolly 1995, Gil et al. 2006, Meysick et al. 2019, Yeager et al. 2019), macrophytal complexity (Edgar & Robertson 1992, Nakamura & Sano 2005) and meadow patch size (Källén et al. 2012, Yeager et al. 2019). Ecological patterning appears regulated at various scales by multiple structural elements such as degree of patchiness or proximity to patch edges (Bologna & Heck 2002, Hovel et al. 2002, Healey & Hovel 2004, Tanner 2005, 2006, Moore & Hovel 2010).

Seagrass meadows around the world show strong seasonal patterns of growth and change in canopy structure. Seagrasses often exhibit summer growth as vertical and horizontal elongation of plants, followed by winter decay of above-ground blades (Marbà et al. 1996, Cebrián et al. 1997, Fourqurean et al. 2001, Metz et al. 2020). This results in strong seasonal variations in primary production that make seagrasses ephemeral hosts for epifauna attaching on their leaves. Such seasonal dynamics of seagrass canopies and primary production can significantly affect the distribution and abundance of epifauna, manifest as temporal fluctuations in epifaunal communities (Edgar 1990a, Gambi et al. 1992, Nakaoka et al. 2001, Kouchi et al. 2006).

Extensive losses of seagrass habitat have been reported from many coastal regions worldwide over the past decade, resulting in an overall annual decline of 7% globally (Waycott et al. 2009, Boström et al. 2011, Unsworth et al. 2018). These losses are predominantly due to anthropogenic activities (e.g. mooring, anchor damage, plant harvesting) and to climate-associated disturbances (Thomson et al. 2015, Hyndes et al. 2016). Such degradation and loss of seagrass habitats arising from multiple perturbations presumably affect epifaunal communities (i.e. abundance and diversity) over large scales, and the functions they provide (e.g. levels of secondary production) (Meysick et al. 2019, Tuya et al. 2019). In addition, loss and fragmentation of seagrass meadows result in significant declines in epifaunal diversity and abundance (Reed & Hovel 2006, Gustafsson & Salo 2012, Cadier & Frouws 2019, Githaiga et al. 2019), with potential implications for higher-order predators reliant on epifaunal production, and perturbations to food web structures. Nevertheless, some studies have shown the opposite response, with increases in epifaunal abundance following seagrass fragmentation (Tanner 2005, Arponen & Boström 2012), although this occurred in situations where the distance between fragments was low. Critical tipping points may thus exist, beyond which epifaunal communities will respond negatively to habitat disturbance. In addition, the net rate of decline in coverage of some seagrass species has slowed and even experienced a reversal in certain areas (for example, rates of coverage of *Posidonia* and *Zoster*a meadows in Europe). This has often been due to management interventions including improvement of water quality, reduction of industrial sewage discharge, and introduction of regulations governing anchoring and trawling. These reversals of seagrass habitat decline offer hope that associated ecosystem services, including the contribution to habitat quality by the epifaunal communities in terms of secondary production and food resources for invertivorous fishes within these meadows, can also recover (Vaudrey et al. 2010, Dolch et al. 2013, de los Santos et al. 2019).

Macroalgal meadows

Along with seagrasses, macroalgae rank among the most important contributors to global carbon and oxygen cycles in shallow marine environments (Hatcher 1990, Titlyanov & Titlyanova 2012, Unsworth et al. 2018). While seagrasses occupy soft sediment areas surrounding reefs, adjacent areas of hard pavement can be dominated by a great diversity of macroalgae, ranging from short algal turfs that form an epilithic algal matrix (EAM), to foliose understory macroalgae without canopies (e.g. *Dictyota* spp., *Padina* spp.), to fleshy canopy-forming laminarian (*Laminaria* spp.) and fucoid species (e.g. *Sargassum* spp., *Cystoseira* spp.) that attain heights over 1 m. In tropical marine ecosystems, macroalgal meadows have been estimated to cover 16–46% of shallow inshore habitats (Fulton et al. 2019).

Although macroalgae can be highly productive components of these ecosystems, they generally attract less attention than coral-dominated areas in coastal conservation and management (Fulton et al. 2019). Nevertheless, in clear tropical waters, macroalgae can produce up to 0.5 $kg{\cdot}C{\cdot}m^{-2}{\cdot}yr^{-1}$, suggesting that the net primary production of dense macroalgal communities within tropical marine ecosystems is as vital as the energy produced by corals (Hatcher 1990, Schaffelke & Klumpp 1997, Eidens et al. 2014). Notably, corals have tight symbiotic cycling of photosynthetic materials between the coral host and zooxanthellae, meaning that relatively low amounts of their net production become available to consumers (Hatcher 1990). The reverse is true for macroalgae, where the net production of primary biomass can be readily consumed by a range of invertebrate and vertebrate herbivores, aiding transfer of energy and nutrients to carnivores (Titlyanov & Titlyanova 2012, Fulton et al. 2019). In tropical macroalgal meadows, abundant and diverse epifauna are a key food resource, making macroalgal meadows important feeding sites for a large variety of reef fishes (Wilson et al. 2014, Tano et al. 2016, van Lier et al. 2018).

Macroalgae belonging to the genus *Sargassum* (family Sargassaceae) are dominant canopy-forming species globally. The large and dense meadows of *Sargassum* trap nutrients from sea water and contribute to high primary productivity within these habitats. They generally harbour abundant and diverse invertebrate assemblages through expanded surface area and complex canopy structure (Taylor & Cole 1994). *Sargassum* canopies host a broad biodiversity of epifaunal invertebrates that are targeted by carnivorous fishes (Edgar 1990b, Edgar & Aoki 1993, Tano et al. 2016). For example, gammarid amphipods, harpacticoid copepods, tanaidaceans, gastropods, bivalves, ophiuroids and polychaetes are common epifauna in the canopy-forming *Sargassum* meadows of Ningaloo Reef, Western Australia, where an individual *Sargassum* can host more than 6000 invertebrates, providing sufficient food for a large guild of higher-order predators (Wenger et al. 2018, Chen et al. 2020).

The biomass and canopy structure of *Sargassum* meadows fluctuate seasonally with sea temperature, influencing the biodiversity, abundance and trophodynamics of associated animals such as epifaunal invertebrates and reef fishes. While a basic knowledge of seasonal fluctuations in *Sargassum* biomass exists (Santelices 1977, Glenn et al. 1990, Trono & Lluisma 1990, Vuki & Price 1994, Schaffelke & Klumpp 1997, Leite & Turra 2003, Hwang et al. 2004, Tsai et al. 2004, Wong & Phang 2004, Ateweberhan et al. 2005, Ang 2006, Ateweberhan et al. 2006, 2008, 2009, Mattio et al. 2008, Lefevre & Bellwood 2010, Fulton et al. 2014, Wilson et al. 2014, Lim et al. 2016), we still have little understanding of how such fluctuations may influence the biodiversity of associated invertebrates, as well as trophic flows within tropical reef ecosystems. In temperate macroalgal meadows, seasonal fluctuations in epifaunal abundance and composition have been recorded (Edgar 1983, Taylor 1998b), with faunal densities reaching a peak in late summer and dropping to low levels in winter. In some cases, this pattern corresponds with seasonal variations in canopy size and shape structure (Edgar & Klumpp 2003, Ba-Akdah et al. 2016, Tano et al. 2016).

In highly productive tropical *Sargassum* meadows, epifaunal fluctuations can show typical annual cycles (Leite & Turra 2003, Ba-Akdah et al. 2016), with seasonality related to the growth and decay of the canopy, which in turn presumably responds to a variety of physical (e.g. light, sea temperature, wave action) and biological (e.g. food resource, competition, predation) drivers. Shifts in habitat availability and complexity can alter habitat area, food supply and/or niche availability for epifaunal different species, as well as influence the strength of biological interactions (e.g. predation, competition; Ledet et al. 2018, Wenger et al. 2018, Chen et al. 2020).

Moving from tropical to temperate macroalgal habitats, research has focused on the community structure and spatio-temporal variation of epifaunal communities associated with the habitat-forming fucoids *Cystoseira* (Fraschetti et al. 2002, Bedini et al. 2014, Casamajor et al. 2019) and *Laminaria* (Seed & Harris 1980, Schmidt & Scheibling 2006, Cacabelos et al. 2010, Tuya et al. 2011, Walls et al. 2016). *Laminaria*-associated epifauna have been particularly well studied in terms of their community structure, secondary production, contribution to energy flows, spatio-temporal variation, biological interactions and response to disturbances. Strong seasonality in these temperate marine environments will have the potential to trigger large trophic cascades associated with the temporal fluctuations in algal biomass. Understanding the responses of epifaunal communities to seasonal habitat changes within these important temperate marine ecosystems represents a key research priority.

The contribution of epifauna to seagrass and macroalgal "nurseries"

Notably, the roles described above of epifauna as contributing to the quality and quantity of food resources provided by seagrass and macroalgal meadows make them a contributor to the critical role meadows play in providing nursery habitats for juvenile reef fish species, including species that are key fisheries targets (Nagelkerken et al. 2000, Evans et al. 2014, Fulton et al. 2020). Nursery habitats can only be defined as such if their contribution to the adult population biomass is greater than the average production of all juvenile habitats (see Dahlgren et al. 2006, Nagelkerken 2009). Given this definition, high food abundance is likely to be one of the key contributing factors to making a particular area "nursery" habitat. This means that macroalgal-associated and seagrass-associated epifauna are fundamental to the development of fish nurseries and to the quality of that nursery habitat in terms of its nutritional load. Studies have shown, via use of stable isotopes and gut content analysis, that epifauna, in particular small crustaceans, are an important contributor to the diet of juvenile fishes within these habitats (de la Morinière et al. 2003) and that food availability is a key factor in attracting juvenile fishes to particular nursery sites (Verweij et al. 2006). In this sense, epifaunal communities associated with seagrass and macroalgal habitats are likely to be integral to the development of fish nurseries and, hence, to the life cycle of many commercially important reef fish species.

Effects of environmental disturbance on epifaunal communities

Although some studies have looked at the effects of natural disturbance events on epifaunal communities (such as typhoons, tsunamis and storm events (Posey et al. 1996, Roberts et al. 2007, Lomovasky et al. 2011, Salmo et al. 2019), coastal habitat alteration (such as marina operations (Turner et al. 1997), construction of pier pilings (on the artificial substrata *per se*, Glasby 1999a,b, or on macroalgae growing on pilings, Marzinelli et al. 2009, 2011) and coastal structures (Sedano et al. 2020) in the context of invasive species, or pollution (e.g. Johnston et al. 2011), investigations of effects of anthropogenic disturbance on epifauna have historically focused on impacts of fishing, including trawling and dredging (e.g. Hutchings 1990, Collie et al. 1997, Freese et al. 1999, Collie et al. 2000a,b, Rumohr & Kujawski 2000, Veale et al. 2000, Jennings et al. 2001a,b, Thrush et al. 2001, Gage et al. 2005, de Juan et al. 2007, 2011, de Juan & Demestre 2012, Strain et al. 2012). Together, these studies demonstrate high sensitivity of epifaunal communities to fishing, which can affect population size structure (Hinz et al. 2009), alter community composition (Hinz et al. 2009) and reduce the maximum size of organisms within the community (e.g. 17% reduction in mean size, Lambert et al. 2011), overall epifaunal biomass (Hinz et al. 2009, Lambert et al. 2011) and species richness. The focus on benthic habitat degradation via fishing methods continues to the present (e.g. Mangano et al. 2013, Lambert et al. 2017, Lundquist et al. 2018), although research on impacts of other environmental factors is expanding, such as shifts driven by eutrophication (Cebrian et al. 2014) and coastal acidification (Hossain 2019, Hossain et al. 2019), along with interactions between environmental factors and trawling effort (e.g. Couce et al. 2020).

Somewhat surprisingly, far fewer studies have investigated potential effects of climate change (e.g. pulse heatwaves, ocean warming, ocean acidification) on marine epifaunal communities. Only a handful of studies to date have considered likely changes in epifaunal community structure wrought by climate-related factors (e.g. Osman et al. 2010, Powell et al. 2019). Two studies have demonstrated the potential for experimental mesocosms to enhance our understanding of the effects of global change on epifauna. In a five-week study, Eklöf et al. (2015) tested the effect of temperature (ambient versus + 3.2°C), ocean acidification and simulated consumer loss (the omnivorous crustacean, *Gammarus locusta*), on the diversity and composition of macrofaunal communities in eelgrass (*Zostera marina*) beds. While acidification had little impact on macrofaunal communities over this relatively short study period, rapid warming and loss of consumer diversity led to an increase in macrofauna richness and abundance, but shifted the balance of organisms with particular life-history traits: warmer conditions favoured poorly defended epifaunal crustaceans such as tube-building amphipods and organisms that brooded their offspring.

The suggestion that epifaunal communities will be more affected by rapid warming than by rapid ocean acidification echoes the findings of Nagelkerken et al. (2020). In their mesocosm study, replicated benthic communities including primary producers (cyanobacteria and algae) and primary and secondary consumers typical of epibenthic communities (e.g. molluscs, copepods, polychaetes, fish) were established within 1800 L tanks and exposed to different temperature and acidification conditions. Alterations to food web structure, biomass and productivity under each scenario were documented. Food web structure was relatively unaffected by temperature and acidification, whereas biomass and productivity significantly changed. Secondary consumer biomass and productivity actually increased under combined warming and acidification, but primary consumption decreased. Over the longer term, this imbalance is obviously unsustainable and suggests that this particular climate scenario could ultimately see the system tip into a new stable state dominated by primary producers, with an associated reduction in the higher-order consumers, such as fish species that are the target of food fisheries (see Figure 1 in Chown 2020).

Managing the effects of environmental disturbance: The inextricable link to habitat

While the idea of “managing” organisms <10 mm in size may seem a somewhat sisyphean task, it is nevertheless a critical one. As described above, the inextricable link to habitat means that the task of “managing” epifaunal communities essentially reduces to managing marine habitats. Research findings clearly indicate that changes in habitat structural elements flow on to taxonomic changes in the epifaunal community (Taylor & Cole 1994). This is evident for macroalgal canopies (Chemello & Milazzo 2002, Marzinelli et al. 2009, 2011, 2012, 2016) and coral reefs (Stella et al. 2010, Kramer et al. 2014). The abundance, biomass and size structure of epifaunal communities can all vary with different structural aspects of the particular habitat (Edgar et al. 1994, Taylor 1998a,b, Kramer et al. 2014, 2017), meaning that any disturbance that causes a habitat change will also affect epifaunal community structure and function.

Potential drivers of structural changes to individual marine habitats and their associated epifaunal communities include marine heatwave events that induce loss of macroalgal canopy structure (Smale & Wernberg 2013, Wernberg et al. 2013, 2016), heat-induced coral bleaching events (Hughes et al. 2017), high-intensity cyclones (Salmo et al. 2019) or coastal development (Partyka & Peterson 2008, Blake et al. 2014, Callaway et al. 2020) (Figure 9). Changes in habitat structural characteristics could result in, for example, eutrophication-driven loss of parts of the seagrass canopy that leads to fragmentation of the remaining habitat (e.g. Waycott et al. 2009). Evidence for the effects of seagrass fragmentation on epifauna is currently somewhat equivocal, with some studies showing higher species richness in a number of small patches compared to a large patch of the same area (e.g. McNeill & Fairweather 1993, Eggleston et al. 1999, Reed & Hovel 2006), but with variable responses through time among individual taxa (Healey & Hovel 2004). Studies looking at edge effects on densities of epifauna in seagrass habitats have also yielded inconsistent results, with some showing positive effects (Bowden et al. 2001, Warry et al. 2009, Arponen & Boström 2012), some negative (Hovel & Lipcius 2002, Uhrin & Holmquist 2003) and some no effect (Connolly & Hindell

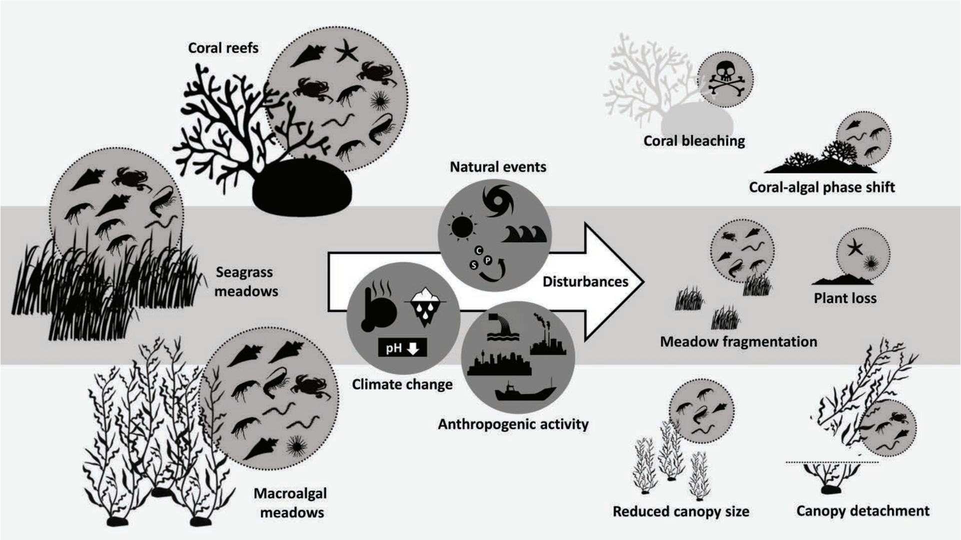

Figure 9 Potential impacts of disturbance events on the structure of three main marine habitats: coral reefs, seagrass meadows and macroalgal meadows, and the associated consequences for epifaunal communities associated with those microhabitats. Healthy habitats and their associated epifaunal communities are pictured on the left of the figure. Examples of disturbance events that could impact these habitats are given within centre grey circles, while the white arrow points in the direction of potential changes to habitat structure following such events. On the right-hand side of the figure, the altered habitat is shown, along with the potential impact on the epifaunal community.

2006). In reality, as Warry et al. (2009) point out, patchy landscapes will benefit certain taxa (e.g. harpacticoid copepods), but the net effect will ultimately be dependent on how patchiness came about, as well as patch size and distances between patches (Arponen & Boström 2012).

In other cases, disturbance events could set the ecosystem onto a new trajectory, with the habitat undergoing a phase shift and tipping into a new stable state (Holling 1973). For example, a thermal anomaly leading to a severe coral bleaching event that results in coral death and the overgrowth of dead skeleton by algal turf. Fraser et al. (2020a) found that live branching coral and turfing algae are host to significantly different epifaunal communities, meaning that as the ecosystem shifts from coral to turf following a bleaching event, invertebrate communities are likely to transform in predictable ways. We still, however, need to understand the implications of habitat change on ecosystem nutrient cycling and production levels. For each of the cases highlighted in Figure 9, knowledge gaps include whether the changes will lead to reduced or enhanced epifaunal abundance and biomass (and lower or higher secondary production levels, respectively), or sustained community abundance but altered biodiversity or size structure, and hence altered biomass and production.

The fact that minor changes in habitat structure might fundamentally alter a community of organisms almost too small for the eye to see is a powerful reminder of the need to consider all the potential consequences of environmental change, before they yield unforeseen consequences, including impacts on fisheries production and human food security. Thus, a better understanding of epifaunal assemblages in anthropogenically altered habitats should be seen as a research priority in the current era of rapid change in marine ecosystems. For example, we know that *Sargassum* meadows display temporal fluctuations in canopy structure (e.g. biomass, cover, canopy height) corresponding to variations in sea temperature (Glenn et al. 1990, Ateweberhan et al. 2006, Fulton

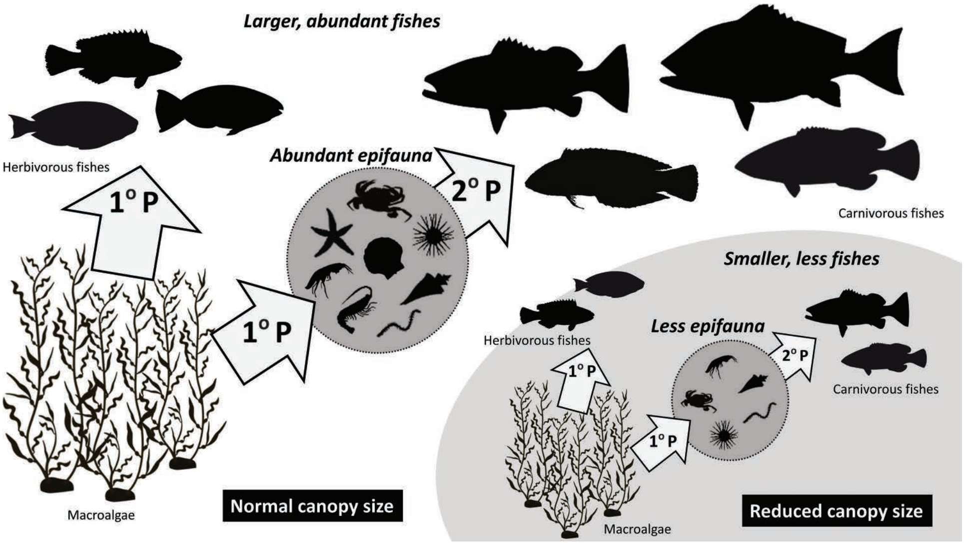

Figure 10 Conceptual diagram highlighting the potential consequences of climate-driven alterations to tropical *Sargassum* canopy structure over and above those currently experienced on a seasonal basis, and the flow-on food chain effects for epifaunal communities and higher-order consumers (invertivorous and carnivorous fishes). (1°P: primary production, 2°P: secondary production.)

et al. 2014) (Figure 10), but currently have little understanding of how changes to *Sargassum* growth and survival driven by warming ocean temperatures (e.g. Graba-Landry et al. 2020) may influence epifaunal production. While current evidence indicates *Sargassum* supports elevated abundance and diversity of epifaunal invertebrates and fishes (Wilson et al. 2014, Tano et al. 2016, Wenger et al. 2018), we lack good information on mechanisms underlying tropical reef ecosystems, including the size structure and diversity of fish populations that can be supported by different levels of epifaunal secondary production (Figure 10). Similarly, better understanding is needed as to how subtle changes to structural elements within marine habitats will impact the abundance, population size structure and productivity of epifaunal communities within those habitats, and ultimately their ability to maintain current levels of ecosystem production and food web stability.

Conclusions and future research directions

This review has explored the history of the study of epifauna and considered the different nomenclature used within the research field to describe similar communities with similar ecosystem functions. We highlight the challenge that this can pose when trying to present a unified perspective on the contribution of these organisms to marine ecosystems. Much of the confusion surrounding nomenclature can be avoided by defining organisms according to the role they play in marine ecosystems, i.e. by considering a functional rather than a taxonomic or habitat-based classification.

This review has also highlighted that, despite their ubiquity, epifauna are a relatively poorly studied group of animals. Three main reasons likely contribute to this: (1) their small body size and cryptic habits; (2) challenges associated with quantitatively sampling and processing communities within structurally diverse habitats; and (3) the difficulty of providing high taxonomic resolution when describing the constituent organisms within diverse epifaunal samples. However, new sampling techniques have immense potential to break down some of these barriers, providing an opportunity for a renaissance in the field in coming years. A quantum advance in epifaunal research is likely through eDNA sampling and analysis of metagenomic structure (Kelly et al. 2017, Stæhr et al. 2017, Garlapati et al. 2019), advances that can surmount all three sampling and taxonomic challenges listed above. An important research front that is currently very active is the estimation of abundance, which remains to be accurately assessed using eDNA methodologies (Kelly et al. 2016, Garlapati et al. 2019, Leduc et al. 2019).

Epifaunal communities potentially provide a critical indicator of marine ecosystem health, including as an early warning sign of issues higher up the food chain. Reduced cost barriers associated with sampling and processing also open up the possibility of repeated sampling of individual locations over the longer term, and the ability to build long-term datasets that can offer insights into community responses to changing environmental conditions. Long-term databases will also likely be key to improving our understanding of the impact of epifaunal production and nutrient cycling on marine ecosystems, and for modelling projections of the biomass of higher-order consumers that can be supported under various climate scenarios.

Additional opportunities for breaking down barriers associated with sampling and taxonomic identification are provided through citizen science. Technological developments that offer more tractable sampling protocols could see the routine inclusion of epifaunal community metrics in marine ecosystem management plans, as well as the chance to build large teams of citizen scientists engaged in sampling eDNA, and monitoring epifaunal communities across broad scales (Duffy et al. 2019). This approach builds on the success of other citizen science programs, such as iNaturalist, eBird and Reef Life Survey (Edgar et al. 2021).

Experimental approaches also offer exciting opportunities to explore how ecological interactions may alter under future climate scenarios (Edgar et al. 2016), as highlighted by the recent study by Nagelkerken et al. (2020). Mesocosm studies, which replicate marine benthic communities and then quantify how food web structure, biomass and productivity are altered under various environmental scenarios, have the potential to yield further insights into the resilience of marine ecosystems under global change. Coordinated experimental networks, where controlled manipulative experiments are replicated in different regions worldwide, similarly include huge capacity for expanding generality of knowledge. Thus, both mesocosm and experimental network approaches are likely to offer important insights into changes to marine trophic structures, including impacts on fish populations and global food security. Epifaunal communities, by virtue of their critical role in marine food web structures, need to feature more significantly in marine research agendas. This is more than a "research push", but a call for investment in studies that can fill the gaps in our understanding of the quantitative contribution that epifauna make to global biodiversity and services provided by marine ecosystems, as well as the potential impacts of global change on abundance, community composition and biomass of epifauna themselves.

Acknowledgements

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Appendix A

Published studies on marine epifaunal communities based on a literature search conducted in the ISI Web of Science database up to and including 21 July 2020 using the terms "epifauna" and "epifaunal".

Year	Authors	Title	Journal
1953	Allen	Observations on the epifauna of the deep-water muds of the Clyde Sea Area, with special reference to *Chlamys septemradiata* (Müller)	*Journal of Animal Ecology*
1964	Pequegnat	Epifauna of California siltstone reef	*Ecology*
1967	Calder & Brehmer	Seasonal occurrence of epifauna on test panels in Hampton Roads, Virginia	*International Journal of Oceanology and Limnology*
1967	Driscoll	Attached epifauna-substrate relations	*Limnology and Oceanography*
1967	Richards & Riley	Benthic epifauna of Long Island Sound	*Bulletin of the Bingham Oceanographic Collection*
1968	Fager	A sand-bottom epifaunal community of invertebrates in shallow water	*Limnology and Oceanography*
1968	Matthews	Folliculinids (protozoa) of Ago Bay, Japan, and their relation to epifauna of pearl oyster (*Pinctada martensii*)	*Pacific Science*
1968	Pequegnat	Distribution of epifaunal biomass on a sublittoral rock-reef	*Pacific Science*
1968	Snell	The Lithothamnion community in Nord-Möre, Norway with notes on the epifauna of *Desmarestia viridis* (Müller)	*Sarsia*
1971	Bourget & Lacroix	Two simple durable epifaunal collectors	*Journal of the Fisheries Research Board of Canada*
1972	Sassaman & Mangum	Adaptations to environmental oxygen levels in infaunal and epifaunal sea anemones	*Biological Bulletin*
1973	Bourget & Lacroix	Seasonal aspects of settlement of benthic epifauna on infralittoral stratum of Saint Lawrence Estuary	*Journal of the Fisheries Research Board of Canada*
1973	Jackson et al.	Epifaunal invertebrates of ornate diamondback terrapin, *Malaclemys terrapin macrospilota*	*American Midland Naturalist*
1977	Koechlin	Settlement of epifauna of *Spirographis spallanzani*, *Sycon ciliatum* and *Ciona intestinalis* in harbor of Lezardrieux	*Cahiers De Biologie Marine*
1978	Anger	Development of a subtidal epifaunal community at the island of Helgoland	*Helgoländer wissenschaftliche Meeresuntersuchungen*
1978	Davis & Vanblaricom	Spatial and temporal heterogeneity in a sand bottom epifaunal community of invertebrates in shallow-water	*Limnology and Oceanography*
1978	Karlson	Predation and space utilization patterns in a marine epifaunal community	*Journal of Experimental Marine Biology and Ecology*
1979	Conover	Effect of gastropod shell characteristics and hermit crabs on shell epifauna	*Journal of Experimental Marine Biology and Ecology*
1979	Peterson	The importance of predation and competition in organizing the intertidal epifaunal communities of Barnegat Inlet, New Jersey	*Oecologia*
1980	Beckley & McLachlan	Studies on the littoral seaweed epifauna of St. Croix Island 2. Composition and summer standing stock	*South African Journal of Zoology*
1980	Fradette & Bourget	Ecology of benthic epifauna of the estuary and Gulf of St. Lawrence: factors influencing their distribution and abundance on buoys	*Canadian Journal of Fisheries and Aquatic Sciences*
1980	Jokiel	Solar ultraviolet radiation and coral reef epifauna	*Science*
1980	Russ	Effects of predation by fishes, competition, and structural complexity of the substratum on the establishment of a marine epifaunal community	*Journal of Experimental Marine Biology and Ecology*
1980	Seed & Harris	The epifauna of the fronds of *Laminaria digitata* Lamour in Strangford Lough, Northern Ireland	*Proceedings of the Royal Irish Academy Section B: Biological Geological and Chemical Science*

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Year	Authors	Title	Journal
1980	Stoner	Perception and choice of substratum by epifaunal amphipods associated with seagrasses	*Marine Ecology Progress Series*
1980	Vandolah & Bird	A comparison of reproductive patterns in epifaunal and infaunal gammaridean amphipods	*Estuarine and Coastal Marine Science*
1980	Wood & Seed	The effects of shore level on the epifaunal communities associated with *Fucus serratus* (L) in the Menai Strait, North Wales	*Cahiers De Biologie Marine*
1981	Kay & Keough	Occupation of patches in the epifaunal communities on pier pilings and the bivalve *Pinna bicolor* at Edithburgh, South Australia	*Oecologia*
1981	Seed & O'connor	Epifaunal associates of *Fucus serratus* at Dale, southwest Wales	*Holarctic Ecology*
1981	Seed et al.	The composition and seasonal changes amongst the epifauna associated with *Fucus serratus* L. in Strangford Lough, Northern Ireland	*Cahiers De Biologie Marine*
1981	Shin	The development of sessile epifaunal communities in Kylesalia, Kilkieran Bay (west coast of Ireland)	*Journal of Experimental Marine Biology and Ecology*
1982	Bak et al.	Complexity of coral interactions: influence of time, location of interaction and epifauna	*Marine Biology*
1982	Beckley	Studies on the littoral seaweed epifauna of St. Croix Island 3. *Gelidium pristoides* (Rhodophyta) and its epifauna	*South African Journal of Zoology*
1982	Lewis & Hollingworth	Leaf epifauna of the seagrass *Thalassia testudinum*	*Marine Biology*
1982	Russ	Overgrowth in a marine epifaunal community: competitive hierarchies and competitive networks	*Oecologia*
1983	Fletcher & Day	The distribution of epifauna on *Ecklonia radiata* (C. Agardh) J. Agardh and the effect of disturbance	*Journal of Experimental Marine Biology and Ecology*
1983	Karlson & Shenk	Epifaunal abundance, association, and overgrowth patterns on large hermit crab shells	*Journal of Experimental Marine Biology and Ecology*
1983	McDonald	A sampler for quantitatively assessing the macrobenthic epifaunal community of a hard substrate	*Estuarine, Coastal and Shelf Science*
1983	Shepherd	The epifauna of megaripples: specie's adaptations and population responses to disturbance	*Australian Journal of Ecology*
1983	Sheridan & Livingston	Abundance and seasonality of infauna and epifauna inhabiting a *Halodule wrightii* meadow in Apalachicola Bay, Florida	*Estuaries*
1983	Ward & Young	The depauperation of epifauna on *Pinna bicolor* near a lead smelter, Spencer Gulf, South Australia	*Environmental Pollution Series A: Ecological and Biological*
1984	Keough	Dynamics of the epifauna of the bivalve *Pinna bicolor*: interactions among recruitment, predation, and competition	*Ecology*
1984	Lópezjamar et al.	Contribution of infauna and mussel-raft epifauna to demersal fish diets	*Marine Ecology Progress Series*
1984	Patterson	Distribution patterns of some epifauna in the Irish Sea and their ecological interactions	*Marine Biology*
1984	Schmidt & Warner	Effects of caging on the development of a sessile epifaunal community	*Marine Ecology Progress Series*
1984	Virnstein et al.	Latitudinal patterns in seagrass epifauna: do patterns exist, and can they be explained?	*Estuaries*

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Year	Authors	Title	Journal
1985	Dewitt & Levinton	Disturbance, emigration, and refugia: how the mud snail, *Ilyanassa obsoleta* (Say), affects the habitat distribution of an epifaunal amphipod, *Microdeutopus gryllotalpa* (Costa)	*Journal of Experimental Marine Biology and Ecology*
1985	Hootsmans & Vermaat	The effect of periphyton-grazing by three epifaunal species on the growth of *Zostera marina* L. under experimental conditions	*Aquatic Botany*
1985	Howard	Measurements of short-term turnover of epifauna within seagrass beds using an *in situ* staining method	*Marine Ecology Progress Series*
1985	Woodhead & Jacobson	Epifaunal settlement, the processes of community development and succession over two years on an artificial reef in the New York bight	*Bulletin of Marine Science*
1986	Fishelson & Haran	Epifauna of algae on a rocky platform near Mikhmoret (Mediterranean Sea, Israel): composition and dynamics	*Israel Journal of Zoology*
1986	Oswald & Seed	Organization and seasonal progression within the epifaunal communities of coastal macroalgae	*Cahiers De Biologie Marine*
1986	Persson & Olafsson	Distribution and abundance of mobile epifauna and macrozoobenthos in south Swedish shallow marine areas	*Ophelia*
1986	Todd & Turner	Ecology of intertidal and sublittoral cryptic epifaunal assemblages. I. Experimental rationale and the analysis of larval settlement	*Journal of Experimental Marine Biology and Ecology*
1987	Cancino et al.	Effects of epifauna on algal growth and quality of the agar produced by *Gracilaria verrucosa* (Hudson) Papenfuss	*Hydrobiologia*
1987	Demurguia & Seed	Some observations on the occurrence and vertical-distribution of mites (Arachnida: Acari) and other epifaunal associates of intertidal barnacles on two contrasted rocky shores in North Wales	*Cahiers De Biologie Marine*
1987	Howard	Diel variation in the abundance of epifauna associated with seagrasses of the Indian River, Florida, USA	*Marine Biology*
1987	Johnson & Scheibling	Structure and dynamics of epifaunal assemblages on intertidal macroalgae *Ascophyllum nodosum* and *Fucus Vesiculosus* in Nova Scotia, Canada	*Marine Ecology Progress Series*
1987	Lewis	Crustacean epifauna of seagrass and macroalgae in Apalachee Bay, Florida, USA	*Marine Biology*
1987	Rosman et al.	Epifaunal aggregations of Vesicomyidae on the continental slope off Louisiana	*Oceanographic Research Papers*
1987	Virnstein & Howard	Motile epifauna of marine macrophytes in the Indian River Lagoon, Florida. 1. Comparisons among three species of seagrasses from adjacent beds	*Bulletin of Marine Science*
1987	Virnstein & Howard	Motile epifauna of marine macrophytes in the Indian River Lagoon, Florida. 2. Comparisons between drift algae and three species of seagrasses	*Bulletin of Marine Science*
1988	Feder & Pearson	The benthic ecology of Loch Linnhe and Loch Eil, a sea-loch system on the west coast of Scotland. V. Biology of the dominant soft-bottom epifauna and their interaction with the infauna	*Journal of Experimental Marine Biology and Ecology*
1988	Hall & Bell	Response of small motile epifauna to complexity of epiphytic algae on seagrass blades	*Journal of Marine Research*
1988	Okamura	The influence of neighbors on the feeding of an epifaunal bryozoan	*Journal of Experimental Marine Biology and Ecology*

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Year	Authors	Title	Journal
1988	Todd & Turner	Ecology of intertidal and sublittoral cryptic epifaunal assemblages. II. Nonlethal overgrowth of encrusting bryozoans by colonial ascidians	*Journal of Experimental Marine Biology and Ecology*
1989	Basford et al.	The epifauna of the Northern North Sea (56°–61°N)	*Journal of the Marine Biological Association of the United Kingdom*
1989	Costello & Myers	Breeding periodicity and sex ratios in epifaunal marine amphipoda in Lough Hyne, Ireland	*Estuarine, Coastal and Shelf Science*
1989	Harrison	Are deep-sea asellote isopods infaunal or epifaunal	*Crustaceana*
1989	Mullineaux	Vertical distributions of the epifauna on manganese nodules: implications for settlement and feeding	*Limnology and Oceanography*
1990	Baden	The cryptofauna of *Zostera marina* (L.): abundance, biomass and population dynamics	*Netherlands Journal of Sea Research*
1990	Basford et al.	The infauna and epifauna of the northern North Sea	*Netherlands Journal of Sea Research*
1990	Daniel & Robertson	Epibenthos of mangrove waterways and open embayments: community structure and the relationship between exported mangrove detritus and epifaunal standing stocks	*Estuarine, Coastal and Shelf Science*
1990	Davoult	Biofacies and trophic structure of the "pebbles-with-sessile-epifauna" community in the Dover Strait	*Oceanologica Acta*
1990	Edgar	Population regulation, population dynamics and competition amongst mobile epifauna associated with seagrass	*Journal of Experimental Marine Biology and Ecology*
1990	Edgar	Predator-prey interactions in seagrass beds. III. Impacts of the western rock lobster *Panulirus cygnus* George on epifaunal gastropod populations	*Journal of Experimental Marine Biology and Ecology*
1990	Edgar	The use of the size structure of benthic macrofaunal communities to estimate faunal biomass and secondary production	*Marine Biology and Ecology*
1990	Hendrickx	The stomatopod and decapod crustaceans collected during the GUAYTEC II Cruise in the Central Gulf Of California, mexico, with the description of a new species of *Plesionika* Bate (Caridea, Pandalidae)	*Revista De Biologia Tropical*
1990	Hutchings	Review of the effects of trawling on macrobenthic epifaunal communities	*Australian Journal of Marine and Freshwater Research*
1990	Kunitzer	The infauna and epifauna of the central North Sea	*Meeresforschung-Reports on Marine Research*
1990	Lambshead & Gooday	The impact of seasonally deposited phytodetritus on epifaunal and shallow infaunal benthic foraminiferal populations in the bathyal northeast Atlantic: the assemblage response	*Deep Sea Research Part I: Oceanographic Research Papers*
1991	Anderson et al.	*Gelidium pristoides* in South Africa	*Hydrobiologia*
1991	Ansari et al.	Seagrass habitat complexity and macroinvertebrate abundance in Lakshadweep coral reef lagoons, Arabian Sea	*Coral Reefs*
1991	Edgar	Artificial algae as habitats for mobile epifauna: factors affecting colonization in a Japanese *Sargassum* bed	*Hydrobiologia*
1991	Edgar	Distribution patterns of mobile epifauna associated with rope fibre habitats within the Bathurst Harbour estuary, south-western Tasmania	*Estuarine, Coastal and Shelf Science*

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Year	Authors	Title	Journal
1991	Hopkinson et al.	Community metabolism and nutrient cycling at Gray's Reef, a hard bottom habitat in the Georgia Bight	*Marine Ecology Progress Series*
1991	Karande	Use of epifaunal communities in pollution monitoring	*Journal of Environmental Biology*
1991	Lana & Guiss	Influence of *Spartina alterniflora* on structure and temporal variability of macrobenthic associations in a tidal flat of Paranagua Bay (southeastern Brazil)	*Marine Ecology Progress Series*
1991	Marshall et al.	New southern geographical records of intertidal sea urchins (Echinodermata: Echinoidea), with notes on abundance	*South African Journal of Zoology*
1991	Rainer & Unsworth	Ecology and production of *Nebalia* sp. (Crustacea: Leptostraca) in a shallow-water seagrass community	*Australian Journal of Marine and Freshwater Research*
1991	Russo	Do predatory fishes affect the structure of an epiphytal amphipod assemblage on a protected algal reef in Hawaii?	*Hydrobiologia*
1991	Schneider & Mann	Rapid recovery of fauna following simulated ice rafting in a Nova Scotian seagrass bed	*Marine Ecology Progress Series*
1991	Schneider & Mann	Species specific relationships of invertebrates to vegetation in a seagrass bed. I. Correlational studies	*Journal of Experimental Marine Biology and Ecology*
1991	Schneider & Mann	Species specific relationships of invertebrates to vegetation in a seagrass bed. II. Experiments on the importance of macrophyte shape, epiphyte cover and predation	*Journal of Experimental Marine Biology and Ecology*
1991	Stephens & Bertness	Mussel facilitation of barnacle survival in a sheltered bay habitat	*Journal of Experimental Marine Biology and Ecology*
1991	Takeuchi & Hirano	Growth and reproduction of *Caprella danilevskii* (Crustacea: Amphipoda) reared in the laboratory	*Marine Biology*
1991	Turner & Todd	The effects of *Gibbula cineraria* (L.), *Nucella lapillus* (L.) and *Asterias rubens* L. on developing epifaunal assemblages	*Journal of Experimental Marine Biology and Ecology*
1991	Ward & Thorpe	Distribution of encrusting bryozoans and other epifauna on the subtidal bivalve *Chlamys opercularis*	*Marine Biology*
1991	Webb & Parsons	Impact of predation-disturbance by large epifauna on sediment-dwelling harpacticoid copepods: field experiments in a subtidal seagrass bed	*Marine Biology*
1991	Zvyagintsev	Seasonal changes in the epifauna on valvas of the oyster *Crassostrea gigas* in Amur Bay, the Sea of Japan	*Biologiya Morya-Marine Biology*
1992	Ardisson & Bourget	Large-scale ecological patterns: discontinuous distribution of marine benthic epifauna	*Marine Ecology Progress Series*
1992	Aronson	Biology of a scale-independent predator-prey interaction	*Marine Ecology Progress Series*
1992	Bingham	Life histories in an epifaunal community: coupling of adult and larval processes	*Ecology*
1992	Dalby & Young	Role of early post-settlement mortality in setting the upper depth limit of ascidians in Florida epifaunal communities	*Marine Ecology Progress Series*
1992	Dewarumez et al.	Is the 'muddy heterogeneous sediment assemblage' an ecotone between the pebbles community and the *Abra alba* community in the southern bight of the North Sea?	*Netherlands Journal of Sea Research*
1992	Edgar	Patterns of colonization of mobile epifauna in a Western Australian seagrass bed	*Journal of Experimental Marine Biology and Ecology*
1992	Edgar & Robertson	The influence of seagrass structure on the distribution and abundance of mobile epifauna: pattern and process in a Western Australian *Amphibolis* bed	*Journal of Experimental Marine Biology and Ecology*

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Year	Authors	Title	Journal
1992	Eleftheriou & Robertson	The effects of experimental scallop dredging on the fauna and physical environment of a shallow sandy community	*Netherlands Journal of Sea Research*
1992	Hily & Floch	Structure of subtidal algal assemblages on soft-bottom sediments: fauna/flora interactions and role of disturbances in the Bay of Brest, France	*Marine Ecology Progress Series*
1992	Isaksson & Pihl	Structural changes in benthic macrovegetation and associated epibenthic faunal communities	*Netherlands Journal of Sea Research*
1992	Klumpp et al.	The role of epiphytic periphyton and macroinvertebrate grazers in the trophic flux of a tropical seagrass community	*Aquatic Botany*
1992	Lana & Guiss	Macrofauna-plant-biomass interactions in a euhaline salt marsh in Paranagua Bay (SE Brazil)	*Marine Ecology Progress Series*
1992	Namikawa et al.	Role of the tentaculozooids of the polymorphic hydroid *Stylactaria conchicola* (Yamada) in interactions with some epifaunal space competitors	*Journal of Experimental Marine Biology and Ecology*
1992	Pearson & Rosenberg	Energy flow through the SE Kattegat: a comparative examination of the eutrophication of a coastal marine ecosystem	*Netherlands Journal of Sea Research*
1992	Takeuchi & Hirano	Duration and size of embryos in epifaunal amphipods *Caprella danilevskii* Czerniavski and *C. okadai* Arimoto (Crustacea: Amphipoda: Caprellidea)	*Journal of Experimental Marine Biology and Ecology*
1992	Takeuchi & Hirano	Growth and reproduction of the epifaunal amphipod *Caprella okadai* Arimoto (Crustacea: Amphipoda: Caprellidea)	*Journal of Experimental Marine Biology and Ecology*
1993	Duineveld et al.	The trawlfauna of the Mauritanian shelf (Northwest Africa): density, species composition, and biomass	*Hydrobiologia*
1993	Edgar	Measurement of the carrying capacity of benthic habitats using a metabolic-rate based index	*Oecologia*
1993	Edgar & Aoki	Resource limitation and fish predation: their importance to mobile epifauna associated with Japanese *Sargassum*	*Oecologia*
1993	Fowler & Laffoley	Stability in Mediterranean-Atlantic sessile epifaunal communities at the northern limits of their range	*Journal of Experimental Marine Biology and Ecology*
1993	Gonzalez et al.	Epifauna of *Spondylus princeps unicolor* (Mollusca: Bivalvia) in Puerto Escondido, Gulf of California, Mexico	*Revista De Biologia Tropical*
1993	Martin-Smith	Abundance of mobile epifauna: the role of habitat complexity and predation by fishes	*Journal of Experimental Marine Biology and Ecology*
1993	Mellors & Marsh	Relationship between seagrass standing crop and the spatial distribution and abundance of the natantian fauna at Green Island, Northern Queensland	*Australian Journal of Marine and Freshwater Research*
1993	Trowbridge	Local and regional abundance patterns of the ascoglossan (= sacoglossan) opisthobranch *Alderia modesta* (Loven, 1844) in the northeastern Pacific	*Veliger*
1993	Turner & Todd	The early development of epifaunal assemblages on artificial substrata at two intertidal sites on an exposed rocky shore in St. Andrews Bay, N.E. Scotland	*Journal of Experimental Marine Biology and Ecology*
1993	Wang & Widdows	Calorimetric studies on the energy metabolism of an infaunal bivalve, *Abra tenuis*, under normoxia, hypoxia and anoxia	*Marine Biology*
1994	Cattrijsse et al.	Nekton communities of an intertidal creek of a European estuarine brackish marsh	*Marine Ecology Progress Series*

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Year	Authors	Title	Journal
1994	Connolly	Removal of seagrass canopy: effects on small fish and their prey	*Journal of Experimental Marine Biology and Ecology*
1994	Cruzabrego et al.	Community ecology of marine gastropods (Molusca: Gastropoda) in Contoy Island, Mexico	*Revista De Biologia Tropical*
1994	Edgar	Observations on the size-structure of macrofaunal assemblages	*Journal of Experimental Marine Biology and Ecology*
1994	Edgar et al.	Comparisons of species richness, size-structure and production of benthos in vegetated and unvegetated habitats in Western Port, Victoria	*Journal of Experimental Marine Biology and Ecology*
1994	Everett	Macroalgae in marine soft-sediment communities: effects on benthic faunal assemblages	*Journal of Experimental Marine Biology and Ecology*
1994	Gee & Warwick	Body-size distribution in a marine metazoan community and the fractal dimensions of macroalgae	*Journal of Experimental Marine Biology and Ecology*
1994	Gee & Warwick	Metazoan community structure in relation to the fractal dimensions of marine macroalgae	*Marine Ecology Progress Series*
1994	Hardin et al.	Spatial variation in hard-bottom epifauna in the Santa Maria basin, California: the importance of physical factors	*Marine Environmental Research*
1994	Hostens & Hamerlynck	The mobile epifauna of the soft bottoms in the subtidal Oosterschelde estuary: structure, function and impact of the storm-surge barrier	*Hydrobiologia*
1994	Jean & Hilly	Quantitative sampling of soft-bottom macroepifauna for assessing the benthic system in the Bay of Brest (France)	*Oceanologica Acta*
1994	Kaiser et al.	Improving quantitative surveys of epibenthic communities using a modified 2m-beam trawl	*Marine Ecology Progress Series*
1994	Levin et al.	Contrasting effects of substrate mobility on infaunal assemblages inhabiting two high-energy settings on fieberling Guyot	*Journal of Marine Research*
1994	Mangum	Multiple sites of gas exchange	*American Zoologist*
1994	Martin-Smith	Short-term dynamics of tropical macroalgal epifauna: patterns and processes in recolonization of *Sargassum fissifolium*	*Marine Ecology Progress Series*
1994	Matsumasa	Effect of secondary substrate on associated small crustaceans in a brackish lagoon	*Journal of Experimental Marine Biology and Ecology*
1994	Monteforte & Garcia-Gasca	Spat collection studies on pearl oysters *Pinctada mazatlanica* and *Pteria sterna* (Bivalvia, Pteriidae) in Bahia de La Paz, South Baja California, Mexico	*Hydrobiologia*
1994	Rathburn & Corliss	The ecology of living (stained) deep-sea benthic foraminifera from the Sulu Sea	*Paleoceanography*
1994	Taylor & Cole	Mobile epifauna on subtidal brown seaweeds in northeastern New Zealand	*Marine Ecology Progress Series*
1994	Todd & Keough	Larval settlement in hard substratum epifaunal assemblages: a manipulative field study of the effects of substratum filming and the presence of incumbents	*Journal of Experimental Marine Biology and Ecology*
1995	Bingham & Young	Stochastic events and dynamics of a mangrove root epifaunal community	*Marine Ecology*
1995	Connolly	Effects of removal of seagrass canopy on assemblages of small, motile invertebrates	*Marine Ecology Progress Series*
1995	Edgar & Shaw	The production and trophic ecology of shallow-water fish assemblages in southern Australia II. Diets of fishes and trophic relationships between fishes and benthos at Western Port, Victoria	*Journal of Experimental Marine Biology and Ecology*

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Year	Authors	Title	Journal
1995	Klitgaard	The fauna associated with outer shelf and upper slope sponges (Porifera, Demospongiae) at the Faroe Islands, northeastern Atlantic	*Sarsia*
1995	McDermott & Fives	The diet of an assemblage of small demersal fish in the western Irish Sea	*Biology and Environment: Proceedings of the Royal Irish Academy*
1995	Migné & Davoult	Multi-scale heterogeneity in a macrobenthic epifauna community	*Hydrobiologia*
1995	Nalesso et al.	Tube epifauna of the Polychaete *Phyllochaetopterus socialis* Claparède	*Estuarine, Coastal and Shelf Science*
1995	Nelson	Amphipod crustaceans of the Indian River Lagoon: current status and threats to biodiversity	*Bulletin of Marine Science*
1995	Osman & Whitlatch	Predation on early ontogenic life stages and its effect on recruitment into a marine epifaunal community	*Marine Ecology Progress Series*
1995	Takeuchi & Hirano	Clinging behavior of the epifaunal caprellids (Amphipoda) inhabiting the *Sargassum* zone on the Pacific coast of Japan, with its evolutionary implications	*Journal of Crustacean Biology*
1995	Taylor et al.	A portable battery-powered suction device for the quantitative sampling of small benthic invertebrates	*Journal of Experimental Marine Biology and Ecology*
1995	Ulrich et al.	Tube-building in two epifaunal amphipod species, *Corophium insidiosum* and *Jassa falcata*	*Helgolander Meeresuntersuchungen*
1995	Vilela	Ecology of Quaternary benthic foraminiferal assemblages on the Amazon shelf, northern Brazil	*Geo-Marine Letters*
1995	Virnstein	Anomalous diversity of some seagrass-associated fauna in the Indian-River Lagoon, Florida	*Bulletin of Marine Science*
1996	Aller & Stupakoff	The distribution and seasonal characteristics of benthic communities on the Amazon shelf as indicators of physical processes	*Continental Shelf Research*
1996	Barry et al.	Trophic ecology of the dominant fishes in Elkhorn Slough, California, 1974–1980	*Estuaries*
1996	Barthel et al.	A wandering population of the hexactineliid sponge *Pheronema carpenteri* on the continental slope off Morocco, northwest Africa	*Marine Ecology*
1996	Benedetti-Cecchi et al.	Estimating the abundance of benthic invertebrates: a comparison of procedures and variability between observers	*Marine Ecology Progress Series*
1996	Boaden	Habitat provision for meiofauna by *Fucus serratus* epifauna with particular data on the flatworm *Monocelis lineata*	*Marine Ecology*
1996	Castricfey	Richness and biodiversity in megatidal seas: rocky sublittoral communities of the Trebeurden-Ploumanach region (Northern Brittany, France)	*Cahiers De Biologie Marine*
1996	Chauvaud et al.	Experimental collection of great scallop postlarvae and other benthic species in the Bay of Brest: settlement patterns in relation to spatio-temporal variability of environmental factors	*Aquaculture International*
1996	Connolly & Butler	The effects of altering seagrass canopy height on small, motile invertebrates of shallow Mediterranean embayments	*Marine Ecology*
1996	Davenport et al.	Mixed fractals and anisotropy in subantarctic marine macroalgae from south Georgia: implications for epifaunal biomass and abundance	*Marine Ecology Progress Series*

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Year	Authors	Title	Journal
1996	Drake & Arias	The effect of epibenthic predators and macroalgal cover on the benthic macroinvertebrate community of a shallow lagoon in the Bay of Cádiz (SW Spain)	*Hydrobiologia*
1996	Ellis et al.	Effects of gas producing platforms on continental shelf macroepifauna in the northwestern Gulf of Mexico: abundance and size structure	*Canadian Journal of Fisheries and Aquatic Sciences*
1996	Gee & Warwick	A study of global biodiversity patterns in the marine motile fauna of hard substrata	*Journal of the Marine Biological Association of the United Kingdom*
1996	Gooday	Epifaunal and shallow infaunal foraminiferal communities at three abyssal NE Atlantic sites subject to differing phytodetritus input regimes	*Deep Sea Research Part I: Oceanographic Research Papers*
1996	Jacobi & Langevin	Habitat geometry of benthic substrata: effects on arrival and settlement of mobile epifauna	*Marine Biology and Ecology*
1996	Kuhne & Rachor	The macrofauna of a stony sand area in the German Bight (North Sea)	*Helgolander Meeresunters*
1996	Lemmens et al.	Filtering capacity of seagrass meadows and other habitats of Cockburn Sound, Western Australia	*Marine Ecology Progress Series*
1996	Levin et al.	Succession of macrobenthos in a created salt marsh	*Marine Ecology Progress Series*
1996	Li et al.	Foraminiferal biofacies on the mid-latitude Lincoln Shelf, South Australia: oceanographic and sedimentological implications	*Marine Geology*
1996	Posey et al.	Influence of storm disturbance on an offshore benthic community	*Bulletin of Marine Science*
1996	Rathburn et al.	Comparisons of the ecology and stable isotopic compositions of living (stained) benthic foraminifera from the Sulu and South China Seas	*Deep Sea Research Part I: Oceanographic Research Papers*
1996	Schlacher & Wooldridge	Origin and trophic importance of detritus – evidence from stable isotopes in the benthos of a small, temperate estuary	*Oecologia*
1996	Schrijvers et al.	Resource competition between macrobenthic epifauna and infauna in a Kenyan *Avicennia marina* mangrove forest	*Marine Ecology Progress Series*
1996	Thomas	Origin and community structure of the Harrington Sound Notch, Bermuda	*Bulletin of Marine Science*
1996	Williamson & Creese	Small invertebrates inhabiting the crustose alga *Pseudolithoderma* sp. (Ralfsiaceae) in northern New Zealand	*New Zealand Journal of Marine and Freshwater Research*
1997	Aller	Benthic community response to temporal and spatial gradients in physical disturbance within a deep-sea western boundary region	*Deep Sea Research Part I: Oceanographic Research Papers*
1997	Boström & Bonsdorff	Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L.) beds in the northern Baltic Sea	*Journal of Sea Research*
1997	Buhs & Reise	Epibenthic fauna dredged from tidal channels in the Wadden Sea of Schleswig-Holstein: spatial patterns and a long-term decline	*Helgolander Meeresuntersuchungen*
1997	Collie et al.	Effects of bottom fishing on the benthic megafauna of Georges Bank	*Marine Ecology Progress Series*
1997	Connolly	Differences in composition of small, motile invertebrate assemblages from seagrass and unvegetated habitats in a southern Australian estuary	*Hydrobiologia*

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Year	Authors	Title	Journal
1997	LeClair & LaBarbera	An *in vivo* comparative study of intersegmental flexibility in the ophiuroid arm	*Biological Bulletin*
1997	Livingston	Trophic response of estuarine fishes to long-term changes of river runoff	*Bulletin of Marine Science*
1997	Livingston et al.	Freshwater input to a gulf estuary: long-term control of trophic organization	*Ecological Applications*
1997	Manley & Shaw	Geotaxis and phototaxis in *Elphidium crispum* (Protozoa: Foraminiferida)	*Journal of the Marine Biological Association of the United Kingdom*
1997	McClanahan & Sala	A Mediterranean rocky-bottom ecosystem fisheries model	*Ecological Modelling*
1997	McCorkle et al.	Vertical distributions and stable isotopic compositions of live (stained) benthic foraminifera from the North Carolina and California continental margins	*Deep Sea Research Part I: Oceanographic Research Papers*
1997	McKnight & Probert	Epibenthic communities on the Chatham Rise, New Zealand	*New Zealand Journal of Marine and Freshwater Research*
1997	Russo	Epifauna living on sublittoral seaweeds around Cyprus	*Hydrobiologia*
1997	Sala	The role of fishes in the organization of a Mediterranean sublittoral community II: epifaunal communities	*Journal of Experimental Marine Biology and Ecology*
1997	Takeuchi & Hino	Community structure of caprellid amphipods (Crustacea) on seagrasses in Otsuchi Bay, northeastern Japan, with reference to the association of *Caprella japonica* (Schurin) and *Phyllospadix iwatensis* Makino	*Fisheries Science*
1997	Turner et al.	Changes in epifaunal assemblages in response to marina operations and boating activities	*Marine Environmental Research*
1997	Warner	Occurrence of epifaunshers on the periwinkle, *Littorina littorea* (L.), and interactions with the the polychaete *Polydora ciliata* (Johnston)	*Hydrobiologia*
1997	Wright et al.	Biological mediation of bottom boundary layer processes and sediment suspension in the lower Chesapeake Bay	*Marine Geology*
1998	Bacon et al.	Physiological responses of infaunal (*Mya arenaria*) and epifaunal (*Placopecten magellanicus*) bivalves to variations in the concentration and quality of suspended particles: I. Feeding activity and selection	*Journal of Experimental Marine Biology and Ecology*
1998	Chapman	Relationships between spatial patterns of benthic assemblages in a mangrove forest using different levels of taxonomic resolution	*Marine Ecology Progress Series*
1998	Engel & Kvitek	Effects of otter trawling on a benthic community in Monterey Bay National Marine Sanctuary	*Conservation Biology*
1998	Flynn et al.	Macrobenthic associations of the lower and upper marshes of a tidal flat colonized by *Spartina alterniflora* in Cananeia Lagoon estuarine region	*Bulletin of Marine Science*
1998	Glasby	Estimating spatial variability in developing assemblages of epibiota on subtidal hard substrata	*Marine and Freshwater Research*
1998	Hata & Nakata	Evaluation of eelgrass bed nitrogen cycle using an ecosystem model	*Environmental Modelling & Software*
1998	Hatcher	Epibenthic colonisation patterns on slabs of stabilised coal-waste in Poole Bay, UK	*Hydrobiologia*

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Year	Authors	Title	Journal
1998	Jernakoff & Nielsen	Plant–animal associations in two species of seagrasses in Western Australia	*Aquatic Botany*
1998	Knowles & Bell	The influence of habitat structure in faunal-habitat associations in a Tampa Bay seagrass system, Florida	*Bulletin of Marine Science*
1998	MacDonald et al.	Physiological responses of infaunal (*Mya arenaria*) and epifaunal (*Placopecten magellanicus*) bivalves to variations in the concentration and quality of suspended particles: II. Absorption efficiency and scope for growth	*Journal of Experimental Marine Biology and Ecology*
1998	Magorrian & Service	Analysis of underwater visual data to identify the impact of physical disturbance on horse mussel (*Modiolus modiolus*) beds	*Marine Pollution Bulletin*
1998	Mazouni et al.	Influence of oyster culture on water column characteristics in a coastal lagoon (Thau, France)	*Hydrobiologia*
1998	Osman & Whitlatch	Local control of recruitment in an epifaunal community and the consequences to colonization processes	*Hydrobiologia*
1998	Sardá et al.	The impact of epifaunal predation on the structure of macroinfaunal invertebrate communities of tidal saltmarsh creeks	*Estuarine, Coastal and Shelf Science*
1998	Sasekumar & Chong	Faunal diversity in Malaysian mangroves	*Global Ecology and Biogeography*
1998	Schrijvers et al.	The infaunal macrobenthos under East African *Ceriops tagal* mangroves impacted by epibenthos	*Journal of Experimental Marine Biology and Ecology*
1998	Tanaka & Leite	The effect of sieve mesh size on the abundance and composition of macrophyte-associated macrofaunal assemblages	*Hydrobiologia*
1998	Taylor	Density, biomass and productivity of animals in four subtidal rocky reef habitats: the importance of small mobile invertebrates	*Marine Ecology Progress Series*
1998	Taylor	Seasonal variation in assemblages of mobile epifauna inhabiting three subtidal brown seaweeds in northeastern New Zealand	*Hydrobiologia*
1998	Taylor	Short-term dynamics of a seaweed epifaunal assemblage	*Journal of Experimental Marine Biology and Ecology*
1998	Taylor & Rees	Excretory products of mobile epifauna as a nitrogen source for seaweeds	*Limnology and Oceanography*
1998	Thrush et al.	Disturbance of the marine benthic habitat by commercial fishing: impacts at the scale of the fishery	*Ecological Applications*
1998	Walsh & Mitchell	Factors associated with variations in abundance of epifaunal caridean shrimps between and within estuarine seagrass meadows	*Marine and Freshwater Research*
1998	Whitlatch & Osman	A new device for studying benthic invertebrate recruitment	*Limnology and Oceanography*
1998	Widdows et al.	Use of annular flumes to determine the influence of current velocity and bivalves on material flux at the sediment-water interface	*Estuaries*
1998	Wieczorek & Todd	Inhibition and facilitation of settlement of epifaunal marine invertebrate larvae by microbial biofilm cues	*Biofouling*
1998	Wildish & Fader	Pelagic–benthic coupling in the Bay of Fundy	*Hydrobiologia*
1998	Witman & Grange	Links between rain, salinity, and predation in a rocky subtidal community	*Ecology*

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Year	Authors	Title	Journal
1998	Wolff et al.	A trophic flow model of the Golfo de Nicoya, Costa Rica	*Revista De Biologia Tropical*
1999	Bologna & Heck	Macrofaunal associations with seagrass epiphytes: relative importance of trophic and structural characteristics	*Journal of Experimental Marine Biology and Ecology*
1999	Brown & Taylor	Effects of trampling by humans on animals inhabiting coralline algal turf in the rocky intertidal	*Journal of Experimental Marine Biology and Ecology*
1999	Connell	Effects of surface orientation on the cover of epibiota	*Biofouling*
1999	Connell & Anderson	Predation by fish on assemblages of intertidal epibiota: effects of predator size and patch size	*Journal of Experimental Marine Biology and Ecology*
1999	Cranfield et al.	Changes in the distribution of epifaunal reefs and oysters during 130 years of dredging for oysters in Foveaux Strait, southern New Zealand	*Aquatic Conservation: Marine and Freshwater Ecosystems*
1999	Davenport et al.	Epifaunal composition and fractal dimensions of marine plants in relation to emersion	*Journal of the Marine Biological Association of the United Kingdom*
1999	Edgar	Experimental analysis of structural versus trophic importance of seagrass beds. I. Effects on macrofaunal and meiofaunal invertebrates	*Vie et Milieu – Life and Environment*
1999	Edgar	Experimental analysis of structural versus trophic importance of seagrass beds. II. Effects on fishes, decapods and cephalopods	*Vie et Milieu – Life and Environment*
1999	Freese et al.	Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska	*Marine Ecology Progress Series*
1999	Glasby	Differences between subtidal epibiota on pier pilings and rocky reefs at marinas in Sydney, Australia	*Estuarine, Coastal and Shelf Science*
1999	Glasby	Effects of shading on subtidal epibiotic assemblages	*Journal of Experimental Marine Biology and Ecology*
1999	Glasby	Interactive effects of shading and proximity to the seafloor on the development of subtidal epibiotic assemblages	*Marine Ecology Progress Series*
1999	Hily & Bouteille	Modifications of the specific diversity and feeding guilds in an intertidal sediment colonized by an eelgrass meadow (*Zostera marina*) (Brittany, France)	*Comptes Rendus de l'Académie des Sciences*
1999	Jewett et al.	'Exxon Valdez' oil spill: impacts and recovery in the soft-bottom benthic community in and adjacent to eelgrass beds	*Marine Ecology Progress Series*
1999	Kenyon et al.	Abundance of fish and crustacean postlarvae on portable artificial seagrass units: daily sampling provides quantitative estimates of the settlement of new recruits	*Journal of Experimental Marine Biology and Ecology*
1999	Lavery et al.	Ecological effects of macroalgal harvesting on beaches in the Peel-Harvey Estuary, Western Australia	*Estuarine, Coastal and Shelf Science*
1999	Lepoint et al.	Fauna vs flora contribution to the leaf epiphytes biomass in a *Posidonia oceanica* seagrass bed (Revellata Bay, Corsica)	*Hydrobiologia*
1999	Morri et al.	Biodiversity of marine sessile epifauna at an Aegean island subject to hydrothermal activity: Milos, eastern Mediterranean Sea	*Marine Biology*
1999	Prena et al.	Experimental otter trawling on a sandy bottom ecosystem of the Grand Banks of Newfoundland: analysis of trawl bycatch and effects on epifauna	*Marine Ecology Progress Series*
1999	Ramos	The megazoobenthos of the Scotia Arc islands	*Scientia Marina*
1999	Rees et al.	A comparison of benthic biodiversity in the North Sea, English Channel, and Celtic Seas	*ICES Journal of Marine Science*

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Year	Authors	Title	Journal
1999	Rees et al.	Surveys of the epibenthos of the Crouch Estuary (UK) in relation to TBT contamination	*Journal of the Marine Biological Association of the United Kingdom*
1999	Rose et al.	Overgrazing of a large seagrass bed by the sea urchin *Lytechinus variegatus* in Outer Florida Bay	*Marine Ecology Progress Series*
1999	Saiz-Salinas & Urkiaga-Alberdi	Use of faunal indicators for assessing the impact of a port enlargement near Bilbao (Spain)	*Environmental Monitoring and Assessment*
1999	Sánchez-Jerez et al.	Comparison of the epifauna spatial distribution in *Posidonia oceanica*, *Cymodocea nodosa* and unvegetated bottoms: importance of meadow edges	*Acta Oecologica*
1999	Sánchez-Jerez et al.	Daily vertical migrations in the epifauna associated with *Posidonia oceanica* meadows	*Journal of the Marine Biological Association of the United Kingdom*
1999	Smallwood et al.	Megafauna can control the quality of organic matter in marine sediments	*Naturwissenschaften*
1999	Smith & Witman	Species diversity in subtidal landscapes: maintenance by physical processes and larval recruitment	*Ecology*
1999	Tarasov et al.	Effect of shallow-water hydrothermal venting on the biota of Matupi Harbour (Rabaul Caldera, New Britain Island, Papua New Guinea)	*Continental Shelf Research*
1999	Viejo	Mobile epifauna inhabiting the invasive *Sargassum muticum* and two local seaweeds in northern Spain	*Aquatic Botany*
2000	Cocito et al.	First survey of sessile communities on subtidal rocks in an area with hydrothermal vents: Milos Island, Aegean Sea	*Hydrobiologia*
2000	Cohen et al.	Epibenthic community structure in Port Phillip Bay, Victoria, Australia	*Marine and Freshwater Research*
2000	Collie et al.	A quantitative analysis of fishing impacts on shelf-sea benthos	*Journal of Animal Ecology*
2000	Collie et al.	Photographic evaluation of the impacts of bottom fishing on benthic epifauna	*ICES Journal of Marine Science*
2000	Dando et al.	Hydrothermal studies in the Aegean Sea	*Physics and Chemistry of the Earth, Part B: Hydrology, Oceans and Atmosphere*
2000	Edgar & & Barrett	Effects of catchment activities on macrofaunal assemblages in Tasmanian estuaries	*Estuarine Coastal and Shelf Science*
2000	Ellis et al.	Demersal assemblages in the Irish Sea, St George's Channel and Bristol Channel	*Estuarine, Coastal and Shelf Science*
2000	Gage et al.	Patterns in deep-sea macrobenthos at the continental margin: standing crop, diversity and faunal change on the continental slope off Scotland	*Hydrobiologia*
2000	Glasby	Surface composition and orientation interact to affect subtidal epibiota	*Journal of Experimental Marine Biology and Ecology*
2000	Jablonski et al.	Analysing the latitudinal diversity gradient in marine bivalves	*Evolutionary Biology of the Bivalvia*[a]
2000	Kaiser et al.	Fishing-gear restrictions and conservation of benthic habitat complexity	*Conservation Biology*
2000	Roy et al.	Dissecting latitudinal diversity gradients: functional groups and clades of marine bivalves	*Proceedings of the Royal Society B: Biological Sciences*

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Year	Authors	Title	Journal
2000	Rumohr & Kujawski	The impact of trawl fishery on the epifauna of the southern North Sea	*ICES Journal of Marine Science*
2000	Sagasti et al.	Epifaunal communities thrive in an estuary with hypoxic episodes	*Estuaries*
2000	Sánchez-Moyano et al.	The molluscan epifauna of the alga *Halopteris Scoparia* in southern Spain as a bioindicator of coastal environmental conditions	*Journal of Molluscan Studies*
2000	Smith	The effects of a small sewage outfall on an algal epifaunal community at Macquarie Island (sub-Antarctic): a drop in the southern ocean?	*Marine Pollution Bulletin*
2000	Sutherland et al.	Predation on meiofaunal and macrofaunal invertebrates by western sandpipers (*Calidris mauri*): evidence for dual foraging modes	*Marine Biology*
2000	Tuck et al.	The impact of water jet dredging for razor clams, *Ensis* spp., in a shallow sandy subtidal environment	*Journal of Sea Research*
2000	Veale et al.	Effects of long-term physical disturbance by commercial scallop fishing on subtidal epifaunal assemblages and habitats	*Marine Biology*
2001	Beaulieu	Colonization of habitat islands in the deep sea: recruitment to glass sponge stalks	*Deep Sea Research Part I: Oceanographic Research Papers*
2001	Beaulieu	Life on glass houses: sponge stalk communities in the deep sea	*Marine Biology*
2001	Bradshaw et al.	The effect of scallop dredging on Irish Sea benthos: experiments using a closed area	*Hydrobiologia*
2001	Brooks & Bell	Mobile corridors in marine landscapes: enhancement of faunal exchange at seagrass/sand ecotones	*Journal of Experimental Marine Biology and Ecology*
2001	Cranfield et al.	Promising signs of regeneration of blue cod and oyster habitat changed by dredging in Foveaux Strait, southern New Zealand	*New Zealand Journal of Marine and Freshwater Research*
2001	Dean & Jewett	Habitat-specific recovery of shallow subtidal communities following the Exxon Valdez oil spill	*Ecological Applications*
2001	Duffy et al.	Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test	*Ecology*
2001	Dumbauld et al.	Response of an estuarine benthic community to application of the pesticide carbaryl and cultivation of pacific oysters (*Crassostrea gigas*) in Willapa Bay, Washington	*Marine Pollution Bulletin*
2001	Glasby	Development of sessile marine assemblages on fixed versus moving substrata	*Marine Ecology Progress Series*
2001	Gooday et al.	The foraminiferan macrofauna from three North Carolina (USA) slope sites with contrasting carbon flux: a comparison with the metazoan macrofauna	*Deep Sea Research Part I: Oceanographic Research Papers*
2001	Henry	Hydroids associated with deep-sea corals in the boreal north-west Atlantic	*Journal of the Marine Biological Association of the United Kingdom*
2001	Jennings et al.	Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities	*Marine Ecology Progress Series*
2001	Jennings et al.	Trawling disturbance can modify benthic production processes	*Journal of Animal Ecology*

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Year	Authors	Title	Journal
2001	Kollmann & Stachowitsch	Long-term changes in the benthos of the northern Adriatic Sea: a phototransect approach	*Marine Ecology*
2001	Lee et al.	The effects of seagrass (*Zostera japonica*) canopy structure on associated fauna: a study using artificial seagrass units and sampling of natural beds	*Journal of Experimental Marine Biology and Ecology*
2001	Mancinelli & Rossi	Influence of allochthonous plant detritus on *Gammarus insensibilis* Stock (Amphipoda) occurrence in the soft-bottom epifauna of the northern Adriatic Sea	*Mediterranean Ecosystems: Structures and Processes*
2001	Maughan	The effects of sedimentation and light on recruitment and development of a temperate, subtidal, epifaunal community	*Journal of Experimental Marine Biology and Ecology*
2001	Nakaoka et al.	Seasonal and between-substrate variation in mobile epifaunal community in a multispecific seagrass bed of Otsuchi Bay, Japan	*Marine Ecology*
2001	Oh et al.	Feeding ecology of the common shrimp *Crangon crangon* in Port Erin Bay, Isle of Man, Irish Sea	*Marine Ecology Progress Series*
2001	Parker et al.	Plant species diversity and composition: experimental effects on marine epifaunal assemblages	*Marine Ecology Progress Series*
2001	Prieto et al.	Mollusc diversity in an *Arca zebra* (Mollusca : Bivalvia) community, Chacopata, Sucre, Venezuela	*Revista De Biologia Tropical*
2001	Robinson et al.	The impact of scallop drags on sea urchin populations and benthos in the Bay of Fundy, Canada	*Hydrobiologia*
2001	Sagasti et al.	Effects of periodic hypoxia on mortality, feeding and predation in an estuarine epifaunal community	*Journal of Experimental Marine Biology and Ecology*
2001	Sánchez-Moyano et al.	Effect of the vegetative cycle of *Caulerpa prolifera* on the spatio-temporal variation of invertebrate macrofauna	*Aquatic Botany*
2001	Sfriso et al.	Benthic macrofauna changes in areas of Venice lagoon populated by seagrasses or seaweeds	*Marine Environmental Research*
2001	Smith	Historical regulation of local species richness across a geographic region	*Ecology*
2001	Sudo & Azeta	The microhabitat and size of gammarid species selectively predated by young red sea bream *Pagrus major*	*Fisheries Science*
2001	Thrush et al.	Fishing disturbance and marine biodiversity: role of habitat structure in simple soft-sediment systems	*Marine Ecology Progress Series*
2001	Vytopil & Willis	Epifaunal community structure in *Acropora* spp. (Scleractinia) on the Great Barrier Reef: implications of coral morphology and habitat complexity	*Coral Reefs*
2001	Wright	*In situ* modification of modern submarine hyaloclastic/pyroclastic deposits by oceanic currents: an example from the Southern Kermadec arc (SW Pacific)	*Marine Geology*
2001	Zühlke et al.	Epibenthic diversity in the North Sea	*Senckenbergiana maritima*
2002	Bologna & Heck	Impact of habitat edges on density and secondary production of seagrass-associated fauna	*Estuaries*
2002	Brooks et al.	Environmental effects associated with marine netpen waste with emphasis on salmon farming in the Pacific northwest	*Responsible Marine Aquaculture*[a]
2002	Brown et al.	Small-scale mapping of sea-bed assemblages in the eastern English Channel using sidescan sonar and remote sampling techniques	*Estuarine, Coastal and Shelf Science*

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Year	Authors	Title	Journal
2002	Burton et al.	Assessment of out-of-kind mitigation success of an artificial reef deployed in Delaware Bay, USA	*ICES Journal of Marine Science*
2002	Callaway et al.	Diversity and community structure of epibenthic invertebrates and fish in the North Sea	*ICES Journal of Marine Science*
2002	Callaway et al.	Mesh-size matters in epibenthic surveys	*Journal of the Marine Biological Association of the United Kingdom*
2002	Cartes et al.	Comparing production-biomass ratios of benthos and suprabenthos in macrofaunal marine crustaceans	*Canadian Journal of Fisheries and Aquatic Sciences*
2002	Dolmer	Mussel dredging: impact on epifauna in Limfjorden, Denmark	*Journal of Shellfish Research*
2002	Dulvy et al.	Scale-dependant control of motile epifaunal community structure along a coral reef fishing gradient	*Journal of Experimental Marine Biology and Ecology*
2002	Edgar & Barrett	Benthic macrofauna in Tasmanian estuaries: scales of distribution and relationships with environmental variables	*Journal of Experimental Marine Biology and Ecology*
2002	Fraschetti et al.	Spatio-temporal variation of hydroids and polychaetes associated with *Cystoseira amentacea* (Fucales: Phaeophyceae)	*Marine Biology*
2002	Germano & Read	Natural recovery at a submarine wood waste site	*Remediation and Beneficial Reuse of Contaminated Sediments*[a]
2002	Holloway & Keough	An introduced polychaete affects recruitment and larval abundance of sessile invertebrates	*Ecological Applications*
2002	Holloway & Keough	Effects of an introduced polychaete, *Sabella spallanzanii*, on the development of epifaunal assemblages	*Marine Ecology Progress Series*
2002	Hovel et al.	Effects of seagrass landscape structure, structural complexity and hydrodynamic regime on macrofaunal densities in North Carolina seagrass beds	*Marine Ecology Progress Series*
2002	Jayaprada	Composition and distribution of epigrowth fauna in Visakhapatnam harbor, east coast of India	*Indian Journal of Marine Sciences*
2002	Koch & Wolff	Energy budget and ecological role of mangrove epibenthos in the Caete estuary, North Brazil	*Marine Ecology Progress Series*
2002	Labarta et al.	Enzymatic digestive activity in epifaunal (*Mytilus chilensis*) and infaunal (*Mulinia edulis*) bivalves in response to changes in food regimes in a natural environment	*Marine Biology*
2002	Mancinelli et al.	Role of microorganisms and macrofauna in benthic phosphorus dynamics in the po river-Adriatic Sea frontal system: an experimental approach	*Chemistry and Ecology*
2002	Matsumoto & Kohda	The effect of feeding habitats on dietary shifts during the growth in a benthophagous suction-feeding fish	*Zoological Science*
2002	Nakaoka et al.	Impacts of dugong foraging on benthic animal communities in a Thailand seagrass bed	*Ecological Research*
2002	Saier	Subtidal and intertidal mussel beds (*Mytilus edulis* L.) in the Wadden Sea: diversity differences of associated epifauna	*Helgoland Marine Research*
2002	Sánchez-Moyano et al.	Effect of environmental factors on the spatial variation of the epifaunal polychaetes of the alga *Halopteris scoparia* in Algeciras Bay (Strait of Gibraltar)	*Hydrobiologia*

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Year	Authors	Title	Journal
2002	Smith & Rule	Artificial substrata in a shallow sublittoral habitat: do they adequately represent natural habitats or the local species pool?	*Journal of Experimental Marine Biology and Ecology*
2002	Stachowicz et al.	Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process	*Ecology*
2002	Steimle et al.	Benthic macrofauna productivity enhancement by an artificial reef in Delaware Bay, USA	*ICES Journal of Marine Science*
2002	Thiel	The zoogeography of algae-associated peracarids along the Pacific coast of Chile	*Journal of Biogeography*
2002	Velasco & Navarro	Feeding physiology of infaunal (*Mulinia edulis*) and epifaunal (*Mytilus chilensis*) bivalves under a wide range of concentrations and qualities of seston	*Marine Ecology Progress Series*
2002	Yu et al.	Seasonal zonation patterns of benthic amphipods in a sandy shore surf zone of Korea	*Journal of Crustacean Biology*
2003	Ashton et al.	A baseline study of the diversity and community ecology of crab and molluscan macrofauna in the Sematan mangrove forest, Sarawak, Malaysia	*Journal of Tropical Ecology*
2003	Beaver et al.	Secondary productivity within biotic fouling community elements on two artificial reef structures in the northwestern Gulf of Mexico	*Fisheries, Reefs, and Offshore Development*[a]
2003	Bolduc & Afton	Effects of structural marsh management and salinity on invertebrate prey of waterbirds in marsh ponds during winter on the Gulf Coast Chenier Plain	*Wetlands*
2003	Bone et al.	Ecological aspects of syllids (Annelida : Polychaeta : Syllidae) on *Thalassia testudinum* beds in Venezuela	*Hydrobiologia*
2003	Bradshaw et al.	To what extent does upright sessile epifauna affect benthic biodiversity and community composition?	*Marine Biology*
2003	Burrows et al.	Topography as a determinant of search paths of fishes and mobile macrocrustacea on the sediment surface	*Journal of Experimental Marine Biology and Ecology*
2003	Colloca et al.	Pattern of distribution and diversity of demersal assemblages in the central Mediterranean Sea	*Estuarine, Coastal and Shelf Science*
2003	Deidun et al.	Low faunal diversity on Maltese sandy beaches: fact or artefact?	*Estuarine, Coastal and Shelf Science*
2003	Diaz & Arana	Epifaunal polychaetes on *Pinctada imbricata* Röding, 1798 (Bivalvia : Pteriidae) from the Gulf of Cariaco, Venezuela	*Interciencia*
2003	Edgar & Klumpp	Consistencies over regional scales in assemblages of mobile epifauna associated with natural and artificial plants of different shape	*Aquatic Botany*
2003	Haggitt & Babcock	The role of grazing by the lysianassid amphipod *Orchomenella aahu* in dieback of the kelp *Ecklonia radiata* in north-eastern New Zealand	*Marine Biology*
2003	Hirst	Encounter 2002 Expedition to the Isles of St Francis, South Australia: peracarid crustacean epifauna of subtidal macroalgal canopies	*Transactions of the Royal Society of South Australia*
2003	Kumagai & Aoki	Seasonal changes in the epifaunal community on the shallow-water gorgonian *Melithaea flabellifera*	*Journal of the Marine Biological Association of the United Kingdom*
2003	Leite & Turra	Temporal variation in *Sargassum* biomass, *Hypnea* epiphytism and associated fauna	*Brazilian Archives of Biology and Technology*

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Year	Authors	Title	Journal
2003	Nash	Interactions of Atlantic salmon in the Pacific Northwest: VI. A synopsis of the risk and uncertainty	*Fisheries Research*
2003	Pardo & Dauer	Particle size selection in individuals from epifaunal versus infaunal populations of the nereidid polychaete *Neanthes succinea* (Polychaeta: Nereididae)	*Hydrobiologia*
2003	Prieto et al.	Diversity and abundance of molluscs in *Thalassia testudinum* prairies of the Bay of Mochima, Mochima National Park, Venezuela	*Revista De Biologia Tropical*
2003	Ribeiro et al.	Macrofauna associated to *Mycale microsigmatosa* (Porifera, Demospongiae) in Rio de Janeiro State, SE Brazil	*Estuarine, Coastal and Shelf Science*
2003	Sagasti et al.	Estuarine epifauna recruit despite periodic hypoxia stress	*Marine Biology*
2003	Schreider et al.	Effects of height on the shore and complexity of habitat on abundances of amphipods on rocky shores in New South Wales, Australia	*Journal of Experimental Marine Biology and Ecology*
2003	Sepúlveda et al.	The peracarid epifauna associated with the ascidian *Pyura chilensis* (Molina, 1782) (Ascidiacea : Pyuridae)	*Journal of Natural History*
2003	Tanaka & Leite	Spatial scaling in the distribution of macrofauna associated with *Sargassum stenophyllum* (Mertens) Martius: analyses of faunal groups, gammarid life habits, and assemblage structure	*Journal of Experimental Marine Biology and Ecology*
2003	Tanner	Patch shape and orientation influences on seagrass epifauna are mediated by dispersal abilities	*Oikos*
2003	Tanner	The influence of prawn trawling on sessile benthic assemblages in Gulf St. Vincent, South Australia	*Canadian Journal of Fisheries and Aquatic Sciences*
2003	Thorbjorn & Petersen	The epifauna on the carbonate reefs in the Arctic Ikka Fjord, SW Greenland	*Ophelia*
2003	Velasco & Navarro	Energetic balance of infaunal (*Mulinia edulis* King, 1831) and epifaunal (*Mytilus chilensis* Hupé, 1854) bivalves in response to wide variations in concentration and quality of seston	*Journal of Experimental Marine Biology and Ecology*
2003	Viejo & Åberg	Temporal and spatial variation in the density of mobile epifauna and grazing damage on the seaweed *Ascophyllum nodosum*	*Marine Biology*
2003	Witman & Smith	Rapid community change at a tropical upwelling site in the Galápagos Marine Reserve	*Biodiversity & Conservation*
2004	Bouillon et al.	Resource utilization patterns of epifauna from mangrove forests with contrasting inputs of local versus imported organic matter	*Marine Ecology Progress Series*
2004	Diaz et al.	Potential impacts of sand mining offshore of Maryland and Delaware: part 2 – biological considerations	*Journal of Coastal Research*
2004	Escapa et al.	The distribution and ecological effects of the introduced Pacific oyster *Crassostrea gigas* (Thunberg, 1793) in northern Patagonia	*Journal of Shellfish Research*
2004	Gaymer et al.	Prey selection and predatory impact of four major sea stars on a soft bottom subtidal community	*Journal of Experimental Marine Biology and Ecology*
2004	Hargrave et al.	Benthic epifauna assemblages, biomass and respiration in The Gully region on the Scotian Shelf, NW Atlantic Ocean	*Marine Ecology Progress Series*
2004	Healey & Hovel	Seagrass bed patchiness: effects on epifaunal communities in San Diego Bay, USA	*Journal of Experimental Marine Biology and Ecology*

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Year	Authors	Title	Journal
2004	Henry & Kenchington	Ecological and genetic evidence for impaired sexual reproduction and induced clonality in the hydroid *Sertularia cupressina* (Cnidaria: Hydrozoa) on commercial scallop grounds in Atlantic Canada	*Marine Biology*
2004	Hinz et al.	Seasonal and annual variability in an epifaunal community in the German Bight	*Marine Biology*
2004	Kaiser et al.	Demersal fish and epifauna associated with sandbank habitats	*Estuarine, Coastal and Shelf Science*
2004	Larsen & Gilfillan	Preliminary survey of the subtidal macrobenthic invertebrates of Cobscook Bay, Maine	*Northeastern Naturalist*
2004	Mathot et al.	Evidence for sexual partitioning of foraging mode in Western Sandpipers (*Calidris mauri*) during migration	*Canadian Journal of Zoology*
2004	Osman & Whitlatch	The control of the development of a marine benthic community by predation on recruits	*Journal of Experimental Marine Biology and Ecology*
2004	Tanaka & Leite	Distance effects on short-term recolonization of *Sargassum stenophyllum* by mobile epifauna, with an analysis of gammarid life habits	*Journal of the Marine Biological Association of the United Kingdom*
2004	Welsh & Castadelli	Bacterial nitrification activity directly associated with isolated benthic marine animals	*Marine Biology*
2004	Wernberg et al.	Epibiota communities of the introduced and indigenous macroalgal relatives *Sargassum muticum* and *Halidrys siliquosa* in Limfjorden (Denmark)	*Helgoland Marine Research*
2004	Wikström & Kautsky	Invasion of a habitat-forming seaweed: effects on associated biota	*Biological Invasions*
2004	Witman et al.	The relationship between regional and local species diversity in marine benthic communities: a global perspective	*Proceedings of the National Academy of Sciences of the United States of America*
2005	Andersen et al.	Feeding ecology and growth of age 0 year *Platichthys flesus* (L.) in a vegetated and a bare sand habitat in a nutrient rich fjord	*Journal of Fish Biology*
2005	Bishop	Compensatory effects of boat wake and dredge spoil disposal on assemblages of macroinvertebrates	*Estuaries*
2005	Brown	Epifaunal colonization of the Loch Linnhe artificial reef: influence of substratum on epifaunal assemblage structure	*Biofouling*
2005	Castañeda-Fernández-de-Lara et al.	Feeding ecology of juvenile spiny lobster, *Panulirus interruptus*, on the Pacific coast of Baja California Sur, Mexico	*New Zealand Journal of Marine and Freshwater Research*
2005	Clark & Johnston	Manipulating larval supply in the field: a controlled study of marine invasibility	*Marine Ecology Progress Series*
2005	Davidson et al.	Structural gradients in an intertidal hard-bottom community: examining vertical, horizontal, and taxonomic clines in zoobenthic biodiversity	*Marine Biology*
2005	Gage et al.	Potential impacts of deep-sea trawling on the benthic ecosystem along the Northern European continental margin: a review	*Benthic Habitats and the Effects of Fishing*[a]
2005	Govenar et al.	Epifaunal community structure associated with *Riftia pachyptila* aggregations in chemically different hydrothermal vent habitats	*Marine Ecology Progress Series*
2005	Hamazaki et al.	Analyses of Bering Sea bottom-trawl surveys in Norton Sound: absence of regime shift effect on epifauna and demersal fish	*ICES Journal of Marine Science*

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Year	Authors	Title	Journal
2005	Hepburn & Hurd	Conditional mutualism between the giant kelp *Macrocystis pyrifera* and colonial epifauna	*Marine Ecology Progress Series*
2005	Jewett et al.	Epifaunal disturbance by periodic low levels of dissolved oxygen: native vs. invasive species response	*Marine Ecology Progress Series*
2005	Klumpp & Kwak	Composition and abundance of benthic macrofauna of a tropical sea-grass bed in North Queensland, Australia	*Pacific Science*
2005	Luckenbach et al.	Oyster reef habitat restoration: relationships between oyster abundance and community development based on two studies in Virginia and South Carolina	*Journal of Coastal Research*
2005	McConnaughey et al.	Effects of chronic bottom trawling on the size structure of soft-bottom benthic invertebrates	*Benthic Habitats and the Effects of Fishing*[a]
2005	Nakamura & Sano	Comparison of invertebrate abundance in a seagrass bed and adjacent coral and sand areas at Amitori Bay, Iriomote Island, Japan	*Fisheries Science*
2005	Nakaoka	Plant–animal interactions in seagrass beds: ongoing and future challenges for understanding population and community dynamics	*Population Ecology*
2005	Pagliosa & Lana	Impact of plant cover removal on macrobenthic community structure of a subtropical salt marsh	*Bulletin of Marine Science*
2005	Polte et al.	Effects of current exposure on habitat preference of mobile 0-group epibenthos for intertidal seagrass beds (*Zostera noltii*) in the northern Wadden Sea	*Estuarine, Coastal and Shelf Science*
2005	Polte et al.	The contribution of seagrass beds (*Zostera noltii*) to the function of tidal flats as a juvenile habitat for dominant, mobile epibenthos in the Wadden Sea	*Marine Biology*
2005	Prieto et al.	Diversity and abundance of mollusks in the sublittoral epifaunal community of Punta Patilla, Venezuela	*Revista De Biologia Tropical*
2005	Raes & Vanreusel	The metazoan meiofauna associated with a cold-water coral degradation zone in the Porcupine Seabight (NE Atlantic)	*Cold-Water Corals and Ecosystems*[a]
2005	Rule & Smith	Spatial variation in the recruitment of benthic assemblages to artificial substrata	*Marine Ecology Progress Series*
2005	Sgro et al.	Functional responses and scope for growth of two non-indigenous bivalve species in the Sacca di Goro (northern Adriatic Sea, Italy)	*Italian Journal of Zoology*
2005	Stone et al.	Effects of bottom trawling on soft-sediment epibenthic communities in the Gulf of Alaska	*Benthic Habitats and the Effects of Fishing*[a]
2005	Tanner	Edge effects on fauna in fragmented seagrass meadows	*Austral Ecology*
2005	Thomasson & Tunberg	Composition and vertical distribution of the motile epifauna on a vertical rock wall in Gullmarsfjorden, western Sweden, using an alternative sampling approach	*Marine Biology Research*
2005	Velasco & Navarro	Feeding physiology of two bivalves under laboratory and field conditions in response to variable food concentrations	*Marine Ecology Progress Series*
2005	Winston & Migotto	A new encrusting interstitial marine fauna from Brazil	*Invertebrate Biology*
2006	Alfaro	Benthic macro-invertebrate community composition within a mangrove/seagrass estuary in northern New Zealand	*Estuarine, Coastal and Shelf Science*
2006	Beaumont et al.	Evaluation of techniques used in the assessment of subtidal epibiotic assemblage structure	*Biofouling*

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Year	Authors	Title	Journal
2006	Burone & Pires-Vanin	Foraminiferal assemblages in Ubatuba Bay, south-eastern Brazilian coast	*Scientia Marina*
2006	Cruz-Rivera & Paul	Feeding by coral reef mesograzers: algae or cyanobacteria?	*Coral Reefs*
2006	Eklöf et al.	Effects of tropical open-water seaweed farming on seagrass ecosystem structure and function	*Marine Ecology Progress Series*
2006	Gil et al.	Nutrient impacts on epifaunal density and species composition in a subtropical seagrass bed	*Hydrobiologia*
2006	Guerra-García et al.	Assessing a quick monitoring method using rocky intertidal communities as a bioindicator: a multivariate approach in Algeciras Bay	*Environmental Monitoring and Assessment*
2006	Henry et al.	Impacts of otter trawling on colonial epifaunal assemblages on a cobble bottom ecosystem on Western Bank (northwest Atlantic)	*Marine Ecology Progress Series*
2006	Hepburn et al.	Colony structure and seasonal differences in light and nitrogen modify the impact of sessile epifauna on the giant kelp *Macrocystis pyrifera* (L.) C Agardh	*Hydrobiologia*
2006	Hinchey et al.	Responses of estuarine benthic invertebrates to sediment burial: the importance of mobility and adaptation	*Hydrobiologia*
2006	Hooper & Davenport	Epifaunal composition and fractal dimensions of intertidal marine macroalgae in relation to emersion	*Journal of the Marine Biological Association of the United Kingdom*
2006	Hosack et al.	Habitat associations of estuarine species: comparisons of intertidal mudflat, seagrass (*Zostera marina*), and oyster (*Crassostrea gigas*) habitats	*Estuaries and Coasts*
2006	Kenchington et al.	Effects of experimental otter trawling on benthic assemblages on Western Bank, northwest Atlantic Ocean	*Journal of Sea Research*
2006	Kogan et al.	ATOC/Pioneer Seamount cable after 8 years on the seafloor: observations, environmental impact	*Continental Shelf Research*
2006	Kouchi et al.	Effects of temporal dynamics and vertical structure of the seagrass *Zostera caulescens* on distribution and recruitment of the epifaunal encrusting bryozoa *Microporella trigonellata*	*Marine Ecology*
2006	Lindsay et al.	Recruitment in epifaunal communities: an experimental test of the effects of species composition and age	*Marine Ecology Progress Series*
2006	Mendez	Deep-water polychaetes (Annelida) from the southeastern Gulf of California, Mexico	*Revista De Biologia Tropical*
2006	O'Brien et al.	Effects of *Sabella spallanzanii* physical structure on soft sediment macrofaunal assemblages	*Marine and Freshwater Research*
2006	Pereira et al.	Biogeographic patterns of intertidal macroinvertebrates and their association with macroalgae distribution along the Portuguese coast	*Hydrobiologia*
2006	Rae & Vanreusel	Microhabitat type determines the composition of nematode communities associated with sediment-clogged cold-water coral framework in the Porcupine Seabight (NE Atlantic)	*Deep Sea Research Part I: Oceanographic Research Papers*
2006	Reed & Hovel	Seagrass habitat disturbance: how loss and fragmentation of eelgrass *Zostera marina* influences epifaunal abundance and diversity	*Marine Ecology Progress Series*
2006	Reiss et al.	Estimating the catching efficiency of a 2-m beam trawl for sampling epifauna by removal experiments	*ICES Journal of Marine Science*

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Year	Authors	Title	Journal
2006	Roberts & Poore	Habitat configuration affects colonisation of epifauna in a marine algal bed	*Biological Conservation*
2006	Roberts et al.	Ecological consequences of copper contamination in macroalgae: effects on epifauna and associated herbivores	*Environmental Toxicology and Chemistry*
2006	Rodney & Paynter	Comparisons of macrofaunal assemblages on restored and non-restored oyster reefs in mesohaline regions of Chesapeake Bay in Maryland	*Journal of Experimental Marine Biology and Ecology*
2006	Royer et al.	Presence of spionid worms and other epibionts in Pacific oysters (*Crassostrea gigas*) cultured in Normandy, France	*Aquaculture*
2006	Schmidt & Scheibling	A comparison of epifauna and epiphytes on native kelps (*Laminaria species*) and an invasive alga (*Codium fragile* ssp *tomentosoides*) in Nova Scotia, Canada	*Botanica Marina*
2006	Sibaja-Cordero & Vargas-Zamora	The vertical zonation of epifauna and algae species in rocky substrates of the Gulf of Nicoya, Costa Rica	*Revista De Biologia Tropical*
2006	Sirota & Hovel	Simulated eelgrass *Zostera marina* structural complexity: effects of shoot length, shoot density, and surface area on the epifaunal community of San Diego Bay, California, USA	*Marine Ecology Progress Series*
2006	Skilleter et al.	Effects of physical disturbance on infaunal and epifaunal assemblages in subtropical, intertidal seagrass beds	*Marine Ecology Progress Series*
2006	Smith et al.	Effects of dredging activity on epifaunal communities – Surveys following cessation of dredging	*Estuarine, Coastal and Shelf Science*
2006	Sun et al.	The effect of primary productivity and seasonality on the distribution of deep-sea benthic foraminifera in the North Atlantic	*Deep Sea Research Part I: Oceanographic Research Papers*
2006	Tanner	Landscape ecology of interactions between seagrass and mobile epifauna: the matrix matters	*Estuarine, Coastal and Shelf Science*
2006	Valente	Response of benthic infauna and epifauna to ocean disposal of red clay dredged material in the New York Bight: a study using sediment-profile imaging, surface imaging and traditional methods	*Journal of Marine Systems*
2006	Vizzini & Mazzola	Sources and transfer of organic matter in food webs of a Mediterranean coastal environment: evidence for spatial variability	*Estuarine, Coastal and Shelf Science*
2006	Ward et al.	Epifaunal assemblages of the eastern Great Australian Bight: effectiveness of a benthic protection zone in representing regional biodiversity	*Continental Shelf Research*
2006	Yahel et al.	Phytoplankton grazing by epi- and infauna inhabiting exposed rocks in coral reefs	*Coral Reefs*
2006	Zintzen et al.	Epifaunal inventory of two shipwrecks from the Belgian Continental Shelf	*Hydrobiologia*
2007	Aníbal et al.	Mudflat surface morphology as a structuring agent of algae and associated macroepifauna communities: a case study in the Ria Formosa	*Journal of Sea Research*
2007	Antoniadou & Chintiroglou	Zoobenthos associated with the invasive red alga *Womersleyella setacea* (Rhodomelacea) in the northern Aegean Sea	*Journal of the Marine Biological Association of the United Kingdom*
2007	Aravind et al.	Life history and population dynamics of an estuarine amphipod, *Eriopisa chilkensis* Chilton (Gammaridae)	*Estuarine, Coastal and Shelf Science*

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Year	Authors	Title	Journal
2007	Bates & DeWreede	Do changes in seaweed biodiversity influence associated invertebrate epifauna?	*Journal of Experimental Marine Biology and Ecology*
2007	de Juan et al.	Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea)	*Marine Ecology Progress Series*
2007	Duineveld et al.	Effects of an area closed to fisheries on the composition of the benthic fauna in the southern North Sea	*ICES Journal of Marine Science*
2007	Fujiwara et al.	Three-year investigations into sperm whale-fall ecosystems in Japan	*Marine Ecology*
2007	Ganesh & Raman	Macrobenthic community structure of the northeast Indian shelf, Bay of Bengal	*Marine Ecology Progress Series*
2007	Govenar & Fisher	Experimental evidence of habitat provision by aggregations of *Riftia pachyptila* at hydrothermal vents on the East Pacific Rise	*Marine Ecology*
2007	Harries et al.	The establishment of the invasive alga *Sargassum muticum* on the west coast of Scotland: a preliminary assessment of community effects	*Journal of the Marine Biological Association of the United Kingdom*
2007	Hirst	Vertical stratification of mobile epiphytal arthropod assemblages between the canopy and understorey of subtidal macroalgae	*Marine Biology*
2007	Huntley et al.	Towards establishing a modern baseline for paleopathology: trace-producing parasites in a bivalve host	*Journal of Shellfish Research*
2007	Ince et al.	Marine macrophytes directly enhance abundances of sandy beach fauna through provision of food and habitat	*Estuarine, Coastal and Shelf Science*
2007	Irving et al.	Priority effects on faunal assemblages within artificial seagrass	*Journal of Experimental Marine Biology and Ecology*
2007	Itoh et al.	Fate of organic matter in faecal pellets egested by epifaunal mesograzers in a *Sargassum* forest and implications for biogeochemical cycling	*Marine Ecology Progress Series*
2007	Jing et al.	Foraging strategies involved in habitat use of shorebirds at the intertidal area of Chongming Dongtan, China	*Ecological Research*
2007	Jorgensen et al.	Top-down and bottom-up stabilizing mechanisms in eelgrass meadows differentially affected by coastal upwelling	*Marine Ecology Progress Series*
2007	Juan et al.	Effects of commercial trawling activities in the diet of the flat fish *Citharus linguatula* (Osteichthyes: Pleuronectiformes) and the starfish *Astropecten irregularis* (Echinodermata: Asteroidea)	*Journal of Experimental Marine Biology and Ecology*
2007	Kenchington et al.	Multi-decadal changes in the megabenthos of the Bay of Fundy: the effects of fishing	*Journal of Sea Research*
2007	Leite et al.	Diel density variation of amphipods associated with *Sargassum* beds from two shores of Ubatuba, Southeastern, Brazil	*Iheringia Serie Zoologia*
2007	McDermott	Ectosymbionts of the non-indigenous Asian shore crab, *Hemigrapsus sanguineus* (Decapoda: Varunidae), in the Western North Atlantic, and a search for its parasites	*Journal of Natural History*
2007	Murray et al.	Changes in the biodiversity of mussel assemblages induced by two methods of cultivation	*Journal of Shellfish Research*
2007	O'Neill et al.	Lack of epifaunal response to the application of salt for managing the noxious green alga *Caulerpa taxifolia* in a coastal lake	*Hydrobiologia*

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Year	Authors	Title	Journal
2007	Owada et al.	Functional morphology and phylogeny of the rock-boring bivalves *Leiosolenus* and *Lithophaga* (Bivalvia : Mytilidae): a third functional clade	*Marine Biology*
2007	Powers et al.	Macroalgal growth on bivalve aquaculture netting enhances nursery habitat for mobile invertebrates and juvenile fishes	*Marine Ecology Progress Series*
2007	Roberts et al.	MBACI sampling of an episodic disturbance: stormwater effects on algal epifauna	*Marine Environmental Research*
2007	Robertson & Weis	Interactions between the grass shrimp *Palaemonetes pugio* and the salt marsh grasses *Phragmites australis* and *Spartina alterniflora*	*Biological Invasions*
2007	Rule & Smith	Depth-associated patterns in the development of benthic assemblages on artificial substrata deployed on shallow, subtropical reefs	*Journal of Experimental Marine Biology and Ecology*
2007	Sánchez-Moyano et al.	Effects of temporal variation of the seaweed *Caulerpa prolifera* cover on the associated crustacean community	*Marine Ecology*
2007	Szarek et al.	Living deep-sea benthic foraminifera from the warm and oxygen-depleted environment of the Sulu Sea	*Deep Sea Research Part II: Topical Studies in Oceanography*
2007	Unsworth et al.	Faunal relationships with seagrass habitat structure: a case study using shrimp from the Indo-Pacific	*Marine and Freshwater Research*
2007	Voultsiadou et al.	The habitat engineering tunicate *Microcosmus sabatieri* Roule, 1885 and its associated peracarid epifauna	*Estuarine, Coastal and Shelf Science*
2007	Walker et al.	Spatial heterogeneity of epibenthos on artificial reefs: fouling communities in the early stages of colonization on an East Australian shipwreck	*Marine Ecology*
2008	Asch & Collie	Changes in a benthic megafaunal community due to disturbance from bottom fishing and the establishment of a fishery closure	*Fishery Bulletin*
2008	Commito et al.	Species diversity in the soft-bottom intertidal zone: biogenic structure, sediment, and macrofauna across mussel bed spatial scales	*Journal of Experimental Marine Biology and Ecology*
2008	Erbland & Ozbay	Comparison of the macrofaunal communities inhabiting a *Crassostrea vircinica* oyster reef and oyster aquaculture gear in Indian River Bay, Delaware	*Journal of Shellfish Research*
2008	Felley et al.	Small-scale distribution of deep-sea demersal nekton and other megafauna in the Charlie-Gibbs Fracture Zone of the Mid-Atlantic Ridge	*Deep Sea Research Part II: Topical Studies in Oceanography*
2008	Fukunaga	Invertebrate community associated with the macroalga *Halimeda kanaloana* meadow in Maui, Hawaii	*International Review of Hydrobiology*
2008	Garcia et al.	Macrofauna associated with branching fire coral *Millepora alcicornis* (Cnidaria : Hydrozoa)	*Thalassas*
2008	Guillén et al.	Alteration of bottom roughness by benthic organisms in a sandy coastal environment	*Continental Shelf Research*
2008	Guyonnet et al.	Modified otter trawl legs to reduce damage and mortality of benthic organisms in North East Atlantic fisheries (Bay of Biscay)	*Journal of Marine Systems*
2008	Hirst	Surrogate measures for assessing cryptic faunal biodiversity on macroalgal-dominated subtidal reefs	*Biological Conservation*
2008	Jennings et al.	Body-size dependent temporal variations in nitrogen stable isotope ratios in food webs	*Marine Ecology Progress Series*

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Year	Authors	Title	Journal
2008	Kochmann et al.	Shift from native mussels to alien oysters: differential effects of ecosystem engineers	*Journal of Experimental Marine Biology and Ecology*
2008	Lam et al.	Shell-bearing Mollusca (Bivalvia and Gastropoda) from submarine caves in Hong Kong	*Journal of Natural History*
2008	Metcalfe & Glasby	Diversity of polychaeta (Annelida) and other worm taxa in mangrove habitats of Darwin Harbour, northern Australia	*Journal of Sea Research*
2008	Micheli et al.	Alteration of seagrass species composition and function over two decades	*Ecological Monographs*
2008	Morton & Bamber	The joint Swire Institute of Marine Science, Hong Kong, and Natural History Museum, London, Hong Kong Submarine Caves Expedition, 2002: discussion, conclusions and recommendations for conservation	*Journal of Natural History*
2008	Moura et al.	Is surface orientation a determinant for colonisation patterns of vagile and sessile macrobenthos on artificial reefs?	*Biofouling*
2008	Muir & Bamber	New polychaete (Annelida) records and a new species from Hong Kong: the families Polynoidae, Sigalionidae, Chrysopetalidae, Pilargiidae, Nereididae, Opheliidae, Ampharetidae and Terebellidae	*Journal of Natural History*
2008	Mutlu & Ergev	Spatio-temporal distribution of soft-bottom epibenthic fauna on the Cilician shelf (Turkey), Mediterranean Sea	*Revista De Biologia Tropical*
2008	Nagelkerken et al.	The habitat function of mangroves for terrestrial and marine fauna: a review	*Aquatic Botany*
2008	Nakaoka et al.	Animals on marine flowers: does the presence of flowering shoots affect mobile epifaunal assemblage in an eelgrass meadow?	*Marine Biology*
2008	Neumann et al.	Effects of cold winters and climate on the temporal variability of an epibenthic community in the German Bight	*Climate Research*
2008	Neumann et al.	Spatial variability of epifaunal communities in the North Sea in relation to sampling effort	*Helgoland Marine Research*
2008	Paetzold et al.	Responses of *Mitrella lunata* and *Caprella* spp., potential tunicate micropredators, in Prince Edward Island estuaries to acetic acid anti-fouling treatments	*Aquaculture*
2008	Partyka & Peterson	Habitat quality and salt-marsh species assemblages along an anthropogenic estuarine landscape	*Journal of Coastal Research*
2008	Prescott & Cudney-Bueno	Mobile 'reefs' in the northeastern Gulf of California: aggregations of black murex snails *Hexaplex nigritus* as habitat for invertebrates	*Marine Ecology Progress Series*
2008	Printrakoon et al.	Distribution of molluscs in mangroves at six sites in the upper Gulf of Thailand	*Raffles Bulletin of Zoology*
2008	Raes et al.	Walking with worms: coral-associated epifaunal nematodes	*Journal of Biogeography*
2008	Rees et al.	Small-scale variation within a *Modiolus modiolus* (Mollusca: Bivalvia) reef in the Irish Sea. III. Crevice, sediment infauna and epifauna from targeted cores	*Journal of the Marine Biological Association of the United Kingdom*
2008	Riedel et al.	Oxygen depletion under glass: behavioural responses of benthic macrofauna to induced anoxia in the Northern Adriatic	*Journal of Experimental Marine Biology and Ecology*
2008	Roberts et al.	Biomonitors and the assessment of ecological impacts: distribution of herbivorous epifauna in contaminated macroalgal beds	*Environmental Pollution*

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Year	Authors	Title	Journal
2008	Roberts et al.	Contamination of marine biogenic habitats and effects upon associated epifauna	*Marine Pollution Bulletin*
2008	Roberts et al.	Field and laboratory simulations of storm water pulses: behavioural avoidance by marine epifauna	*Environmental Pollution*
2008	Rueda & Salas	Molluscs associated with a subtidal *Zostera marina* L. bed in southern Spain: linking seasonal changes of fauna and environmental variables	*Estuarine, Coastal and Shelf Science*
2008	Sanderson et al.	Small-scale variation within a *Modiolus modiolus* (Mollusca: Bivalvia) reef in the Irish Sea. II. Epifauna recorded by divers and cameras	*Journal of the Marine Biological Association of the United Kingdom*
2008	Thistle et al.	Large, motile epifauna interact strongly with harpacticoid copepods and polychaetes at a bathyal site	*Deep Sea Research Part I: Oceanographic Research Papers*
2008	Tomašových	Substrate exploitation and resistance to biotic disturbance in the brachiopod *Terebratalia transversa* and the bivalve *Pododesmus macrochisma*	*Marine Ecology Progress Series*
2008	Vázquez-Bader et al.	Seasonal changes in the density and species composition of the epifaunal echinoderms recorded from the southwestern Gulf of Mexico	*Revista De Biologia Tropical*
2008	Vázquez-Luis et al.	Changes in amphipod (Crustacea) assemblages associated with shallow-water algal habitats invaded by *Caulerpa racemosa* var. *cylindracea* in the western Mediterranean Sea	*Marine Environmental Research*
2008	Vermeij et al.	The trans-Atlantic history of diversity and body size in ecological guilds	*Ecology*
2008	Witman et al.	The relation between productivity and species diversity in temperate-arctic marine ecosystems	*Ecology*
2009	Armitage & Fourqurean	Stable isotopes reveal complex changes in trophic relationships following nutrient addition in a coastal marine ecosystem	*Estuaries and Coasts*
2009	Bates	Host taxonomic relatedness and functional-group affiliation as predictors of seaweed-invertebrate epifaunal associations	*Marine Ecology Progress Series*
2009	Blanchard et al.	How does abundance scale with body size in coupled size-structured food webs?	*Journal of Animal Ecology*
2009	Brusati & Grosholz	Does invasion of hybrid cordgrass change estuarine food webs?	*Biological Invasions*
2009	Bruschetti et al.	An invasive intertidal reef-forming polychaete affect habitat use and feeding behavior of migratory and locals birds in a SW Atlantic coastal lagoon	*Journal of Experimental Marine Biology and Ecology*
2009	Cannicci et al.	Effects of urban wastewater on crab and mollusc assemblages in equatorial and subtropical mangroves of East Africa	*Estuarine, Coastal and Shelf Science*
2009	Carbines & Cole	Using a remote drift underwater video (DUV) to examine dredge impacts on demersal fishes and benthic habitat complexity in Foveaux Strait, Southern New Zealand	*Fisheries Research*
2009	Cartes et al.	The distribution of megabenthic, invertebrate epifauna in the Balearic Basin (western Mediterranean) between 400 and 2300 m: environmental gradients influencing assemblages composition and biomass trends	*Journal of Sea Research*

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Year	Authors	Title	Journal
2009	Collie et al.	Recolonization of gravel habitats on Georges Bank (northwest Atlantic)	*Deep Sea Research Part II: Topical Studies in Oceanography*
2009	Dafforn et al.	Shallow moving structures promote marine invader dominance	*Biofouling*
2009	de Juan et al.	Defining ecological indicators of trawling disturbance when everywhere that can be fished is fished: a Mediterranean case study	*Marine Policy*
2009	Gheerardyn et al.	Harpacticoida (Crustacea: Copepoda) associated with cold-water coral substrates in the Porcupine Seabight (NE Atlantic): species composition, diversity and reflections on the origin of the fauna	*Scientia Marina*
2009	Grizzle et al.	Effects of a large fishing closure on benthic communities in the western Gulf of Maine: recovery from the effects of gillnets and otter trawls	*Fishery Bulletin*
2009	Gustafsson et al.	Effects of plant species richness and composition on epifaunal colonization in brackish water angiosperm communities	*Journal of Experimental Marine Biology and Ecology*
2009	Gutow et al.	Rapid changes in the epifaunal community after detachment of buoyant benthic macroalgae	*Journal of the Marine Biological Association of the United Kingdom*
2009	Hinz et al.	Trawl disturbance on benthic communities: chronic effects and experimental predictions	*Ecological Applications*
2009	Jacobucci et al.	Temporal variation of amphipod assemblages associated with *Sargassum filipendula* (Phaeophyta) and its epiphytes in a subtropical shore	*Aquatic Ecology*
2009	Jeffreys et al.	Influence of oxygen on heterotrophic reworking of sedimentary lipids at the Pakistan margin	*Deep Sea Research Part II: Topical Studies in Oceanography*
2009	Johnson et al.	Large-scale manipulations reveal that top-down and bottom-up controls interact to alter habitat utilization by saltmarsh fauna	*Marine Ecology Progress Series*
2009	Margreth et al.	Benthic foraminifera as bioindicator for cold-water coral reef ecosystems along the Irish margin	*Deep Sea Research Part I: Oceanographic Research Papers*
2009	Marzinelli et al.	Do modified habitats have direct or indirect effects on epifauna?	*Ecology*
2009	McKinnon et al.	Differences in soft-sediment macrobenthic assemblages invaded by *Caulerpa taxifolia* compared to uninvaded habitats	*Marine Ecology Progress Series*
2009	Montagna et al.	Long-term biological effects of coastal hypoxia in Corpus Christi Bay, Texas, USA	*Journal of Experimental Marine Biology and Ecology*
2009	Morsan	Impact on biodiversity of scallop dredging in San Matías Gulf, northern Patagonia (Argentina)	*Hydrobiologia*
2009	Neumann et al.	Temporal variability in southern North Sea epifauna communities after the cold winter of 1995/1996	*ICES Journal of Marine Science*
2009	Neumann et al.	Variability of epifauna and temperature in the northern North Sea	*Marine Biology*
2009	Poore et al.	Natural densities of mesograzers fail to limit growth of macroalgae or their epiphytes in a temperate algal bed	*Journal of Ecology*

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Year	Authors	Title	Journal
2009	Rabaoui et al.	Associated fauna of the fan shell *Pinna nobilis* (Mollusca: Bivalvia) in the northern and eastern Tunisian coasts	*Scientia Marina*
2009	Rueda et al.	A highly diverse molluscan assemblage associated with eelgrass beds (*Zostera marina* L.) in the Alboran Sea: micro-habitat preference, feeding guilds and biogeographical distribution	*Scientia Marina*
2009	Rueda et al.	Changes in the composition and structure of a molluscan assemblage due to eelgrass loss in southern Spain (Alboran Sea)	*Journal of the Marine Biological Association of the United Kingdom*
2009	Spivak et al.	Epifaunal community composition and nutrient addition alter sediment organic matter composition in a natural eelgrass *Zostera marina* bed: a field experiment	*Marine Ecology Progress Series*
2009	Summerhayes et al.	Effects of oyster death and shell disarticulation on associated communities of epibiota	*Journal of Experimental Marine Biology and Ecology*
2009	Yu et al.	Seasonal variation in diel and tidal effects among benthic amphipods with different lifestyles in a sandy surf zone of Korea	*Crustaceana*
2010	Ayres-Peres & Mantelatto	Epibiont occurrence on gastropod shells used by the hermit crab *Loxopagurus loxochelis* (Anomura: Diogenidae) on the northern coast of Sao Paulo, Brazil	*Zoologia*
2010	Barnes et al.	Oyster reef community interactions: the effect of resident fauna on oyster (*Crassostrea* spp.) larval recruitment	*Journal of Experimental Marine Biology and Ecology*
2010	Borg et al.	Spatial variation in the composition of motile macroinvertebrate assemblages associated with two bed types of the seagrass *Posidonia oceanica*	*Marine Ecology Progress Series*
2010	Cacabelos et al.	Effects of habitat structure and tidal height on epifaunal assemblages associated with macroalgae	*Estuarine, Coastal and Shelf Science*
2010	Gartner et al.	Light reductions drive macroinvertebrate changes in *Amphibolis griffithii* seagrass habitat	*Marine Ecology Progress Series*
2010	Gedan & Bertness	How will warming affect the salt marsh foundation species *Spartina patens* and its ecological role?	*Oecologia*
2010	Gestoso et al.	Variability of epifaunal assemblages associated with native and invasive macroalgae	*Marine and Freshwater Research*
2010	Khan et al.	Biodiversity of epibenthic community in the inshore waters of southeast coast of India	*Biologia*
2010	Kon et al.	Effects of the physical structure of mangrove vegetation on a benthic faunal community	*Journal of Experimental Marine Biology and Ecology*
2010	Marenghi et al.	A comparison of the habitat value of sub-tidal and floating oyster (*Crassostrea virginica*) aquaculture gear with a created reef in Delaware's Inland Bays, USA	*Aquaculture International*
2010	Martinetto et al.	High abundance and diversity of consumers associated with eutrophic areas in a semi-desert macrotidal coastal ecosystem in Patagonia, Argentina	*Estuarine, Coastal and Shelf Science*
2010	Moore & Hovel	Relative influence of habitat complexity and proximity to patch edges on seagrass epifaunal communities	*Oikos*
2010	Newcombe & Taylor	Trophic cascade in a seaweed-epifauna-fish food chain	*Marine Ecology Progress Series*
2010	Nikula et al.	Circumpolar dispersal by rafting in two subantarctic kelp-dwelling crustaceans	*Marine Ecology Progress Series*

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Year	Authors	Title	Journal
2010	Norkko et al.	Conditional responses to increasing scales of disturbance, and potential implications for threshold dynamics in soft-sediment communities	*Marine Ecology Progress Series*
2010	Osman et al.	Thresholds and multiple community states in marine fouling communities: integrating natural history with management strategies	*Marine Ecology Progress Series*
2010	Poirier et al.	Influence of hydro-sedimentary factors on mollusc death assemblages in a temperate mixed tide-and-wave dominated coastal environment: implications for the fossil record	*Continental Shelf Research*
2010	Reiss et al.	Spatial patterns of infauna, epifauna, and demersal fish communities in the North Sea	*ICES Journal of Marine Science*
2010	Sellheim et al.	Effects of a nonnative habitat-forming species on mobile and sessile epifaunal communities	*Marine Ecology Progress Series*
2010	Smyth & Roberts	The European oyster (*Ostrea edulis*) and its epibiotic succession	*Hydrobiologia*
2010	Stella et al.	Variation in the structure of epifaunal invertebrate assemblages among coral hosts	*Coral Reefs*
2010	Tang et al.	Associations between macrobenthos and invasive cordgrass, *Spartina anglica*, in the Danish Wadden Sea	*Helgoland Marine Research*
2010	Tanner & Fernandes	Environmental effects of yellowtail kingfish aquaculture in South Australia	*Aquaculture Environment Interactions*
2010	Valanko et al.	Strategies of post-larval dispersal in non-tidal soft-sediment communities	*Journal of Experimental Marine Biology and Ecology*
2010	Vanreusel et al.	The contribution of deep-sea macrohabitat heterogeneity to global nematode diversity	*Marine Ecology*
2010	Voultsiadou et al.	Sponge epibionts on ecosystem-engineering ascidians: the case of *Microcosmus sabatieri*	*Estuarine, Coastal and Shelf Science*
2010	Zintzen & Massin	Artificial hard substrata from the Belgian part of the North Sea and their influence on the distributional range of species	*Belgian Journal of Zoology*
2011	Anderson et al.	Deep-sea bio-physical variables as surrogates for biological assemblages, an example from the Lord Howe Rise	*Deep Sea Research Part II: Topical Studies in Oceanography*
2011	Atkinson et al.	Effects of demersal trawling along the west coast of southern Africa: multivariate analysis of benthic assemblages	*Marine Ecology Progress Series*
2011	Burone et al.	Benthic foraminiferal distribution on the southeastern Brazilian shelf and upper slope	*Marine Biology*
2011	Carr et al.	Spatial patterns of epifaunal communities in San Francisco Bay eelgrass (*Zostera marina*) beds	*Marine Ecology*
2011	Currin et al.	The role of cyanobacteria in Southern California salt marsh food webs	*Marine Ecology*
2011	de Juan et al.	Exploring the degree of trawling disturbance by the analysis of benthic communities ranging from a heavily exploited fishing ground to an undisturbed area in the NW Mediterranean	*Scientia Marina*
2011	Douglass et al.	Food web structure in a Chesapeake Bay eelgrass bed as determined through gut contents and ^{13}C and ^{15}N isotope analysis	*Estuaries and Coasts*

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Year	Authors	Title	Journal
2011	Drouin et al.	Higher abundance and diversity in faunal assemblages with the invasion of *Codium fragile* ssp. *fragile* in eelgrass meadows	*Marine Ecology Progress Series*
2011	Ellis et al.	The benthos and fish of offshore sandbank habitats in the southern North Sea	*Journal of the Marine Biological Association of the United Kingdom*
2011	Fleddum et al.	Impact of hypoxia on the structure and function of benthic epifauna in Tolo Harbour, Hong Kong	*Marine Pollution Bulletin*
2011	Fraser et al.	Oceanic rafting by a coastal community	*Proceedings of the Royal Society B: Biological Sciences*
2011	Freeman & Creese	Predation as a driver of gastropod distribution in north-eastern New Zealand kelp forests	*Marine and Freshwater Research*
2011	Freestone & Osman	Latitudinal variation in local interactions and regional enrichment shape patterns of marine community diversity	*Ecology*
2011	Harris	Benthic environments of the Lord Howe Rise submarine plateau: introduction to the special volume	*Deep Sea Research Part II: Topical Studies in Oceanography*
2011	Harwell et al.	Landscape aspects of oyster reefs: effects of fragmentation on habitat utilization	*Journal of Experimental Marine Biology and Ecology*
2011	Hellyer et al.	Manipulating artificial habitats to benefit seahorses in Sydney Harbour, Australia	*Aquatic Conservation: Marine and Freshwater Ecosystems*
2011	Hinz et al. 2011	Effects of scallop dredging on temperate reef fauna	*Marine Ecology Progress Series*
2011	Johnson	High-marsh invertebrates are susceptible to eutrophication	*Marine Ecology Progress Series*
2011	Kon et al.	Influence of a microhabitat on the structuring of the benthic macrofaunal community in a mangrove forest	*Hydrobiologia*
2011	Lambert et al.	Quantification and prediction of the impact of fishing on epifaunal communities	*Marine Ecology Progress Series*
2011	Liuzzi & Gappa	Algae as hosts for epifaunal bryozoans: role of functional groups and taxonomic relatedness	*Journal of Sea Research*
2011	Lomovasky et al.	Macro benthic community assemblage before and after the 2007 tsunami and earthquake at Paracas Bay, Peru	*Journal of Sea Research*
2011	Luo et al.	Community characteristics of macrobenthos in waters around the Nature Reserve of the Chinese sturgeon *Acipenser sinensis* and the adjacent waters in Yangtze River Estuary	*Journal of Applied Ichthyology*
2011	Metaxas	Spatial patterns of larval abundance at hydrothermal vents on seamounts: evidence for recruitment limitation	*Marine Ecology Progress Series*
2011	Moura et al.	Estimation of secondary production of the faro/ancao artificial reefs	*Brazilian Journal of Oceanography*
2011	Navarro et al.	Filtering capacity and endoscopic analysis of sympatric infaunal and epifaunal bivalves of southern Chile	*Journal of the Marine Biological Association of the United Kingdom*
2011	Neumann & Kröncke	The effect of temperature variability on ecological functioning of epifauna in the German Bight	*Marine Ecology*
2011	Nikula et al.	Evolutionary consequences of microhabitat: population-genetic structuring in kelp- vs. rock-associated chitons	*Molecular Ecology*

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Year	Authors	Title	Journal
2011	Paavo et al.	Macrofaunal community patterns of adjacent coastal sediments with wave-reflecting or wave-dissipating characteristics	*Journal of Coastal Research*
2011	Pacciardi et al.	Effects of *Caulerpa racemosa* invasion on soft-bottom assemblages in the Western Mediterranean Sea	*Biological Invasions*
2011	Stevens & Dunn	Different food preferences in four sympatric deep-sea Macrourid fishes	*Marine Biology*
2011	Tanner	Utilisation of the invasive alga *Caulerpa taxifolia* as habitat by faunal assemblages in the Port River–Barker Inlet Estuary, South Australia	*Estuaries and Coasts*
2011	Tsubaki et al.	Pattern and process of diversification in an ecologically diverse epifaunal bivalve group Pterioidea (Pteriomorphia, Bivalvia)	*Molecular Phylogenetics and Evolution*
2011	Tuya et al.	Patterns of abundance and assemblage structure of epifauna inhabiting two morphologically different kelp holdfasts	*Hydrobiologia*
2011	Wong et al.	Evaluating estuarine habitats using secondary production as a proxy for food web support	*Marine Ecology Progress Series*
2012	Anderson & Lovvorn	Seasonal dynamics of prey size mediate complementary functions of mussel beds and seagrass habitats for an avian predator	*Marine Ecology Progress Series*
2012	Arponen & Boström	Responses of mobile epifauna to small-scale seagrass patchiness: is fragmentation important?	*Hydrobiologia*
2012	Bishop et al.	Density-dependent facilitation cascades determine epifaunal community structure in temperate Australian mangroves	*Ecology*
2012	Byers et al.	Impacts of an abundant introduced ecosystem engineer within mudflats of the southeastern US coast	*Biological Invasions*
2012	Cutajar et al.	Impacts of the invasive grass *Spartina anglica* on benthic macrofaunal assemblages in a temperate Australian saltmarsh	*Marine Ecology Progress Series*
2012	de Juan & Demestre	A Trawl Disturbance Indicator to quantify large scale fishing impact on benthic ecosystems	*Ecological Indicators*
2012	Elahi & Sebens	Consumers mediate natural variation between prey richness and resource use in a benthic marine community	*Marine Ecology Progress Series*
2012	Gestoso et al.	Effects of macroalgal identity on epifaunal assemblages: native species versus the invasive species *Sargassum muticum*	*Helgoland Marine Research*
2012	Gullström et al.	Spatial patterns and environmental correlates in leaf-associated epifaunal assemblages of temperate seagrass (*Zostera marina*) meadows	*Marine Biology*
2012	Gustafsson & Salo	The effect of patch isolation on epifaunal colonization in two different seagrass ecosystems	*Marine Biology*
2012	Hamilton et al.	One species of seagrass cannot act as a surrogate for others in relation to providing habitat for other taxa	*Marine Ecology Progress Series*
2012	Haupt et al.	Intra-regional translocations of epifaunal and infaunal species associated with cultured Pacific oysters *Crassostrea gigas*	*African Journal of Marine Science*
2012	Hepburn et al.	Uptake and transport of nitrogen derived from sessile epifauna in the giant kelp *Macrocystis pyrifera*	*Aquatic Biology*

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Year	Authors	Title	Journal
2012	Janiak & Whitlatch	Epifaunal and algal assemblages associated with the native *Chondrus crispus* (Stackhouse) and the non-native *Grateloupia turuturu* (Yamada) in eastern Long Island Sound	*Journal of Experimental Marine Biology and Ecology*
2012	Källén et al.	*Seagrass*-epifauna relationships in a temperate South African estuary: interplay between patch-size, within-patch location and algal fouling	*Estuarine, Coastal and Shelf Science*
2012	Karlson & Osman	Species composition and geographic distribution of invertebrates in fouling communities along the east coast of the USA: a regional perspective	*Marine Ecology Progress Series*
2012	Lambert et al.	Implications of using alternative methods of vessel monitoring system (VMS) data analysis to describe fishing activities and impacts	*ICES Journal of Marine Science*
2012	Lewis & Anderson	Top-down control of epifauna by fishes enhances seagrass production	*Ecology*
2012	Macias	Faunistic analysis of the caridean shrimps inhabiting seagrasses along the NW coast of the Gulf of Mexico and Caribbean Sea	*Revista De Biologia Tropical*
2012	Martinez et al.	Spatial distribution of epibenthic molluscs on a sandstone reef in the Northeast of Brazil	*Brazilian Journal of Biology*
2012	Marzinelli et al.	Artificial structures influence fouling on habitat-forming kelps	*Biofouling*
2012	Mosch et al.	Factors influencing the distribution of epibenthic megafauna across the Peruvian oxygen minimum zone	*Deep Sea Research Part I: Oceanographic Research Papers*
2012	Nerot et al.	Stable isotope variations in benthic filter feeders across a large depth gradient on the continental shelf	*Estuarine, Coastal and Shelf Science*
2012	Pagliosa et al.	Influence of piers on functional groups of benthic primary producers and consumers in the channel of a subtropical coastal lagoon	*Brazilian Journal of Oceanography*
2012	Przeslawski et al.	Deep-sea *Lebensspuren* of the Australian continental margins	*Deep Sea Research Part I: Oceanographic Research Papers*
2012	Ragnarsson & Burgos	Separating the effects of a habitat modifier, *Modiolus modiolus* and substrate properties on the associated megafauna	*Journal of Sea Research*
2012	Riedel et al.	Tolerance of benthic macrofauna to hypoxia and anoxia in shallow coastal seas: a realistic scenario	*Marine Ecology Progress Series*
2012	Spicer & Widdicombe	Acute extracellular acid–base disturbance in the burrowing sea urchin *Brissopsis lyrifera* during exposure to a simulated CO_2 release	*Science of The Total Environment*
2012	Strain et al.	The long-term impacts of fisheries on epifaunal assemblage function and structure, in a Special Area of Conservation	*Journal of Sea Research*
2012	Tait & Hovel	Do predation risk and food availability modify prey and mesopredator microhabitat selection in eelgrass (*Zostera marina*) habitat?	*Journal of Experimental Marine Biology and Ecology*
2012	Tyrrell et al.	Salt marsh fucoid algae: overlooked ecosystem engineers of north temperate salt marshes	*Estuaries and Coasts*
2012	Wilkie et al.	Are native *Saccostrea glomerata* and invasive *Crassostrea gigas* oysters' habitat equivalents for epibenthic communities in south-eastern Australia?	*Journal of Experimental Marine Biology and Ecology*

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Year	Authors	Title	Journal
2012	Yorke & Metaxas	Relative importance of kelps and fucoids as substrata of the invasive epiphytic bryozoan *Membranipora membranacea* in Nova Scotia, Canada	*Aquatic Biology*
2013	Barnes et al.	Biodiversity in saline coastal lagoons: patterns of distribution and human impacts on sponge and ascidian assemblages	*Diversity and Distributions*
2013	Bell et al.	Lebensspuren of the bathyal Mid-Atlantic Ridge	*Deep Sea Research Part II: Topical Studies in Oceanography*
2013	Bilkovic et al.	Ecological tradeoffs of stabilized salt marshes as a shoreline protection strategy: effects of artificial structures on macrobenthic assemblages	*Ecological Engineering*
2013	Bishop et al.	Morphological traits and density of foundation species modulate a facilitation cascade in Australian mangroves	*Ecology*
2013	Bowden et al.	Cold seep epifaunal communities on the Hikurangi Margin, New Zealand: composition, succession, and vulnerability to human activities	*Plos One*
2013	Brandt et al.	Epifauna of the Sea of Japan collected via a new epibenthic sledge equipped with camera and environmental sensor systems	*Deep Sea Research Part II: Topical Studies in Oceanography*
2013	Broszeit et al.	Seasonal oxygen-driven migration of mobile benthic fauna affected by natural water column stratification	*Estuarine, Coastal and Shelf Science*
2013	Cartes et al.	Geomorphological, trophic and human influences on the bamboo coral Isidella elongata assemblages in the deep Mediterranean: to what extent does Isidella form habitat for fish and invertebrates?	*Deep Sea Research Part I: Oceanographic Research Papers*
2013	Coleman et al.	Using a no-take zone to assess the impacts of fishing: sessile epifauna appear insensitive to environmental disturbances from commercial potting	*Journal of Experimental Marine Biology and Ecology*
2013	Cook et al.	The substantial first impact of bottom fishing on rare biodiversity hotspots: a dilemma for evidence-based conservation	*Plos One*
2013	Dauvin et al.	Interactions between aggregations and environmental factors explain spatio-temporal patterns of the brittle-star *Ophiothrix fragilis* in the eastern Bay of Seine	*Estuarine, Coastal and Shelf Science*
2013	de Juan et al.	Benthic habitat characterisation of soft-bottom continental shelves: integration of acoustic surveys, benthic samples and trawling disturbance intensity	*Estuarine, Coastal and Shelf Science*
2013	Delgado et al.	Spatial characterization of megabenthic epifauna of soft bottoms around mud volcanoes in the Gulf of Cadiz	*Journal of Natural History*
2013	Dhib et al.	Contrasting key roles of *Ruppia cirrhosa* in a southern Mediterranean lagoon: reservoir for both biodiversity and harmful species and indicator of lagoon health status	*Marine Pollution Bulletin*
2013	Do et al.	Limited consequences of seagrass decline on benthic macrofauna and associated biotic indicators	*Estuaries and Coasts*
2013	Ellis et al.	Epibenthic assemblages in the Celtic Sea and associated with the Jones Bank	*Progress in Oceanography*
2013	Engelen et al.	Faunal differences between the invasive brown macroalga *Sargassum muticum* and competing native macroalgae	*Biological Invasions*
2013	Fleddum et al.	Changes in biological traits of macro-benthic communities subjected to different intensities of demersal trawling along the west coast of southern Africa	*Journal of the Marine Biological Association of the United Kingdom*

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Year	Authors	Title	Journal
2013	Foveau et al.	Distribution patterns in the benthic diversity of the eastern English Channel	*Marine Ecology Progress Series*
2013	Gartner et al.	Habitat preferences of macroinvertebrate fauna among seagrasses with varying structural forms	*Journal of Experimental Marine Biology and Ecology*
2013	Gribben et al.	Positive versus negative effects of an invasive ecosystem engineer on different components of a marine ecosystem	*Oikos*
2013	Hammerschlag-Peyer et al.	Predator effects on faunal community composition in shallow seagrass beds of The Bahamas	*Journal of Experimental Marine Biology and Ecology*
2013	Krone et al.	Epifauna dynamics at an offshore foundation – implications of future wind power farming in the North Sea	*Marine Environmental Research*
2013	Laboy-Nieves & Muniz-Barretto	Epifauna associated with the sea cucumber *Holothuria mexicana* in Puerto Rico	*Echinoderms in a Changing World*[a]
2013	Lambert et al.	A comparison of two techniques for the rapid assessment of marine habitat complexity	*Methods in Ecology and Evolution*
2013	MacDonald & Weis	Fish community features correlate with prop root epibionts in Caribbean mangroves	*Journal of Experimental Marine Biology and Ecology*
2013	Mangano et al.	Evidence of trawl disturbance on mega-epibenthic communities in the Southern Tyrrhenian Sea	*Marine Ecology Progress Series*
2013	Neumann et al.	Benthos and demersal fish habitats in the German Exclusive Economic Zone (EEZ) of the North Sea	*Helgoland Marine Research*
2013	Ortiz et al.	Network properties and keystoneness assessment in different intertidal communities dominated by two ecosystem engineer species (SE Pacific coast): a comparative analysis	*Ecological Modelling*
2013	Pascal et al.	Response of the benthic food web to short- and long-term nutrient enrichment in saltmarsh mudflats	*Marine Ecology Progress Series*
2013	Popadić et al.	Impact evaluation of the industrial activities in the Bay of Bakar (Adriatic Sea, Croatia): recent benthic foraminifera and heavy metals	*Marine Pollution Bulletin*
2013	Prato et al.	Seasonal fluctuations of some biological traits of the invader *Caprella scaura* (Crustacea: Amphipoda: Caprellidae) in the Mar Piccolo of Taranto (Ionian Sea, southern Italy)	*Scientia Marina*
2013	Reinhardt et al.	Effects of temperature on the recruitment phenology and niche overlap of shallow epifaunal assemblages in southern New England	*Marine Ecology Progress Series*
2013	Riera et al.	Hard and soft-bottom macrozoobenthos in subtidal communities around an inactive harbour area (Gran Canaria, Canary Islands)	*Vie et Milieu – Life and Environment*
2013	Roff et al.	Macroalgal associations of motile epifaunal invertebrate communities on coral reefs	*Marine Ecology*
2013	Ross et al.	Spatially variable effects of a marine pest on ecosystem function	*Oecologia*
2013	Sciberras et al.	Benthic community response to a scallop dredging closure within a dynamic seabed habitat	*Marine Ecology Progress Series*
2013	Sell & Kröncke	Correlations between benthic habitats and demersal fish assemblages — a case study on the Dogger Bank (North Sea)	*Journal of Sea Research*

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Year	Authors	Title	Journal
2013	Smith et al.	Effects of chronic bottom fishing on the benthic epifauna and diets of demersal fishes on northern Georges Bank	*Marine Ecology Progress Series*
2013	Staszak & Armitage	Evaluating salt marsh restoration success with an index of ecosystem integrity	*Journal of Coastal Research*
2013	Tuya et al.	Seagrass responses to nutrient enrichment depend on clonal integration, but not flow-on effects on associated biota	*Marine Ecology Progress Series*
2013	Urra et al.	Seasonal variation of molluscan assemblages in different strata of photophilous algae in the Alboran Sea (western Mediterranean)	*Journal of Sea Research*
2013	Vitaliano et al.	Broad-scale, dense amphipod tube aggregations on the sea bed: implications for resource species that utilize benthic habitats	*Fisheries Oceanography*
2013	Wolf et al.	Synergistic effects of algal overgrowth and corallivory on Caribbean reef-building corals	*Ecology*
2014	Altieri & Witman	Modular mobile foundation species as reservoirs of biodiversity	*Ecosphere*
2014	Bedini et al.	Mobile epifaunal assemblages associated with *Cystoseira* beds: comparison between areas invaded and not invaded by *Lophocladia lallemandii*	*Scientia Marina*
2014	Bhagirathan et al.	Impact of bottom trawling on the epifauna off Veraval coast, India	*Indian Journal of Geo-Marine Sciences*
2014	Blain & Gagnon	Canopy-forming seaweeds in urchin-dominated systems in eastern Canada: structuring forces or simple prey for keystone grazers?	*Plos One*
2014	Blake et al.	Patterns of seagrass community response to local shoreline development	*Estuaries and Coasts*
2014	Boulcott et al.	Impact of scallop dredging on benthic epifauna in a mixed-substrate habitat	*ICES Journal of Marine Science*
2014	Brahim et al.	Bathymetric variation of epiphytic assemblages on *Posidonia oceanica* (L.) Delile leaves in relation to anthropogenic disturbance in the southeastern Mediterranean	*Environmental Science and Pollution Research*
2014	Buzá-Jacobucci & Pereira-Leite	The role of epiphytic algae and different species of *Sargassum* in the distribution and feeding of herbivorous amphipods	*Latin American Journal of Aquatic Research*
2014	Carvalho et al.	Biodiversity patterns of epifaunal assemblages associated with the gorgonians *Eunicella gazella* and *Leptogorgia lusitanica* in response to host, space and time	*Journal of Sea Research*
2014	Cebrian et al.	Eutrophication-driven shifts in primary producers in shallow coastal systems: implications for system functional change	*Estuaries and Coasts*
2014	Corrêa et al.	Diversity and composition of macro- and meiofaunal carapace epibionts of the hawksbill sea turtle (*Eretmochelys imbricata* Linnaeus, 1822) in Atlantic waters	*Marine Biodiversity*
2014	Fariñas-Franco & Roberts	Early faunal successional patterns in artificial reefs used for restoration of impacted biogenic habitats	*Hydrobiologia*
2014	Fernandez et al.	Temporal variation in richness and composition of recruits in a diverse cnidarian assemblage of subtropical Brazil	*Journal of Experimental Marine Biology and Ecology*

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Year	Authors	Title	Journal
2014	Fukunaga et al.	Epifaunal community structure and ammonium uptake compared for the invasive algae, *Gracilaria salicornia* and *Acanthophora specifera*, and the native alga, *Padina thivyi*	*Journal of Experimental Marine Biology and Ecology*
2014	Gatune et al.	Growth and survival of post-larval giant tiger shrimp *Penaeus monodon* feeding on mangrove leaf litter biofilms	*Marine Ecology Progress Series*
2014	Hosono	Temperature explains reproductive dynamics in caprellids at different latitudes	*Marine Ecology Progress Series*
2014	Huang et al.	Do past climate states influence diversity dynamics and the present-day latitudinal diversity gradient?	*Global Ecology and Biogeography*
2014	Hughes	Benthic habitat and megafaunal zonation across the Hebridean Slope, western Scotland, analysed from archived seabed photographs	*Journal of the Marine Biological Association of the United Kingdom*
2014	Jones et al.	Asphalt mounds and associated biota on the Angolan margin	*Deep Sea Research Part I: Oceanographic Research Papers*
2014	Konsulova & Doncheva	Ecological impact assessment of groins in Varna Bay (Black Sea, Bulgaria) – a prerequisite for application of environmentally friendly shore protection structures	*Acta Zoologica Bulgarica*
2014	Kornijow	A quantitative sampler for collecting invertebrates associated with deep submerged vegetation	*Aquatic Ecology*
2014	Lambert et al.	Quantifying recovery rates and resilience of seabed habitats impacted by bottom fishing	*Journal of Applied Ecology*
2014	Lange & Griffiths	Large-scale spatial patterns within soft-bottom epibenthic invertebrate assemblages along the west coast of South Africa, based on the Nansen trawl survey	*African Journal of Marine Science*
2014	Lefcheck et al.	Epifaunal invertebrates as predators of juvenile bay scallops (*Argopecten irradians*)	*Journal of Experimental Marine Biology and Ecology*
2014	Leopardas et al.	Benthic macrofaunal assemblages in multispecific seagrass meadows of the southern Philippines: variation among vegetation dominated by different seagrass species	*Journal of Experimental Marine Biology and Ecology*
2014	Esqueda-González et al.	Species composition, richness, and distribution of marine bivalve molluscs in Bahía de Mazatlán, México	*ZooKeys*
2014	Muntadas et al.	Trawling disturbance on benthic ecosystems and consequences on commercial species: a northwestern Mediterranean case study	*Scientia Marina*
2014	Navarro-Barranco et al.	Mobile epifaunal community in marine caves in comparison to open habitats	*Aquatic Biology*
2014	Nordström et al.	Benthic food-web succession in a developing salt marsh	*Marine Ecology Progress Series*
2014	Palardy & Witman	Flow, recruitment limitation, and the maintenance of diversity in marine benthic communities	*Ecology*
2014	Pierri-Daunt & Tanaka	Assessing habitat fragmentation on marine epifaunal macroinvertebrate communities: an experimental approach	*Landscape Ecology*
2014	Png-Gonzalez et al.	Comparison of epifaunal assemblages between *Cymodocea nodosa* and *Caulerpa prolifera* meadows in Gran Canaria (eastern Atlantic)	*Journal of the Marine Biological Association of the United Kingdom*
2014	Reynolds et al.	Field experimental evidence that grazers mediate transition between microalgal and seagrass dominance	*Limnology and Oceanography*

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Year	Authors	Title	Journal
2014	Ronowicz et al.	Temporal and spatial variability of zoobenthos recruitment in a north-east Atlantic marine reserve	*Journal of the Marine Biological Association of the United Kingdom*
2014	Smeulders et al.	Cold-water coral habitats of Rockall and Porcupine Bank, NE Atlantic Ocean: sedimentary facies and benthic foraminiferal assemblages	*Deep Sea Research Part II: Topical Studies in Oceanography*
2014	Smith et al.	Fish trophic engineering: ecological effects of the invasive ascidian *Didemnum vexillum* (Georges Bank, northwestern Atlantic)	*Journal of Experimental Marine Biology and Ecology*
2014	Trave & Sheaves	Bimini Islands: a characterization of the two major nursery areas; status and perspectives	*Springerplus*
2014	Tuya et al.	Ecological structure and function differs between habitats dominated by seagrasses and green seaweeds	*Marine Environmental Research*
2014	Vassallo et al.	Inventory of invertebrates from the rocky intertidal shore at Montepio, Veracruz, Mexico	*Revista Mexicana De Biodiversidad*
2014	Veiga et al.	Structural complexity of macroalgae influences epifaunal assemblages associated with native and invasive species	*Marine Environmental Research*
2014	Vidović et al.	Benthic foraminifera assemblages as elemental pollution bioindicator in marine sediments around fish farm (Vrgada Island, Central Adriatic, Croatia)	*Marine Pollution Bulletin*
2015	Barry et al.	Generalizing visual fast count estimators for underwater video surveys	*Ecosphere*
2015	Bergman et al.	Effects of a 5-year trawling ban on the local benthic community in a wind farm in the Dutch coastal zone	*ICES Journal of Marine Science*
2015	Carcedo et al.	Macrobenthic surf zone communities of temperate sandy beaches: spatial and temporal patterns	*Marine Ecology*
2015	Chen et al.	Invasive cordgrass facilitates epifaunal communities in a Chinese marsh	*Biological Invasions*
2015	Coolen et al.	Reefs, sand and reef-like sand: a comparison of the benthic biodiversity of habitats in the Dutch Borkum Reef Grounds	*Journal of Sea Research*
2015	Cúrdia et al.	Diversity and abundance of invertebrate epifaunal assemblages associated with gorgonians are driven by colony attributes	*Coral Reefs*
2015	de Jong et al.	Relationships between macrozoobenthos and habitat characteristics in an intensively used area of the Dutch coastal zone	*Ices Journal of Marine Science*
2015	de Jong et al.	Short-term impact of deep sand extraction and ecosystem-based landscaping on macrozoobenthos and sediment characteristics	*Marine Pollution Bulletin*
2015	De Mesel et al.	Succession and seasonal dynamics of the epifauna community on offshore wind farm foundations and their role as stepping stones for non-indigenous species	*Hydrobiologia*
2015	DeAmicis & Foggo	Long-term field study reveals subtle effects of the invasive alga *Sargassum muticum* upon the epibiota of *Zostera marina*	*Plos One*
2015	Dias et al.	Temporal variability in epifaunal assemblages associated with temperate gorgonian gardens	*Marine Environmental Research*
2015	Eklöf et al.	Community-level effects of rapid experimental warming and consumer loss outweigh effects of rapid ocean acidification	*Oikos*

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Year	Authors	Title	Journal
2015	Fernandez et al.	A comparison of temporal turnover of species from benthic cnidarian assemblages in tropical and subtropical harbours	*Marine Biology Research*
2015	Green & Fong	A small-scale test of the species-energy hypothesis in a southern California estuary	*Journal of Experimental Marine Biology and Ecology*
2015	Greene	Habitat characterization of a tidal energy site using an ROV: overcoming difficulties in a harsh environment	*Continental Shelf Research*
2015	Gutow et al.	Castaways can't be choosers – homogenization of rafting assemblages on floating seaweeds	*Journal of Sea Research*
2015	Hemery et al.	Patterns of benthic mega-invertebrate habitat associations in the Pacific Northwest continental shelf waters	*Biodiversity and Conservation*
2015	Howarth et al.	Sessile and mobile components of a benthic ecosystem display mixed trends within a temperate marine reserve	*Marine Environmental Research*
2015	Huang et al.	Top–down control by great blue herons *Ardea herodias* regulates seagrass-associated epifauna	*Oikos*
2015	Knight et al.	A comparison of epifaunal invertebrate communities in native eelgrass *Zostera marina* and non-native *Zostera japonica* at Tsawwassen, BC	*Marine Biology Research*
2015	Kristensen et al.	Establishment of blue mussel beds to enhance fish habitats	*Applied Ecology and Environmental Research*
2015	Lanham et al.	Beyond the border: effects of an expanding algal habitat on the fauna of neighbouring habitats	*Marine Environmental Research*
2015	Lee et al.	Baseline seabed habitat and biotope mapping for a proposed marine reserve	*PeerJ*
2015	Long et al.	Overgrowth of eelgrass by the invasive colonial tunicate *Didemnum vexillum*: consequences for tunicate and eelgrass growth and epifauna abundance	*Journal of Experimental Marine Biology and Ecology*
2015	McDonald et al.	Effects of geoduck (*Panopea generosa* Gould, 1850) aquaculture gear on resident and transient macrofauna communities of Puget Sound, Washington	*Journal of Shellfish Research*
2015	McFarlin et al.	Context-dependent effects of the loss of *Spartina altemiflora* on salt marsh invertebrate communities	*Estuarine Coastal and Shelf Science*
2015	Munari et al.	Epifauna associated to the introduced *Gracilaria vermiculophylla* (Rhodophyta; Florideophyceae: Gracilariales) and comparison with the native *Ulva rigida* (Chlorophyta; Ulvophyceae: Ulvales) in an Adriatic lagoon	*Italian Journal of Zoology*
2015	Navarro-Barranco et al.	Colonization and successional patterns of the mobile epifaunal community along an environmental gradient in a marine cave	*Marine Ecology Progress Series*
2015	Nogueira et al.	Effects of habitat structure on the epifaunal community in *Mussismilia* corals: does coral morphology influence the richness and abundance of associated crustacean fauna?	*Helgoland Marine Research*
2015	Ortiz et al.	Control Strategy scenarios for the alien lionfish *Pterois volitans* in Chinchorro Bank (Mexican Caribbean): based on semi-quantitative loop analysis	*Plos One*
2015	Ortiz et al.	Mass balanced trophic models and short-term dynamical simulations for benthic ecological systems of Mejillones and Antofagasta bays (SE Pacific): comparative network structure and assessment of human impacts	*Ecological Modelling*

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Year	Authors	Title	Journal
2015	Palmer & Montagna	Impacts of droughts and low flows on estuarine water quality and benthic fauna	*Hydrobiologia*
2015	Sepúlveda et al.	Ascidian-associated polychaetes: ecological implications of aggregation size and tube-building chaetopterids on assemblage structure in the Southeastern Pacific Ocean	*Marine Biodiversity*
2015	Sheehan et al.	The ecosystem service value of living versus dead biogenic reef	*Estuarine, Coastal and Shelf Science*
2015	Sokołowski et al.	Habitat-related patterns of soft-bottom macrofaunal assemblages in a brackish, low-diversity system (southern Baltic Sea)	*Journal of Sea Research*
2015	Torres et al.	The role of annual macroalgal morphology in driving its epifaunal assemblages	*Journal of Experimental Marine Biology and Ecology*
2015	Vader & Tandberg	Amphipods as associates of other crustacea: a survey	*Journal of Crustacean Biology*
2015	van der Zee et al.	Habitat modification drives benthic trophic diversity in an intertidal soft-bottom ecosystem	*Journal of Experimental Marine Biology and Ecology*
2015	Veeragurunathan et al.	Cultivation of *Gracilaria dura* in the open sea along the southeast coast of India	*Journal of Applied Phycology*
2015	Whomersley et al.	More bang for your monitoring bucks: detection and reporting of non-indigenous species	*Marine Pollution Bulletin*
2015	Wong & Dowd	Patterns in taxonomic and functional diversity of macrobenthic invertebrates across seagrass habitats: a case study in Atlantic Canada	*Estuaries and Coasts*
2015	Zupo et al.	Chemoreception of the seagrass *Posidonia oceanica* by benthic invertebrates is altered by seawater acidification	*Journal of Chemical Ecology*
2016	Arnold et al.	The structure of biogenic habitat and epibiotic assemblages associated with the global invasive kelp *Undaria pinnatifida* in comparison to native macroalgae	*Biological Invasions*
2016	Ba-Akdah et al.	Habitat preference and seasonal variability of epifaunal assemblages associated with macroalgal beds on the Central Red Sea coast, Saudi Arabia	*Journal of the Marine Biological Association of the United Kingdom*
2016	Bowden et al.	Deep-sea seabed habitats: do they support distinct mega-epifaunal communities that have different vulnerabilities to anthropogenic disturbance?	*Deep Sea Research Part I: Oceanographic Research Papers*
2016	Clark et al.	The NIWA seamount sled: an effective epibenthic sledge for sampling epifauna on seamounts and rough seafloor	*Deep Sea Research Part I: Oceanographic Research Papers*
2016	de Jong et al.	Ecosystem-based design rules for marine sand extraction sites	*Ecological Engineering*
2016	Demers et al.	Under the radar: sessile epifaunal invertebrates in the seagrass *Posidonia australis*	*Journal of the Marine Biological Association of the United Kingdom*
2016	Du Preez et al.	The structure and distribution of benthic communities on a shallow seamount (Cobb Seamount, northeast Pacific Ocean)	*Plos One*
2016	Figueroa et al.	Photosynthetic activity estimated as *in vivo* chlorophyll a fluorescence in calcareous red macroalgae	*Ciencias Marinas*
2016	Filimon et al.	Community structure of zoobenthos associated with *Cystoseira barbata* facies from the southern romanian black sea coast	*Journal of Environmental Protection and Ecology*

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Year	Authors	Title	Journal
2016	Fritz	Commentary: threatened by mining, polymetallic nodules are required to preserve abyssal epifauna	*Frontiers in Marine Science*
2016	Hemery & Henkel	Patterns of benthic mega-invertebrate habitat associations in the Pacific Northwest continental shelf waters: a reassessment	*Biodiversity and Conservation*
2016	Jimenez et al.	Harvesting effects on functional structure and composition of tropical invertebrate assemblages	*ICES Journal of Marine Science*
2016	Kollars et al.	Invasive décor: an association between a native decorator worm and a non-native seaweed can be mutualistic	*Marine Ecology Progress Series*
2016	Lefcheck et al.	Faunal communities are invariant to fragmentation in experimental seagrass landscapes	*Plos One*
2016	Leite et al.	Temporal variation of epi- and endofaunal assemblages associated with the red sponge *Tedania ignis* on a rocky shore (Sao Sebastiao Channel), SE Brazil	*Iheringia Serie Zoologia*
2016	Luckenbach et al.	Effects of clam aquaculture on nektonic and benthic assemblages in two shallow-water estuaries	*Journal of Shellfish Research*
2016	Marzinelli et al.	Does restoration of a habitat-forming seaweed restore associated faunal diversity?	*Restoration Ecology*
2016	McDonald et al.	Fish, macroinvertebrate and epifaunal communities in shallow coastal lagoons with varying seagrass cover of the northern Gulf of Mexico	*Estuaries and Coasts*
2016	McSkimming et al.	Habitat restoration: early signs and extent of faunal recovery relative to seagrass recovery	*Estuarine, Coastal and Shelf Science*
2016	Meyer et al.	*Hyalinoecia artifex*: field notes on a charismatic and abundant epifaunal polychaete on the US Atlantic continental margin	*Invertebrate Biology*
2016	Muntadas et al.	Assessing functional redundancy in chronically trawled benthic communities	*Ecological Indicators*
2016	Murat et al.	Silting up and development of anoxic conditions enhanced by high abundance of the geoengineer species *Ophiothrix fragilis*	*Continental Shelf Research*
2016	Navarro-Barranco et al.	Amphipod community associated with invertebrate hosts in a Mediterranean marine cave	*Marine Biodiversity*
2016	Neumann et al.	Functional composition of epifauna in the south-eastern North Sea in relation to habitat characteristics and fishing effort	*Estuarine, Coastal and Shelf Science*
2016	Piló et al.	How functional traits of estuarine macrobenthic assemblages respond to metal contamination?	*Ecological Indicators*
2016	Piras et al.	A photographic method to identify benthic assemblages based on demersal trawler discards	*Fisheries Research*
2016	Rodrigues et al.	Patterns of mollusc distribution in mangroves from the São Marcos Bay, coast of Maranhão State, Brazil	*Acta Amazonica*
2016	Rodríguez-Zaragoza et al.	Trophic models and short-term dynamic simulations for benthic-pelagic communities at Banco Chinchorro Biosphere Reserve (Mexican Caribbean): a conservation case	*Community Ecology*
2016	Rosli et al.	Differences in meiofauna communities with sediment depth are greater than habitat effects on the New Zealand continental margin: implications for vulnerability to anthropogenic disturbance	*PeerJ*

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Year	Authors	Title	Journal
2016	Tano et al.	Tropical seaweed beds are important habitats for mobile invertebrate epifauna	*Estuarine Coastal and Shelf Science*
2016	Theodor et al.	Stable carbon isotope gradients in benthic foraminifera as proxy for organic carbon fluxes in the Mediterranean Sea	*Biogeosciences*
2016	Vanreusel et al.	Threatened by mining, polymetallic nodules are required to preserve abyssal epifauna	*Scientific Reports*
2016	Walls et al.	Potential novel habitat created by holdfasts from cultivated *Laminaria digitata*: assessing the macroinvertebrate assemblages	*Aquaculture Environment Interactions*
2016	Zharikov & Lysenko	The distribution of macrobenthic epifauna in the far eastern marine reserve based on remote underwater video data	*Russian Journal of Marine Biology*
2017	Agostini et al.	What determines sclerobiont colonization on marine mollusk shells?	*Plos One*
2017	Alfaro-Lucas et al.	Bone-eating *Osedax* worms (Annelida: Siboglinidae) regulate biodiversity of deep-sea whale-fall communities	*Deep Sea Research Part II: Topical Studies in Oceanography*
2017	Balestra et al.	Coccolithophore and benthic foraminifera distribution patterns in the Gulf of Cadiz and Western Iberian Margin during Integrated Ocean Drilling Program (IODP) Expedition 339	*Journal of Marine Systems*
2017	Boyé et al.	Constancy despite variability: local and regional macrofaunal diversity in intertidal seagrass beds	*Journal of Sea Research*
2017	Collie et al.	Indirect effects of bottom fishing on the productivity of marine fish	*Fish and Fisheries*
2017	Cox et al.	Community assessment techniques and the implications for rarefaction and extrapolation with Hill numbers	*Ecology and Evolution*
2017	Davoult et al.	Multiple effects of a *Gracilaria vermiculophylla* invasion on estuarine mudflat functioning and diversity	*Marine Environmental Research*
2017	Donadi et al.	A cross-scale trophic cascade from large predatory fish to algae in coastal ecosystems	*Proceedings of the Royal Society B: Biological Sciences*
2017	Eddy et al.	Ecosystem effects of invertebrate fisheries	*Fish and Fisheries*
2017	Fernandez-Gonzalez & Sanchez-Jerez	Fouling assemblages associated with off-coast aquaculture facilities: an overall assessment of the Mediterranean Sea	*Mediterranean Marine Science*
2017	Foveau & Dauvin	Surprisingly diversified macrofauna in mobile gravels and pebbles from high-energy hydrodynamic environment of the ‘Raz Blanchard’ (English Channel)	*Regional Studies in Marine Science*
2017	Gribben et al.	Positive and negative interactions control a facilitation cascade	*Ecosphere*
2017	Hamilton et al.	Modeling local effects on propagule movement and the potential expansion of mangroves and associated fauna: testing in a sub-tropical lagoon	*Hydrobiologia*
2017	Lambert et al.	Defining thresholds of sustainable impact on benthic communities in relation to fishing disturbance	*Scientific Reports*
2017	Lavender et al.	Small-scale habitat complexity of artificial turf influences the development of associated invertebrate assemblages	*Journal of Experimental Marine Biology and Ecology*
2017	Lefcheck et al.	Restored eelgrass (*Zostera marina* L.) as a refuge for epifaunal biodiversity in mid-western Atlantic coastal bays	*Estuaries and Coasts*

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Year	Authors	Title	Journal
2017	Mach et al.	Nonnative species in British Columbia eelgrass beds spread via shellfish aquaculture and stay for the mild climate	*Estuaries and Coasts*
2017	Mariani et al.	Habitat structure and zonation patterns of northwestern Mediterranean shoreline strands	*Scientia Marina*
2017	Neumann et al.	Full-coverage spatial distribution of epibenthic communities in the south-eastern North Sea in relation to habitat characteristics and fishing effort	*Marine Environmental Research*
2017	O'Carroll et al.	Identifying relevant scales of variability for monitoring epifaunal reef communities at a tidal energy extraction site	*Ecological Indicators*
2017	O'Carroll et al.	Tidal Energy: the benthic effects of an operational tidal stream turbine	*Marine Environmental Research*
2017	Pascal et al.	Influences of geothermal sulfur bacteria on a tropical coastal food web	*Marine Ecology Progress Series*
2017	Ramalho et al.	Deep-sea mega-epibenthic assemblages from the SW Portuguese Margin (NE Atlantic) subjected to bottom-trawling fisheries	*Frontiers in Marine Science*
2017	Reynolds et al.	Ghost of invasion past: legacy effects on community disassembly following eradication of an invasive ecosystem engineer	*Ecosphere*
2017	Salmo et al.	Colonization and shift of mollusc assemblages as a restoration indicator in planted mangroves in the Philippines	*Biodiversity and Conservation*
2017	Sokołowski et al.	Recruitment pattern of benthic fauna on artificial substrates in brackish low-diversity system (the Baltic Sea)	*Hydrobiologia*
2017	Suárez-Jiménez et al.	The invasive kelp *Undaria pinnatifida* hosts an epifaunal assemblage similar to native seaweeds with comparable morphologies	*Marine Ecology Progress Series*
2017	Taylor et al.	Assessing oxygen depletion in the Northeastern Pacific Ocean during the last deglaciation using I/Ca ratios from multiple benthic foraminiferal species	*Paleoceanography*
2017	Vermeij	Shell features associated with the sand-burying habit in gastropods	*Journal of Molluscan Studies*
2017	Winkler et al.	Seasonal variation in epifaunal communities associated with giant kelp (*Macrocystis pyrifera*) at an upwelling-dominated site	*Austral Ecology*
2017	Xu et al.	Functional groupings and food web of an artificial reef used for sea cucumber aquaculture in northern China	*Journal of Sea Research*
2017	Yeager & Hovel	Structural complexity and fish body size interactively affect habitat optimality	*Oecologia*
2017	Zaabar et al.	Temporal variation and structure of macro-epifauna associated with macrophytes in the Bizerte lagoon (Tunisia, SW Mediterranean Sea)	*Journal of Natural History*
2018	Alitto et al.	Shallow-water brittle stars (Echinodermata: Ophiuroidea) from Araçá Bay (Southeastern Brazil), with spatial distribution considerations	*Zootaxa*
2018	Audino & Marian	Comparative and functional anatomy of the mantle margin in ark clams and their relatives (Bivalvia: Arcoidea) supports association between morphology and life habits	*Journal of Zoology*
2018	Baker et al.	Potential contribution of surface-dwelling *Sargassum* algae to deep-sea ecosystems in the southern North Atlantic	*Deep Sea Research Part II: Topical Studies in Oceanography*

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Year	Authors	Title	Journal
2018	Belattmania et al.	Similar epiphytic macrofauna inhabiting the introduced *Sargassum muticum* and native fucoids on the Atlantic coast of Morocco	*Cryptogamie Algologie*
2018	Belattmania et al.	The introduction of *Sargassum muticum* modifies epifaunal patterns in a Moroccan seagrass meadow	*Marine Ecology*
2018	Brix et al.	Distributional patterns of isopods (Crustacea) in Icelandic and adjacent waters	*Marine Biodiversity*
2018	Burnett & Koehl	Knots and tangles weaken kelp fronds while increasing drag forces and epifauna on the kelp	*Journal of Experimental Marine Biology and Ecology*
2018	Coffin et al.	Impacts of hypoxia on estuarine macroinvertebrate assemblages across a regional nutrient gradient	*Facets*
2018	Cunha et al.	Epiphytic hydroids (Cnidaria, Hydrozoa) contribute to a higher abundance of caprellid amphipods (Crustacea, Peracarida) on macroalgae	*Hydrobiologia*
2018	das Chagas et al.	Composition of the biofouling community associated with oyster culture in an Amazon estuary, Para State, North Brazil	*Revista De Biologia Marina Y Oceanografia*
2018	Desmond et al.	Epifaunal community structure within southern New Zealand kelp forests	*Marine Ecology Progress Series*
2018	dos Santos et al.	*Eretmochelys imbricata* shells present a dynamic substrate for a facilitative epibiont relationship between macrofauna richness and nematode diversity, structure and function	*Journal of Experimental Marine Biology and Ecology*
2018	Douglass et al.	Fish and seagrass communities vary across a marine reserve boundary, but seasonal variation in small fish abundance overshadows top-down effects of large consumer exclosures	*Journal of Experimental Marine Biology and Ecology*
2018	Eggleton et al.	How benthic habitats and bottom trawling affect trait composition in the diet of seven demersal and benthivorous fish species in the North Sea	*Journal of Sea Research*
2018	Esqueda-González et al.	Spatial analysis of bivalve mollusks diversity in Mazatlan Bay, Mexico	*Marine Biodiversity*
2018	Fariñas-Franco et al.	Protection alone may not promote natural recovery of biogenic habitats of high biodiversity damaged by mobile fishing gears	*Marine Environmental Research*
2018	French & Moore	Canopy functions of *R. maritima* and *Z. marina* in the Chesapeake Bay	*Frontiers in Marine Science*
2018	Gabara et al.	Rhodolith structural loss decreases abundance, diversity, and stability of benthic communities at Santa Catalina Island	*Marine Ecology Progress Series*
2018	Gavira-O'Neill et al.	Mobile epifauna of the invasive bryozoan *Tricellaria inopinata*: is there a potential invasional meltdown?	*Marine Biodiversity*
2018	Glaspie et al.	Effects of estuarine acidification on an oyster-associated community in New South Wales, Australia	*Journal of Shellfish Research*
2018	Ha & Williams	Eelgrass community dominated by native omnivores in Bodega Bay, California, USA	*Bulletin of Marine Science*
2018	Hamoutene et al.	Linking the presence of visual indicators of aquaculture deposition to changes in epibenthic richness at finfish sites installed over hard bottom substrates	*Environmental Monitoring and Assessment*
2018	Hemery et al.	Benthic assemblages of mega epifauna on the Oregon continental margin	*Continental Shelf Research*

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Year	Authors	Title	Journal
2018	Hermosillo-Núñez et al.	Keystone species complexes in kelp forest ecosystems along the northern Chilean coast (SE Pacific): improving multispecies management strategies	*Ecological Indicators*
2018	Hermosillo-Núñez et al.	Trophic network properties of coral ecosystems in three marine protected areas along the Mexican Pacific Coast: assessment of systemic structure and health	*Ecological Complexity*
2018	Howarth et al.	Effects of bottom trawling and primary production on the composition of biological traits in benthic assemblages	*Marine Ecology Progress Series*
2018	Janiak et al.	Artificial structures versus mangrove prop roots: a general comparison of epifaunal communities within the Indian River Lagoon, Florida, USA	*Marine Ecology Progress Series*
2018	Kaiser et al.	Recovery linked to life history of sessile epifauna following exclusion of towed mobile fishing gear	*Journal of Applied Ecology*
2018	Kaminsky et al.	Spatial analysis of benthic functional biodiversity in San Jorge Gulf, Argentina	*Oceanography*
2018	Kennedy et al.	Eelgrass as valuable nearshore foraging habitat for juvenile pacific salmon in the early marine period	*Marine and Coastal Fisheries*
2018	Kniesz et al.	Peritrich epibionts on the hadal isopod species *Macrostylis marionae* n. sp. from the Puerto Rico Trench used as indicator for sex-specific behaviour	*Deep Sea Research Part II: Topical Studies in Oceanography*
2018	Little et al.	Long-term fluctuations in epibiotic bryozoan and hydroid abundances in an Irish sea lough	*Estuarine, Coastal and Shelf Science*
2018	Lundquist et al.	Assessing benthic responses to fishing disturbance over broad spatial scales that incorporate high environmental variation	*Frontiers in Marine Science*
2018	McGann & Conrad	Faunal and stable isotopic analyses of benthic foraminifera from the Southeast Seep on Kimki Ridge offshore southern California, USA	*Deep Sea Research Part II: Topical Studies in Oceanography*
2018	Momota & Nakaoka	Seasonal change in spatial variability of eelgrass epifaunal community in relation to gradients of abiotic and biotic factors	*Marine Ecology*
2018	Monk et al.	An evaluation of the error and uncertainty in epibenthos cover estimates from AUV images collected with an efficient, spatially-balanced design	*Plos One*
2018	Montereale-Gavazzi et al.	Seafloor change detection using multibeam echosounder backscatter: case study on the Belgian part of the North Sea	*Marine Geophysical Research*
2018	Moreno et al.	Coupling biophysical processes that sustain a deep subpopulation of *Loxechinus albus* and its associated epibenthic community over a bathymetric feature	*Estuarine, Coastal and Shelf Science*
2018	Morris et al.	Can coir increase native biodiversity and reduce colonisation of non-indigenous species in eco-engineered rock pools?	*Ecological Engineering*
2018	Mosbahi et al.	Molluscs associated with intertidal *Zostera noltei* Hornemann beds in southern Tunisia (central Mediterranean): seasonal dynamics and environmental drivers	*Vie et Milieu – Life and Environment*
2018	Muntadas et al.	A knowledge platform to inform on the effects of trawling on benthic communities	*Estuarine, Coastal and Shelf Science*
2018	Nakamoto et al.	Phylogenetically diverse macrophyte community promotes species diversity of mobile epi-benthic invertebrates	*Estuarine, Coastal and Shelf Science*
2018	Namba & Nakaoka	Spatial patterns and predictor variables vary among different types of primary producers and consumers in eelgrass (*Zostera marina*) beds	*Plos One*

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Year	Authors	Title	Journal
2018	Navarro-Barranco et al.	Impoverished mobile epifaunal assemblages associated with the invasive macroalga *Asparagopsis taxiformis* in the Mediterranean Sea	*Marine Environmental Research*
2018	Parameswaran et al.	Diversity and distribution of echinoderms in the South Eastern Arabian Sea shelf under the influence of seasonal hypoxia	*Progress in Oceanography*
2018	Saarinen et al.	Epifaunal community composition in five macroalgal species – what are the consequences if some algal species are lost?	*Estuarine, Coastal and Shelf Science*
2018	Scheffel et al.	Tropicalization of the northern Gulf of Mexico: impacts of salt marsh transition to black mangrove dominance on faunal communities	*Estuaries and Coasts*
2018	Schweitzer et al.	Impacts of a multi-trap line on benthic habitat containing emergent epifauna within the Mid-Atlantic Bight	*ICES Journal of Marine Science*
2018	Singh et al.	Changes in standing stock and vertical distribution of benthic foraminifera along a depth gradient (58–2750 m) in the southeastern Arabian Sea	*Marine Biodiversity*
2018	Soler-Hurtado et al.	Structure of gorgonian epifaunal communities in Ecuador (eastern Pacific)	*Coral Reefs*
2018	Sutherland et al.	Influence of salmonid aquaculture activities on a rock-cliff epifaunal community in Jervis Inlet, British Columbia	*Marine Pollution Bulletin*
2018	Tanner et al.	Benthic biogeographic patterns in the southern Australian deep sea: do historical museum records accord with recent systematic, but spatially limited, survey data?	*Ecology and Evolution*
2018	Tilot et al.	The benthic megafaunal assemblages of the CCZ (eastern Pacific) and an approach to their management in the face of threatened anthropogenic impacts	*Frontiers in Marine Science*
2018	Vaughn & Hoellein	Bivalve impacts in freshwater and marine ecosystems	*Annual Review of Ecology, Evolution, and Systematics*[a]
2018	Venturelli et al.	Epifaunal foraminifera in an infaunal world: insights into the influence of heterogeneity on the benthic ecology of oxygen-poor, deep-sea habitats	*Frontiers in Marine Science*
2018	Viola et al.	Anthropogenic disturbance facilitates a non-native species on offshore oil platforms	*Journal of Applied Ecology*
2018	Waters et al.	Rafting dispersal in a brooding southern sea star (Asteroidea : Anasterias)	*Invertebrate Systematics*
2018	Wenger et al.	Microhabitat selectivity shapes the seascape ecology of a carnivorous macroalgae-associated tropical fish	*Marine Ecology Progress Series*
2018	Whippo et al.	Epifaunal diversity patterns within and among seagrass meadows suggest landscape-scale biodiversity processes	*Ecosphere*
2018	Williams et al.	Characterising the invertebrate megafaunal assemblages of a deep-sea (200–3000 m) frontier region for oil and gas exploration: the Great Australian Bight, Australia	*Deep Sea Research Part II: Topical Studies in Oceanography*
2018	Yusa et al.	Spatial–temporal variations in the composition of two *Zostera* species in a seagrass bed: implications for population management of a commercially exploited grass shrimp	*Fisheries Science*
2018	Zwerschke et al.	Limited impact of an invasive oyster on intertidal assemblage structure and biodiversity: the importance of environmental context and functional equivalency with native species	*Marine Biology*

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Year	Authors	Title	Journal
2019	Abdelhady et al.	Water chemistry and substrate type as major determinants of molluscan feeding habit and life–mode in lagoon sediments	*Estuarine, Coastal and Shelf Science*
2019	Audino et al.	Ark clams and relatives (Bivalvia: Arcida) show convergent morphological evolution associated with lifestyle transitions in the marine benthos	*Biological Journal of the Linnean Society*
2019	Barrientos-Lujan et al.	Ecological and functional diversity of gastropods associated with hermatypic corals of the Mexican tropical Pacific	*Marine Biodiversity*
2019	Bentley et al.	Fishers' knowledge improves the accuracy of food web model predictions	*ICES Journal of Marine Science*
2019	Bertolini	Can secondary species maintain a primary role? Consistent inter-regional effects of understory algae on diversity	*Marine Biodiversity*
2019	Bonaglia et al.	Sulfide oxidation in deep Baltic Sea sediments upon oxygenation and colonization by macrofauna	*Marine Biology*
2019	Bremec & Schejter	*Chaetopterus antarcticus* (Polychaeta: Chaetopteridae) in Argentinian shelf scallop beds: from infaunal to epifaunal life habits	*Revista De Biologia Tropical*
2019	Brooks & Crowe	Combined effects of multiple stressors: new insights into the influence of timing and sequence	*Frontiers in Ecology and Evolution*
2019	Cadier & Frouws	Experimental harvest in a tropical seagrass meadow leads to shift in associated benthic communities	*Community Ecology*
2019	Campanyà-Llovet & Snelgrove	Influence of phytodetrital quality on macroinfaunal community structure and epifaunal response	*Marine Ecology Progress Series*
2019	Carmen & Grunden	A preliminary assessment of crab predation on epifaunal fouling organisms attached to eelgrass at Martha's Vineyard, Massachusetts, USA	*Management of Biological Invasions*
2019	Casamajor et al.	*Cystoseira baccata* meadows along the French Basque coast (Bay of Biscay) as a reference for the implementation of the Water Framework and Marine Strategy EU directives	*Continental Shelf Research*
2019	Cavalcante et al.	Spatiotemporal dynamics of the molluscan community associated with seagrass on the western equatorial Atlantic	*Journal of the Marine Biological Association of the United Kingdom*
2019	Ferreira et al.	Temporal variation in peracarid assemblages inhabiting *Caulerpa racemosa* in two Brazilian rocky shores	*Marine Biodiversity*
2019	Fields et al.	Video sleds effectively survey epibenthic communities at dredged material disposal sites	*Environmental Monitoring and Assessment*
2019	Foster et al.	The invasive green alga *Avrainvillea* sp. transforms native epifauna and algal communities on a tropical hard substrate reef	*Phycological Research*
2019	Fulton et al.	Form and function of tropical macroalgal reefs in the Anthropocene	*Functional Ecology*
2019	Gan et al.	Effects of macroalgal morphology on marine epifaunal diversity	*Journal of the Marine Biological Association of the United Kingdom*
2019	Gárate et al.	Potential nitrous oxide production by marine shellfish in response to warming and nutrient enrichment	*Marine Pollution Bulletin*
2019	Garcia et al.	Population and reproductive biology of two caprellid species (Crustacea: Amphipoda) associated to *Sargassum cymosum* (Phaeophyta: Fucales) on the southeast coast of Brazil	*Nauplius*
2019	Gates et al.	Ecological role of an offshore industry artificial structure	*Frontiers in Marine Science*

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Year	Authors	Title	Journal
2019	Githaiga et al.	Seagrass removal leads to rapid changes in fauna and loss of carbon	*Frontiers in Ecology and Evolution*
2019	Guillas et al.	Settlement of juvenile glass sponges and other invertebrate cryptofauna on the Hecate Strait glass sponge reefs	*Invertebrate Biology*
2019	Hayduk et al.	Evidence for regional-scale controls on eelgrass (*Zostera marina*) and mesograzer community structure in upwelling-influenced estuaries	*Limnology and Oceanography*
2019	Henseler et al.	Coastal habitats and their importance for the diversity of benthic communities: a species- and trait-based approach	*Estuarine, Coastal and Shelf Science*
2019	Hossain	Trophic functioning of macrobenthic fauna in a tropical acidified Bornean estuary (Southeast Asia)	*International Journal of Sediment Research*
2019	Hossain et al.	Epibenthic community variation along an acidified tropical estuarine system	*Regional Studies in Marine Science*
2019	Iliff et al.	Effects of chronic pesticide exposure on an epibenthic oyster reef community	*Marine Pollution Bulletin*
2019	Ito et al.	Vertical distribution of epifauna on *Sargassum horneri*, with special reference to the occurrence of bivalve spat	*Plankton & Benthos Research*
2019	Jacobucci et al.	Influence of a narrow depth gradient on the spatial structure of *Sargassum* peracarid assemblages in Southeastern Brazil	*Marine Biodiversity*
2019	Janas et al.	Importance of benthic macrofauna and coastal biotopes for ecosystem functioning – oxygen and nutrient fluxes in the coastal zone	*Estuarine, Coastal and Shelf Science*
2019	Lomeli et al.	Evaluating off-bottom sweeps of a U.S. West Coast groundfish bottom trawl: effects on catch efficiency and seafloor interactions	*Fisheries Research*
2019	Lozano-Cortés et al.	Marine invertebrates colonizing a causeway in the Manifa offshore oilfield, Saudi Arabia	*Marine Biodiversity*
2019	Luff et al.	A simple mooring modification reduces impacts on seagrass meadows	*Scientific Reports*
2019	Lutz et al.	Differences in architecture between native and non-indigenous macroalgae influence associations with epifauna	*Journal of Experimental Marine Biology and Ecology*
2019	Meysick et al.	Context-dependent community facilitation in seagrass meadows along a hydrodynamic stress gradient	*Journal of Sea Research*
2019	Michaelis et al.	Epibenthic assemblages of hard-substrate habitats in the German Bight (south-eastern North Sea) described using drift videos	*Continental Shelf Research*
2019	Michaelis et al.	Hard-substrate habitats in the German Bight (South-Eastern North Sea) observed using drift videos	*Journal of Sea Research*
2019	Navarro-Barranco et al.	Can invasive habitat-forming species play the same role as native ones? The case of the exotic marine macroalga *Rugulopteryx okamurae* in the Strait of Gibraltar	*Biological Invasions*
2019	Olivier et al.	Exploring the temporal variability of a food web using long-term biomonitoring data	*Ecography*
2019	Outinen et al.	Monitoring of sessile and mobile epifauna – considerations for non-indigenous species	*Marine Pollution Bulletin*
2019	Piechaud et al.	Automated identification of benthic epifauna with computer vision	*Marine Ecology Progress Series*
2019	Powell et al.	The intermingling of benthic macroinvertebrate communities during a period of shifting range: the "East of Nantucket" Atlantic Surfclam Survey and the existence of transient multiple stable states	*Marine Ecology*

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Year	Authors	Title	Journal
2019	Price et al.	Using 3D photogrammetry from ROV video to quantify cold-water coral reef structural complexity and investigate its influence on biodiversity and community assemblage	*Coral Reefs*
2019	Salmo et al.	Recolonization of mollusc assemblages in mangrove plantations damaged by Typhoon Chan-hom in the Philippines	*Estuarine, Coastal and Shelf Science*
2019	Seitz et al.	Production and vertical distribution of invertebrates on riprap shorelines in Chesapeake Bay: a novel rocky intertidal habitat	*Estuarine, Coastal and Shelf Science*
2019	Slavik et al.	The large-scale impact of offshore wind farm structures on pelagic primary productivity in the southern North Sea	*Hydrobiologia*
2019	Smith et al.	Detrital traits affect substitutability of a range-expanding foundation species across latitude	*Oikos*
2019	Sutherland et al.	Detecting indicator taxa associated with benthic organic enrichment using different video camera orientations	*Journal of Coastal Research*
2019	Talbot et al.	Uncovering the environmental drivers of short-term temporal dynamics in an epibenthic community from the Western English Channel	*Journal of the Marine Biological Association of the United Kingdom*
2019	Trannum et al.	Epifaunal and infaunal responses to submarine mine tailings in a Norwegian fjord	*Marine Pollution Bulletin*
2019	Tuya et al.	Biogeographical scenarios modulate seagrass resistance to small-scale perturbations	*Journal of Ecology*
2019	Wee et al.	The role of in situ coral nurseries in supporting mobile invertebrate epifauna	*Journal for Nature Conservation*
2019	Yeager et al.	Trait sensitivities to seagrass fragmentation across spatial scales shape benthic community structure	*Journal of Animal Ecology*
2019	Zhang & Silliman	A facilitation cascade enhances local biodiversity in seagrass beds	*Diversity*
2020	Babcock et al.	Changing biogeochemistry and invertebrate community composition at newly deployed artificial reefs in the northeast Gulf of Mexico	*Estuaries and Coasts*
2020	Barbosa & Taylor	Spatial and temporal trends in diet for pinfish (*Lagodon rhomboides*) from turtle grass (*Thalassia testudinum*) beds with contrasting environmental regimes in the Lower Laguna Madre, Texas	*Estuaries and Coasts*
2020	Belattmania et al.	Spatiotemporal variation of the epifaunal assemblages associated to *Sargassum muticumon* the NW Atlantic coast of Morocco	*Environmental Science and Pollution Research*
2020	Callaway et al.	Natural dynamics overshadow anthropogenic impact on marine fauna at an urbanised coastal embayment	*Science of The Total Environment*
2020	Chen et al.	*Sargassum* epifaunal communities vary with canopy size, predator biomass and seascape setting within a fringing coral reef ecosystem	*Marine Ecology Progress Series*
2020	Couce et al.	Capturing threshold responses of marine benthos along gradients of natural and anthropogenic change	*Journal of Applied Ecology*
2020	Cramer et al.	Millennial-scale change in the structure of a Caribbean reef ecosystem and the role of human and natural disturbance	*Ecography*
2020	Fraser et al.	Taxonomic composition of mobile epifaunal invertebrate assemblages on diverse benthic microhabitats from temperate to tropical reefs	*Marine Ecology Progress Series*
2020	Gagnon et al.	Facilitating foundation species: the potential for plant-bivalve interactions to improve habitat restoration success	*Journal of Applied Ecology*

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Year	Authors	Title	Journal
2020	Ge et al.	Succession of macrofaunal communities and environmental properties along a gradient of smooth cordgrass *Spartina alterniflora* invasion stages	*Marine Environmental Research*
2020	González-García et al.	Composition, structure and distribution of epibenthic communities within a mud volcano field of the northern Gulf of Cádiz in relation to environmental variables and trawling activity	*Journal of Sea Research*
2020	Gracia et al.	Meio-epifaunal wood colonization in the vicinity of methane seeps	*Marine Ecology*
2020	Kodama et al.	Effect of algal phenology on seasonal dynamics of gammarid assemblages: differences between canopy and understory strata in a *Sargassum yezoense* bed	*Marine Ecology Progress Series*
2020	Lanham et al.	Facilitation cascades create a predation refuge for biodiversity in a novel connected habitat	*Ecosphere*
2020	Ledbetter & Hovel	Effects of a habitat-modifying eelgrass epibiont on predator success and epifaunal survival	*Journal of Experimental Marine Biology and Ecology*
2020	López-Garrido et al.	ROV's video recordings as a tool to estimate variation in megabenthic epifauna diversity and community composition in the Guaymas Basin	*Frontiers in Marine Science*
2020	Ma et al.	Zonation of mangrove flora and fauna in a subtropical estuarine wetland based on surface elevation	*Ecology and Evolution*
2020	Namba et al.	The effect of environmental gradient on biodiversity and similarity of invertebrate communities in eelgrass (*Zostera marina*) beds	*Ecological Research*
2020	Noble-James et al.	Monitoring shallow methane-derived authigenic carbonate: insights from a UK Marine Protected Area	*Aquatic Conservation: Marine and Freshwater Ecosystems*
2020	Pisapia et al.	Epifaunal invertebrate assemblages associated with branching Pocilloporids in Moorea, French Polynesia	*PeerJ*
2020	Proudfoot et al.	Seafloor mapping to support conservation planning in an ecologically unique fjord in Newfoundland and Labrador, Canada	*Journal of Coastal Conservation*
2020	Rouse et al.	Artificial reef design affects benthic secondary productivity and provision of functional habitat	*Ecology and Evolution*
2020	Rowden et al.	Determining coral density thresholds for identifying structurally complex vulnerable marine ecosystems in the deep sea	*Frontiers in Marine Science*
2020	Sedano et al.	Do artificial structures cause shifts in epifaunal communities and trophic guilds across different spatial scales?	*Marine Environmental Research*
2020	Sedano et al.	From sessile to vagile: understanding the importance of epifauna to assess the environmental impacts of coastal defence structures	*Estuarine, Coastal and Shelf Science*
2020	Shelamoff et al.	Kelp patch size and density influence secondary productivity and diversity of epifauna	*Oikos*
2020	Simpson et al.	Seahorse hotels: use of artificial habitats to support populations of the endangered White's seahorse *Hippocampus whitei*	*Marine Environmental Research*
2020	Stelling-Wood et al.	Habitat variability in an underwater forest: using a trait-based approach to predict associated communities	*Functional Ecology*
2020	Stevens et al.	Diet of six deep-sea grenadiers (Macrouridae)	*Journal of Fish Biology*
2020	Wei et al.	Seafloor biodiversity of Canada's three oceans: patterns, hotspots and potential drivers	*Diversity and Distributions*

[a] Book or book chapter or book series.

Appendix B

Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
1953	Allen	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1964	Pequegnat	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1967	Calder & Brehmer	Temperate	North	No size definition of epifauna given	Artificial structures
1967	Driscoll	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1967	Richards & Riley	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1968	Fager	Subtropical	North	Size range of animals defined	Benthic & unidentified habitats
1968	Matthews	Temperate	North	No size definition of epifauna given	Artificial structures
1968	Pequegnat	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1968	Snell	Temperate	North	No size definition of epifauna given	Macroalgae
1971	Bourget & Lacroix	Na	Na	No size definition of epifauna given	Benthic & unidentified habitats
1972	Sassaman & Mangum	Temperate	North	No size definition of epifauna given	Artificial structures, benthic & unidentified habitats
1973	Bourget & Lacroix	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1973	Jackson et al.	Subtropical	North	Only maximum size specified	Other biogenic habitats
1977	Koechlin	Temperate	North	No size definition of epifauna given	Artificial structures
1978	Anger	Temperate	North	No size definition of epifauna given	Artificial structures
1978	Davis & Vanblaricom	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1978	Karlson	Temperate	North	No size definition of epifauna given	Artificial structures
1979	Conover	Subtropical	North	No size definition of epifauna given	Other biogenic habitats
1979	Peterson	Temperate	North	No size definition of epifauna given	Artificial structures, benthic & unidentified habitats
1980	Beckley & McLachlan	Subtropical	South	No size definition of epifauna given	Macroalgae
1980	Fradette & Bourget	Temperate	North	No size definition of epifauna given	Artificial structures
1980	Jokiel	Tropical	North	No size definition of epifauna given	Corals
1980	Russ	Temperate	South	No size definition of epifauna given	Artificial structures
1980	Seed & Harris	Temperate	North	No size definition of epifauna given	Macroalgae

(*Continued*)

Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
1980	Stoner	Subtropical	North	No size definition of epifauna given	Seagrasses
1980	Vandolah & Bird	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1980	Wood & Seed	Temperate	North	No size definition of epifauna given	Macroalgae
1981	Kay & Keough	Temperate	South	No size definition of epifauna given	Artificial structures
1981	Seed & O'connor	Temperate	North	No size definition of epifauna given	Macroalgae
1981	Seed et al.	Temperate	North	No size definition of epifauna given	Macroalgae
1981	Shin	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1982	Bak et al.	Tropical	North	No size definition of epifauna given	Corals
1982	Beckley	Subtropical	South	No size definition of epifauna given	Macroalgae
1982	Lewis & Hollingworth	Tropical	North	No size definition of epifauna given	Seagrasses
1982	Russ	Temperate	South	No size definition of epifauna given	Artificial structures
1983	Fletcher & Day	Temperate	South	No size definition of epifauna given	Macroalgae
1983	Karlson & Shenk	Temperate	North	No size definition of epifauna given	Other biogenic habitats
1983	McDonald	Na	Na	No size definition of epifauna given	Benthic & unidentified habitats
1983	Shepherd	Subtropical	South	No size definition of epifauna given	Benthic & unidentified habitats
1983	Sheridan & Livingston	Subtropical	North	No size definition of epifauna given	Seagrasses
1983	Ward & Young	Subtropical	South	No size definition of epifauna given	Other biogenic habitats
1984	Keough	Temperate	South	No size definition of epifauna given	Other biogenic habitats
1984	Lópezjamar et al.	Temperate	North	No size definition of epifauna given	Artificial structures
1984	Patterson	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1984	Schmidt & Warner	Temperate	North	No size definition of epifauna given	Macroalgae, benthic & unidentified habitats
1984	Virnstein et al.	Tropical, subtropical, temperate	North, South	No size definition of epifauna given	Seagrasses
1985	Dewitt & Levinton	Temperate	North	Size range of animals defined	Mangroves
1985	Hootsmans & Vermaat	Temperate	North	Only minimum size specified	Seagrasses
1985	Howard	Subtropical	North	No size definition of epifauna given	Seagrasses

(*Continued*)

Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
1985	Woodhead & Jacobson	Temperate	North	No size definition of epifauna given	Artificial structures
1986	Fishelson & Haran	Subtropical	North	No size definition of epifauna given	Macroalgae
1986	Oswald & Seed	Temperate	North	No size definition of epifauna given	Macroalgae
1986	Persson & Olafsson	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1986	Todd & Turner	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1987	Cancino et al.	Temperate	South	No size definition of epifauna given	Macroalgae
1987	Demurguia & Seed	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1987	Howard	Subtropical	North	Only minimum size specified	Seagrasses
1987	Johnson & Scheibling	Temperate	North	Only minimum size specified	Macroalgae
1987	Lewis	Subtropical	North	Only minimum size specified	Macroalgae, seagrasses
1987	Rosman et al.	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1987	Virnstein & Howard	Subtropical	North	Only minimum size specified	Seagrasses
1987	Virnstein & Howard	Subtropical	North	Only minimum size specified	Macroalgae, seagrasses
1988	Feder & Pearson	Temperate	North	Only maximum size specified	Benthic & unidentified habitats
1988	Hall & Bell	Subtropical	North	No size definition of epifauna given	Macroalgae, seagrasses
1988	Okamura	Temperate	North	No size definition of epifauna given	Macroalgae
1988	Todd & Turner	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1989	Basford et al.	Temperate	North	Only maximum size specified	Benthic & unidentified habitats
1989	Costello & Myers	Temperate	North	Only minimum size specified	Other biogenic habitats
1989	Harrison	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1989	Mullineaux	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1990	Baden	Temperate	North	Size range of animals defined	Seagrasses
1990	Basford et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1990	Daniel & Robertson	Tropical	South	No size definition of epifauna given	Mangroves
1990	Davoult	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats

(*Continued*)

Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
1990	Edgar	Subtropical	North, South	Size range of animals defined	Seagrasses
1990	Edgar	Subtropical	South	Size range of animals defined	Seagrasses
1990	Edgar	Subtropical	South	Size range of animals defined	Artificial structures, seagrasses, benthic & unidentified habitats
1990	Hendrickx	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1990	Hutchings	Tropical	South	No size definition of epifauna given	Corals, benthic & unidentified habitats
1990	Kunitzer	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1990	Lambshead & Gooday	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1991	Anderson et al.	Subtropical	South	Only minimum size specified	Macroalgae
1991	Ansari et al.	Tropical	North	Only minimum size specified	Seagrasses
1991	Edgar	Subtropical	North	Only minimum size specified	Artificial structures, macroalgae
1991	Edgar	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
1991	Hopkinson et al.	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1991	Karande	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1991	Lana & Guiss	Subtropical	South	Only minimum size specified	Mangroves
1991	Marshall et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
1991	Rainer & Unsworth	Subtropical	South	No size definition of epifauna given	Seagrasses
1991	Russo	Tropical	North	Only minimum size specified	Corals, macroalgae
1991	Schneider & Mann	Temperate	North	Only minimum size specified	Seagrasses
1991	Schneider & Mann	Temperate	North	Only minimum size specified	Seagrasses
1991	Schneider & Mann	Temperate	North	Only minimum size specified	Seagrasses
1991	Stephens & Bertness	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
1991	Takeuchi & Hirano	Temperate	North	Only minimum size specified	Macroalgae
1991	Turner & Todd	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1991	Ward & Thorpe	Temperate	North	No size definition of epifauna given	Other biogenic habitats
1991	Webb & Parsons	Temperate	North	Only maximum size specified	Seagrasses

(*Continued*)

Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
1991	Zvyagintsev	Temperate	North	No size definition of epifauna given	Other biogenic habitats
1992	Ardisson & Bourget	Temperate	North	No size definition of epifauna given	Artificial structures, mangroves
1992	Aronson	Subtropical, temperate	North	No size definition of epifauna given	Other biogenic habitats
1992	Bingham	Subtropical	North	No size definition of epifauna given	Mangroves
1992	Dalby & Young	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1992	Dewarumez et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1992	Edgar	Subtropical	South	Size range of animals defined	Seagrasses, benthic & unidentified habitats
1992	Edgar & Robertson	Subtropical	South	Only minimum size specified	Seagrasses
1992	Eleftheriou & Robertson	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1992	Hily & Floch	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1992	Isaksson & Pihl	Temperate	North	No size definition of epifauna given	Seagrasses
1992	Klumpp et al.	Tropical	North	Only minimum size specified	Seagrasses
1992	Lana & Guiss	Subtropical	South	Only minimum size specified	Seagrasses
1992	Namikawa et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats
1992	Pearson & Rosenberg	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1992	Takeuchi & Hirano	Temperate	North	No size definition of epifauna given	Macroalgae
1992	Takeuchi & Hirano	Temperate	North	Only maximum size specified	Macroalgae
1993	Duineveld et al.	Tropical	North	Only maximum size specified	Benthic & unidentified habitats
1993	Edgar	Tropical, subtropical, temperate	North, South	Size range of animals defined	Macroalgae, seagrasses
1993	Edgar & Aoki	Subtropical	North	Size range of animals defined	Macroalgae
1993	Fowler & Laffoley	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1993	Gonzalez et al.	Subtropical	North	No size definition of epifauna given	Other biogenic habitats
1993	Martin-Smith	Tropical	South	Only minimum size specified	Macroalgae
1993	Mellors & Marsh	Tropical	South	Only minimum size specified	Seagrasses

(*Continued*)

Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
1993	Trowbridge	Temperate	North	No size definition of epifauna given	Macroalgae
1993	Turner & Todd	Temperate	North	No size definition of epifauna given	Artificial structures
1993	Wang & Widdows	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1994	Cattrijsse et al.	Temperate	North	No size definition of epifauna given	Mangroves
1994	Connolly	Subtropical	South	Size range of animals defined	Seagrasses
1994	Cruzabrego et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1994	Edgar	Tropical, subtropical, temperate	North, South	Size range of animals defined	Macroalgae, seagrasses, benthic & unidentified habitats
1994	Edgar et al.	Temperate	South	No size definition of epifauna given	Seagrasses
1994	Everett	Temperate	North	No size definition of epifauna given	Macroalgae
1994	Gee & Warwick	Temperate	North	Size range of animals defined	Macroalgae
1994	Gee & Warwick	Temperate	North	Only minimum size specified	Macroalgae
1994	Hardin et al.	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1994	Hostens & Hamerlynck	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1994	Jean & Hilly	Temperate	North	Only maximum size specified	Benthic & unidentified habitats
1994	Kaiser et al.	Temperate	North	Only maximum size specified	Benthic & unidentified habitats
1994	Levin et al.	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1994	Mangum	Na	Na	No size definition of epifauna given	Benthic & unidentified habitats
1994	Martin-Smith	Tropical	South	Only minimum size specified	Macroalgae
1994	Matsumasa	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1994	Monteforte & Garcia-Gasca	Subtropical	North	Only minimum size specified	Other biogenic habitats
1994	Rathburn & Corliss	Tropical	North	Only minimum size specified	Benthic & unidentified habitats
1994	Taylor & Cole	Temperate	South	Only minimum size specified	Macroalgae
1994	Todd & Keough	Temperate	South	Only minimum size specified	Artificial structures
1995	Bingham & Young	Subtropical	North	No size definition of epifauna given	Mangroves

(*Continued*)

Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
1995	Connolly	Subtropical	South	Size range of animals defined	Seagrasses
1995	Edgar & Shaw	Temperate	South	Only minimum size specified	Seagrasses
1995	Klitgaard	Temperate	North	Size range of animals defined	Other biogenic habitats
1995	McDermott & Fives	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1995	Migné & Davoult	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1995	Nalesso et al.	Tropical	South	Only minimum size specified	Other biogenic habitats
1995	Nelson	Subtropical	North	Only minimum size specified	Seagrasses
1995	Osman & Whitlatch	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1995	Takeuchi & Hirano	Temperate	North	No size definition of epifauna given	Macroalgae
1995	Taylor et al.	Temperate	South	Only minimum size specified	Turf algae & microalgae, benthic & unidentified habitats
1995	Ulrich et al.	Temperate	North	No size definition of epifauna given	Macroalgae, benthic & unidentified habitats
1995	Vilela	Tropical	North, South	Size range of animals defined	Benthic & unidentified habitats
1995	Virnstein	Subtropical	North	No size definition of epifauna given	Seagrasses
1996	Aller & Stupakoff	Tropical	South	Size range of animals defined	Benthic & unidentified habitats
1996	Barry et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1996	Barthel et al.	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1996	Benedetti-Cecchi et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1996	Boaden	Temperate	North	Only minimum size specified	Macroalgae
1996	Castricfey	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1996	Chauvaud et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1996	Connolly & Butler	Temperate	North	Size range of animals defined	Seagrasses
1996	Davenport et al.	Temperate	South	Only minimum size specified	Macroalgae
1996	Drake & Arias	Temperate	North	Size range of animals defined	Macroalgae
1996	Ellis et al.	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1996	Gee & Warwick	Tropical, subtropical, temperate	North, South	Only minimum size specified	Benthic & unidentified habitats

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
1996	Gooday	Tropical, subtropical, temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1996	Jacobi & Langevin	Tropical	South	No size definition of epifauna given	Artificial structures
1996	Kuhne & Rachor	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1996	Lemmens et al.	Subtropical	South	Only minimum size specified	Seagrasses
1996	Levin et al.	Subtropical	North	No size definition of epifauna given	Mangroves
1996	Li et al.	Subtropical, temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
1996	Posey et al.	Subtropical	North	No size definition of epifauna given	Artificial structures
1996	Rathburn et al.	Tropical	North	Only minimum size specified	Benthic & unidentified habitats
1996	Schlacher & Wooldridge	Subtropical	South	Only minimum size specified	Benthic & unidentified habitats
1996	Schrijvers et al.	Tropical	South	Only minimum size specified	Mangroves
1996	Thomas	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats
1996	Williamson & Creese	Temperate	South	size range of animals defined	Turf algae & microalgae
1997	Aller	Temperate	North	size range of animals defined	Benthic & unidentified habitats
1997	Boström & Bonsdorff	Temperate	North	Only minimum size specified	Seagrasses
1997	Buhs & Reise	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1997	Collie et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1997	Connolly	Subtropical	South	Size range of animals defined	Seagrasses, benthic & unidentified habitats
1997	LeClair & LaBarbera	Tropical	North	No size definition of epifauna given	Corals
1997	Livingston	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats
1997	Livingston et al.	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats
1997	Manley & Shaw	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
1997	McClanahan & Sala	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1997	McCorkle et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1997	McKnight & Probert	Temperate	South	Only minimum size specified	Benthic & unidentified habitats
1997	Russo	Temperate	North	Only minimum size specified	Macroalgae

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
1997	Sala	Temperate	North	No size definition of epifauna given	Macroalgae
1997	Takeuchi & Hino	Temperate	North	Only minimum size specified	Seagrasses
1997	Turner et al.	Temperate	South	No size definition of epifauna given	Artificial structures
1997	Warner	Temperate	North	No size definition of epifauna given	Other biogenic habitats
1997	Wright et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1998	Bacon et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats, benthic & unidentified habitats
1998	Chapman	Subtropical	South	Only minimum size specified	Mangroves
1998	Engel & Kvitek	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1998	Flynn et al.	Subtropical	South	Only minimum size specified	Mangroves
1998	Glasby	Subtropical	South	No size definition of epifauna given	Benthic & unidentified habitats
1998	Hata & Nakata	Temperate	North	No size definition of epifauna given	Seagrasses
1998	Hatcher	Temperate	North	Only minimum size specified	Artificial structures
1998	Jernakoff & Nielsen	Subtropical	South	Size range of animals defined	Seagrasses
1998	Knowles & Bell	Subtropical	North	Only minimum size specified	Seagrasses
1998	MacDonald et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats, benthic & unidentified habitats
1998	Magorrian & Service	Temperate	North	No size definition of epifauna given	Other biogenic habitats
1998	Mazouni et al.	Temperate	North	No size definition of epifauna given	Artificial structures
1998	Osman & Whitlatch	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1998	Sardá et al.	Temperate	North	No size definition of epifauna given	Mangroves
1998	Sasekumar & Chong	Tropical	North	No size definition of epifauna given	Mangroves
1998	Schrijvers et al.	Tropical	South	Size range of animals defined	Mangroves
1998	Tanaka & Leite	Tropical	South	Size range of animals defined	Macroalgae
1998	Taylor	Temperate	South	Size range of animals defined	Macroalgae
1998	Taylor	Temperate	South	Only minimum size specified	Macroalgae, turf algae & microalgae, other biogenic habitats
1998	Taylor	Temperate	South	Only minimum size specified	Macroalgae

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
1998	Taylor & Rees	Temperate	South	Size range of animals defined	Macroalgae
1998	Thrush et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
1998	Walsh & Mitchell	Temperate	South	No size definition of epifauna given	Seagrasses
1998	Whitlatch & Osman	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1998	Widdows et al.	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
1998	Wieczorek & Todd	Na	Na	No size definition of epifauna given	Benthic & unidentified habitats
1998	Wildish & Fader	Temperate	North	No size definition of epifauna given	Other biogenic habitats
1998	Witman & Grange	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
1998	Wolff et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1999	Bologna & Heck	Subtropical	North	Only minimum size specified	Artificial structures, seagrasses
1999	Brown & Taylor	Temperate	South	Only minimum size specified	Turf algae & microalgae
1999	Connell	Temperate	South	No size definition of epifauna given	Artificial structures
1999	Connell & Anderson	Subtropical	South	No size definition of epifauna given	Macroalgae
1999	Cranfield et al.	Temperate	South	No size definition of epifauna given	Other biogenic habitats
1999	Davenport et al.	Temperate	South	Only minimum size specified	Macroalgae
1999	Edgar	Temperate	South	No size definition of epifauna given	Artificial structures, seagrasses
1999	Edgar	Temperate	South	No size definition of epifauna given	Artificial structures, seagrasses
1999	Freese et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1999	Glasby	Subtropical	South	No size definition of epifauna given	Seagrasses
1999	Glasby	Subtropical	South	Only minimum size specified	Artificial structures, seagrassess, benthic & unidentified habitats
1999	Glasby	Subtropical	South	No size definition of epifauna given	Artificial structures, seagrassess, benthic & unidentified habitats
1999	Hily & Bouteille	Temperate	North	Only minimum size specified	Seagrasses
1999	Jewett et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1999	Kenyon et al.	Tropical	South	Only minimum size specified	Artificial structures, seagrasses
1999	Lavery et al.	Subtropical	South	Only minimum size specified	Macroalgae

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
1999	Lepoint et al.	Temperate	North	No size definition of epifauna given	Seagrasses
1999	Morri et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1999	Prena et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1999	Ramos	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
1999	Rees et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1999	Rees et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1999	Rose et al.	Subtropical	North	Only minimum size specified	Seagrasses
1999	Saiz-Salinas & Urkiaga-Alberdi	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1999	Sánchez-Jerez et al.	Temperate	North	Only minimum size specified	Seagrasses
1999	Sánchez-Jerez et al.	Temperate	North	No size definition of epifauna given	Seagrasses
1999	Smallwood et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1999	Smith & Witman	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
1999	Tarasov et al.	Tropical	South	No size definition of epifauna given	Artificial structures
1999	Viejo	Temperate	North	Size range of animals defined	Macroalgae
2000	Cocito et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2000	Cohen et al.	Temperate	South	Only minimum size specified	Benthic & unidentified habitats
2000	Collie et al.	Tropical, subtropical, temperate	North: temperate South: tropical, subtropical, temperate	No size definition of epifauna given	Benthic & unidentified habitats
2000	Collie et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats, benthic & unidentified habitats
2000	Dando et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2000	Edgar & Barrett	Temperate	South	Only minimum size specified	Benthic & unidentified habitats
2000	Ellis et al.	Temperate	North	Only maximum size specified	Benthic & unidentified habitats
2000	Gage et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2000	Glasby	Subtropical	South	No size definition of epifauna given	Benthic & unidentified habitats

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2000	Jablonski et al.	Tropical, subtropical, temperate	North: tropical, subtropical, temperate South: tropical	No size definition of epifauna given	Benthic & unidentified habitats
2000	Kaiser et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2000	Roy et al.	Tropical, subtropical, temperate	North, South	No size definition of epifauna given	Benthic & unidentified habitats
2000	Rumohr & Kujawski	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2000	Sagasti et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2000	Sánchez-Moyano et al.	Temperate	North	Only minimum size specified	Macroalgae
2000	Smith	Temperate	South	Only minimum size specified	Turf algae & microalgae
2000	Sutherland et al.	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
2000	Tuck et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2000	Veale et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2001	Beaulieu	Subtropical	North	Only minimum size specified	Other biogenic habitats
2001	Beaulieu	Subtropical	North	Only minimum size specified	Other biogenic habitats
2001	Bradshaw et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2001	Brooks & Bell	Subtropical	North	No size definition of epifauna given	Macroalgae, seagrasses
2001	Cranfield et al.	Temperate	South	No size definition of epifauna given	Other biogenic habitats
2001	Dean & Jewett	Temperate	North	No size definition of epifauna given	Macroalgae, seagrasses, benthic & unidentified habitats
2001	Duffy et al.	Temperate	North	Only minimum size specified	Seagrasses
2001	Dumbauld et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2001	Glasby	Subtropical	South	Only minimum size specified	Artificial structures, benthic & unidentified habitats
2001	Gooday et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2001	Henry	Temperate	North	No size definition of epifauna given	Corals
2001	Jennings et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2001	Jennings et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2001	Kollmann & Stachowitsch	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2001	Lee et al.	Tropical	North	Only minimum size specified	Artificial structures, seagrasses
2001	Mancinelli & Rossi	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2001	Maughan	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2001	Nakaoka et al.	Temperate	North	Only minimum size specified	Seagrasses
2001	Oh et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2001	Parker et al.	Temperate	North	Only minimum size specified	Seagrasses
2001	Prieto et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2001	Robinson et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2001	Sagasti et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2001	Sánchez-Moyano et al.	Temperate	North	Only minimum size specified	Macroalgae
2001	Sfriso et al.	Temperate	North	Only minimum size specified	Macroalgae, seagrasses, benthic & unidentified habitats
2001	Smith	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2001	Sudo & Azeta	Subtropical	North	Only minimum size specified	Seagrasses, benthic & unidentified habitats
2001	Thrush et al.	Temperate	South	Only minimum size specified	Benthic & unidentified habitats
2001	Vytopil & Willis	Tropical	South	Only minimum size specified	Corals
2001	Wright	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2001	Zühlke et al.	Temperate	North	Only maximum size specified	Benthic & unidentified habitats
2002	Bologna & Heck	Subtropical	North	Only minimum size specified	Seagrasses
2002	Brooks et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2002	Brown et al.	Temperate	North	size range of animals defined	Benthic & unidentified habitats
2002	Burton et al.	Temperate	North	No size definition of epifauna given	Artificial structures
2002	Callaway et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2002	Callaway et al.	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
2002	Cartes et al.	Tropical, subtropical, temperate	North, South	Only minimum size specified	Benthic & unidentified habitats

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2002	Dolmer	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2002	Dulvy et al.	Tropical	South	Size range of animals defined	Corals
2002	Edgar & Barrett	Temperate	South	Size range of animals defined	Benthic & unidentified habitats
2002	Fraschetti et al.	Temperate	North	No size definition of epifauna given	Macroalgae
2002	Germano & Read	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2002	Holloway & Keough	Subtropical	South	No size definition of epifauna given	Artificial structures
2002	Holloway & Keough	Subtropical, temperate	South	No size definition of epifauna given	Artificial structures
2002	Hovel et al.	Subtropical	North	No size definition of epifauna given	Seagrasses
2002	Jayaprada	Tropical	North	Only minimum size specified	Artificial structures
2002	Koch & Wolff	Tropical	South	No size definition of epifauna given	Mangroves
2002	Labarta et al.	Temperate	South	Size range of animals defined	Macroalgae
2002	Mancinelli et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2002	Matsumoto & Kohda	Subtropical	North	Only minimum size specified	Macroalgae
2002	Nakaoka et al.	Tropical	North	Only minimum size specified	Seagrasses
2002	Saier	Temperate	North	Only minimum size specified	Other biogenic habitats
2002	Sánchez-Moyano et al.	Temperate	North	Only minimum size specified	Macroalgae
2002	Smith & Rule	Subtropical	South	Only minimum size specified	Artificial structures, macroalgae, turf algae & microalgae
2002	Stachowicz et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2002	Steimle et al.	Temperate	North	Only minimum size specified	Artificial structures
2002	Thiel	Tropical, subtropical, temperate	South	Only minimum size specified	Macroalgae
2002	Velasco & Navarro	Temperate	South	Size range of animals defined	Macroalgae
2002	Yu et al.	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats
2003	Ribeiro et al.	Tropical	South	Only minimum size specified	Other biogenic habitats
2003	Ashton et al.	Tropical	North	No size definition of epifauna given	Mangroves
2003	Beaver et al.	Subtropical	North	No size definition of epifauna given	Artificial structures

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2003	Bolduc & Afton	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats
2003	Bone et al.	Tropical	North	Only minimum size specified	Seagrasses
2003	Bradshaw et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2003	Burrows et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2003	Colloca et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2003	Deidun et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2003	Diaz & Arana	Tropical	North	No size definition of epifauna given	Other biogenic habitats
2003	Edgar & Klumpp	Tropical	South	Size range of animals defined	Artificial structures, macroalgae, seagrasses
2003	Haggitt & Babcock	Temperate	South	Only minimum size specified	Macroalgae
2003	Hirst	Subtropical	South	Only minimum size specified	Macroalgae
2003	Kumagai & Aoki	Subtropical	North	No size definition of epifauna given	Corals
2003	Leite & Turra	Tropical	South	Only minimum size specified	Macroalgae
2003	Nash	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2003	Pardo & Dauer	Temperate	North	No size definition of epifauna given	Other biogenic habitats, benthic & unidentified habitats
2003	Prieto et al.	Tropical	North	No size definition of epifauna given	Seagrasses
2003	Sagasti et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2003	Schreider et al.	Subtropical	South	Size range of animals defined	Macroalgae
2003	Sepúlveda et al.	Temperate	South	Only maximum size specified	Other biogenic habitats
2003	Tanaka & Leite	Tropical	South	Only minimum size specified	Macroalgae
2003	Tanner	Subtropical	South	Only minimum size specified	Seagrasses
2003	Tanner	Subtropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2003	Thorbjorn & Petersen	Temperate	North	Only minimum size specified	Corals, other biogenic habitats, benthic & unidentified habitats
2003	Velasco & Navarro	Temperate	South	Size range of animals defined	Macroalgae
2003	Viejo & Åberg	Temperate	North	No size definition of epifauna given	Macroalgae
2003	Witman & Smith	Tropical	South	No size definition of epifauna given	Benthic & unidentified habitats

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2004	Bouillon et al.	Tropical	North, South	No size definition of epifauna given	Mangroves
2004	Diaz et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2004	Escapa et al.	Temperate	South	No size definition of epifauna given	Other biogenic habitats
2004	Gaymer et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2004	Hargrave et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2004	Healey & Hovel	Subtropical	North	No size definition of epifauna given	Artificial structures, seagrasses
2004	Henry & Kenchington	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2004	Hinz et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2004	Kaiser et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2004	Larsen & Gilfillan	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2004	Mathot et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2004	Osman & Whitlatch	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2004	Tanaka & Leite	Tropical	South	Only minimum size specified	Macroalgae
2004	Welsh & Castadelli	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2004	Wernberg et al.	Temperate	North	Only minimum size specified	Macroalgae
2004	Wikström & Kautsky	Temperate	North	No size definition of epifauna given	Macroalgae
2004	Witman et al.	Tropical, subtropical, temperate	North, South	No size definition of epifauna given	Benthic & unidentified habitats
2005	Andersen et al.	Temperate	North	Only minimum size specified	Macroalgae, benthic & unidentified habitats
2005	Bishop	Temperate	North	Only minimum size specified	Seagrasses
2005	Brown	Temperate	North	No size definition of epifauna given	Artificial structures
2005	Castañeda-Fernández-de-Lara et al.	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats
2005	Clark & Johnston	Subtropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2005	Davidson et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2005	Gage et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2005	Govenar et al.	Temperate	North	Size range of animals defined	Other biogenic habitats
2005	Hamazaki et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2005	Hepburn & Hurd	Temperate	South	No size definition of epifauna given	Macroalgae
2005	Jewett et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2005	Klumpp & Kwak	Tropical	South	Only minimum size specified	Seagrasses
2005	Luckenbach et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2005	McConnaughey et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2005	Nakamura & Sano	Subtropical	North	Only minimum size specified	Corals, seagrasses, benthic & unidentified habitats
2005	Nakaoka	Tropical, subtropical, temperate	North	No size definition of epifauna given	Seagrasses
2005	Pagliosa & Lana	Subtropical	South	Only minimum size specified	Mangroves
2005	Polte et al.	Temperate	North	Size range of animals defined	Seagrasses
2005	Polte et al.	Temperate	North	Size range of animals defined	Seagrasses
2005	Prieto et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2005	Raes & Vanreusel	Temperate	North	Only minimum size specified	Corals
2005	Rule & Smith	Subtropical	South	Size range of animals defined	Artificial structures
2005	Sgro et al.	Temperate	North	Size range of animals defined	Macroalgae
2005	Stone et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2005	Tanner	Subtropical	South	Only minimum size specified	Seagrasses
2005	Thomasson & Tunberg	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2005	Velasco & Navarro	Temperate	South	Size range of animals defined	Macroalgae
2005	Winston & Migotto	Tropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2006	Alfaro	Temperate	South	Only minimum size specified	Mangroves, seagrasses
2006	Beaumont et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2006	Burone & Pires-Vanin	Tropical	South	Only minimum size specified	Benthic & unidentified habitats

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2006	Cruz-Rivera & Paul	Tropical	North	Size range of animals defined	Macroalgae, turf algae & microalgae, other biogenic habitats
2006	Eklöf et al.	Tropical	South	Only minimum size specified	Macroalgae, seagrasses
2006	Gil et al.	Subtropical	North	No size definition of epifauna given	Macroalgae, seagrasses
2006	Guerra-García et al.	Temperate	North	No size definition of epifauna given	Macroalgae
2006	Henry et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2006	Hepburn et al.	Temperate	South	No size definition of epifauna given	Macroalgae
2006	Hinchey et al.	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
2006	Hooper & Davenport	Temperate	North	Only minimum size specified	Macroalgae
2006	Hosack et al.	Temperate	North	Only minimum size specified	Seagrasses, other biogenic habitats
2006	Kenchington et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2006	Kogan et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2006	Kouchi et al.	Temperate	North	No size definition of epifauna given	Seagrasses
2006	Lindsay et al.	Temperate	North	No size definition of epifauna given	Artificial structures
2006	Mendez	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats
2006	O'Brien et al.	Temperate	South	Only minimum size specified	Benthic & unidentified habitats
2006	Pereira et al.	Temperate	North	Size range of animals defined	Macroalgae
2006	Rae & Vanreusel	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2006	Reed & Hovel	Temperate	North	No size definition of epifauna given	Seagrasses
2006	Reiss et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2006	Roberts & Poore	Subtropical	South	Only minimum size specified	Macroalgae
2006	Roberts et al.	Subtropical	South	No size definition of epifauna given	Macroalgae
2006	Rodney & Paynter	Temperate	North	Only minimum size specified	Other biogenic habitats
2006	Royer et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2006	Schmidt & Scheibling	Temperate	North	Only minimum size specified	Macroalgae

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2006	Sibaja-Cordero & Vargas-Zamora	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2006	Sirota & Hovel	Subtropical	North	Only minimum size specified	Seagrasses
2006	Skilleter et al.	Subtropical	South	Only minimum size specified	Seagrasses
2006	Smith et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2006	Sun et al.	Tropical, subtropical, temperate	North	Only minimum size specified	Benthic & unidentified habitats
2006	Tanner	Subtropical	South	Only minimum size specified	Artificial structures, seagrasses
2006	Valente	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2006	Vizzini & Mazzola	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2006	Ward et al.	Subtropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2006	Yahel et al.	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats
2006	Zintzen et al.	Temperate	North	Only minimum size specified	Artificial structures
2007	Aníbal et al.	Temperate	North	Only minimum size specified	Macroalgae
2007	Antoniadou & Chintiroglou	Temperate	North	Only minimum size specified	Macroalgae
2007	Aravind et al.	Tropical	North	No size definition of epifauna given	Mangroves
2007	Bates & DeWreede	Temperate	North	Only minimum size specified	Macroalgae
2007	de Juan et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2007	Duineveld et al.	Temperate	North	Only minimum size specified	Artificial structures
2007	Fujiwara et al.	Subtropical	North	Size range of animals defined	Other biogenic habitats
2007	Ganesh & Raman	Tropical	North	Only minimum size specified	Benthic & unidentified habitats
2007	Govenar & Fisher	Tropical	North	Size range of animals defined	Benthic & unidentified habitats
2007	Harries et al.	Temperate	North	Only minimum size specified	Macroalgae
2007	Hirst	Temperate	South	Only minimum size specified	Macroalgae
2007	Huntley et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2007	Ince et al.	Subtropical	South	Only minimum size specified	Macroalgae, seagrasses

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2007	Irving et al.	Subtropical	South	No size definition of epifauna given	Artificial structures
2007	Itoh et al.	Temperate	North	No size definition of epifauna given	Macroalgae
2007	Jing et al.	Subtropical	North	Only minimum size specified	Mangroves
2007	Jorgensen et al.	Temperate	North	Only minimum size specified	Seagrasses
2007	Juan et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2007	Kenchington et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2007	Leite et al.	Tropical	South	Only minimum size specified	Macroalgae
2007	McDermott	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2007	Murray et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2007	O'Neill et al.	Subtropical	South	Only minimum size specified	Macroalgae
2007	Owada et al.	Subtropical, temperate	North	No size definition of epifauna given	Artificial structures, corals, benthic & unidentified habitats
2007	Powers et al.	Temperate	North	Only minimum size specified	Macroalgae
2007	Roberts et al.	Subtropical	South	Only minimum size specified	Macroalgae
2007	Robertson & Weis	Temperate	North	No size definition of epifauna given	Mangroves
2007	Rule & Smith	Subtropical	South	Only minimum size specified	Artificial structures
2007	Sánchez-Moyano et al.	Temperate	North	Only minimum size specified	Macroalgae
2007	Szarek et al.	Tropical	North	Only minimum size specified	Benthic & unidentified habitats
2007	Unsworth et al.	Tropical	North	Only minimum size specified	Seagrasses
2007	Voultsiadou et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2007	Walker et al.	Subtropical	South	No size definition of epifauna given	Artificial structures
2008	Asch & Collie	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2008	Commito et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2008	Erbland & Ozbay	Temperate	North	Size range of animals defined	Other biogenic habitats
2008	Felley et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2008	Fukunaga	Tropical	North	No size definition of epifauna given	Macroalgae

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2008	Garcia et al.	Tropical	South	No size definition of epifauna given	Corals
2008	Guillén et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2008	Guyonnet et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2008	Hirst	Subtropical	South	Only minimum size specified	Macroalgae
2008	Jennings et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2008	Kochmann et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2008	Lam et al.	Tropical	North	Only minimum size specified	Benthic & unidentified habitats
2008	Metcalfe & Glasby	Tropical	South	No size definition of epifauna given	Mangroves
2008	Micheli et al.	Subtropical	North	Only minimum size specified	Seagrasses
2008	Morton & Bamber	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2008	Moura et al.	Temperate	North	Only minimum size specified	Artificial structures
2008	Muir & Bamber	Tropical	North	Only minimum size specified	Benthic & unidentified habitats
2008	Mutlu & Ergev	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2008	Nagelkerken et al.	Na	Na	No size definition of epifauna given	Mangroves
2008	Nakaoka et al.	Temperate	North	Size range of animals defined	Seagrasses
2008	Neumann et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2008	Neumann et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2008	Paetzold et al.	Temperate	North	Size range of animals defined	Other biogenic habitats
2008	Partyka & Peterson	Subtropical	North	Only minimum size specified	Mangroves
2008	Prescott & Cudney-Bueno	Subtropical	North	Size range of animals defined	Artificial structures, other biogenic habitats
2008	Printrakoon et al.	Tropical	North	Only minimum size specified	Mangroves
2008	Raes et al.	Tropical, temperate	North: temperate South: tropical	Only minimum size specified	Corals
2008	Rees et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2008	Riedel et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2008	Roberts et al.	Subtropical	South	No size definition of epifauna given	Macroalgae

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2008	Roberts et al.	Subtropical	South	Only minimum size specified	Macroalgae, seagrasses, other biogenic habitats
2008	Roberts et al.	Na	Na	No size definition of epifauna given	Macroalgae
2008	Rueda & Salas	Temperate	North	Only minimum size specified	Seagrasses
2008	Sanderson et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2008	Thistle et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2008	Tomašových	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2008	Vázquez-Bader et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2008	Vázquez-Luis et al.	Temperate	North	Only minimum size specified	Macroalgae
2008	Vermeij et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2008	Witman et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2009	Armitage & Fourqurean	Subtropical	North	Only minimum size specified	Seagrasses
2009	Bates	Temperate	North	Only minimum size specified	Macroalgae
2009	Blanchard et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2009	Brusati & Grosholz	Temperate	North	No size definition of epifauna given	Mangroves
2009	Bruschetti et al.	Temperate	South	No size definition of epifauna given	Other biogenic habitats
2009	Cannicci et al.	Tropical, subtropical	South	No size definition of epifauna given	Mangroves
2009	Carbines & Cole	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2009	Cartes et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2009	Collie et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2009	Dafforn et al.	Subtropical	South	No size definition of epifauna given	Artificial structures
2009	de Juan et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2009	Gheerardyn et al.	Temperate	North	Only minimum size specified	Corals
2009	Grizzle et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2009	Gustafsson et al.	Temperate	North	Only minimum size specified	Mangroves
2009	Gutow et al.	Temperate	North	Only minimum size specified	Macroalgae

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2009	Hinz et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2009	Jacobucci et al.	Tropical	South	Only minimum size specified	Macroalgae
2009	Jeffreys et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2009	Johnson et al.	Temperate	North	Only minimum size specified	Mangroves
2009	Margreth et al.	Temperate	North	Size range of animals defined	Corals
2009	Marzinelli et al.	Subtropical	South	No size definition of epifauna given	Macroalgae
2009	McKinnon et al.	Temperate	South	Only minimum size specified	Macroalgae
2009	Montagna et al.	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2009	Morsan	Temperate	South	No size definition of epifauna given	Other biogenic habitats
2009	Neumann et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2009	Neumann et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2009	Poore et al.	Subtropical	South	Only minimum size specified	Macroalgae
2009	Rabaoui et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2009	Rueda et al.	Temperate	North	Only minimum size specified	Seagrasses
2009	Rueda et al.	Temperate	North	Only minimum size specified	Seagrasses
2009	Spivak et al.	Temperate	North	No size definition of epifauna given	Seagrasses
2009	Summerhayes et al.	Subtropical	South	Only minimum size specified	Other biogenic habitats
2009	Yu et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2010	Ayres-Peres & Mantelatto	Tropical	South	No size definition of epifauna given	Other biogenic habitats
2010	Barnes et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2010	Borg et al.	Temperate	North	Only minimum size specified	Seagrasses
2010	Cacabelos et al.	Temperate	North	Only minimum size specified	Macroalgae
2010	Gartner et al.	Subtropical	South	Size range of animals defined	Seagrasses
2010	Gedan & Bertness	Temperate	North	Only minimum size specified	Mangroves
2010	Gestoso et al.	Temperate	North	Only minimum size specified	Macroalgae

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2010	Khan et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2010	Kon et al.	Tropical	North	Size range of animals defined	Mangroves
2010	Marenghi et al.	Temperate	North	Only minimum size specified	Artificial structures
2010	Martinetto et al.	Temperate	South	Only minimum size specified	Macroalgae, mangroves, benthic & unidentified habitats
2010	Moore & Hovel	Subtropical	North	Only minimum size specified	Seagrasses
2010	Newcombe & Taylor	Temperate	South	Only maximum size specified	Macroalgae
2010	Nikula et al.	Temperate	South	No size definition of epifauna given	Macroalgae
2010	Norkko et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2010	Osman et al.	Temperate	North	No size definition of epifauna given	Macroalgae, seagrasses, benthic & unidentified habitats
2010	Poirier et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2010	Reiss et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2010	Sellheim et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2010	Smyth & Roberts	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2010	Stella et al.	Tropical	South	Only minimum size specified	Corals
2010	Tang et al.	Temperate	North	Only minimum size specified	Mangroves, benthic & unidentified habitats
2010	Tanner & Fernandes	Subtropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2010	Valanko et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2010	Vanreusel et al.	Tropical, subtropical, temperate	North, South	No size definition of epifauna given	Benthic & unidentified habitats
2010	Voultsiadou et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2010	Zintzen & Massin	Temperate	North	Only minimum size specified	Artificial structures
2011	Anderson et al.	Tropical, subtropical, temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2011	Atkinson et al.	Subtropical	South	Only maximum size specified	Benthic & unidentified habitats
2011	Burone et al.	Tropical, subtropical	South	Only minimum size specified	Benthic & unidentified habitats
2011	Carr et al.	Temperate	North	Only minimum size specified	Seagrasses

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2011	Currin et al.	Subtropical	North	No size definition of epifauna given	Mangroves
2011	de Juan et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2011	Douglass et al.	Temperate	North	No size definition of epifauna given	Seagrasses
2011	Drouin et al.	Temperate	North	Only minimum size specified	Macroalgae, seagrasses
2011	Ellis et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2011	Fleddum et al.	Tropical	North	Only minimum size specified	Artificial structures
2011	Fraser et al.	Temperate	South	No size definition of epifauna given	Macroalgae
2011	Freeman & Creese	Temperate	South	No size definition of epifauna given	Macroalgae
2011	Freestone & Osman	Tropical, subtropical, temperate	North	No size definition of epifauna given	Mangroves, benthic & unidentified habitats
2011	Harris	Tropical, subtropical, temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2011	Harwell et al.	Subtropical	North	Only minimum size specified	Other biogenic habitats
2011	Hellyer et al.	Subtropical	South	Only minimum size specified	Artificial structures
2011	Hinz et al. 2011	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2011	Johnson	Temperate	North	No size definition of epifauna given	Mangroves
2011	Kon et al.	Tropical	North	Only minimum size specified	Mangroves
2011	Lambert et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2011	Liuzzi & Gappa	Temperate	South	No size definition of epifauna given	Macroalgae
2011	Lomovasky et al.	Tropical	South	Only minimum size specified	Benthic & unidentified habitats
2011	Luo et al.	Subtropical	North	Only maximum size specified	Benthic & unidentified habitats
2011	Metaxas	Tropical, subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2011	Moura et al.	Temperate	North	Only minimum size specified	Artificial structures
2011	Navarro et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2011	Neumann & Kröncke	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2011	Nikula et al.	Temperate	South	No size definition of epifauna given	Macroalgae

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2011	Paavo et al.	Temperate	South	Only minimum size specified	Benthic & unidentified habitats
2011	Pacciardi et al.	Temperate	North	Only minimum size specified	Macroalgae
2011	Stevens & Dunn	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2011	Tanner	Subtropical	South	Only minimum size specified	Macroalgae
2011	Tsubaki et al.	Na	Na	No size definition of epifauna given	Corals, benthic & unidentified habitats
2011	Tuya et al.	Temperate	North	Only minimum size specified	Macroalgae
2011	Wong et al.	Subtropical	North	Only minimum size specified	Mangroves, seagrasses, other biogenic habitats, benthic & unidentified habitats
2012	Anderson & Lovvorn	Temperate	North	Only minimum size specified	Seagrasses
2012	Arponen & Boström	Temperate	North	No size definition of epifauna given	Seagrasses
2012	Bishop et al.	Subtropical	South	Only minimum size specified	Mangroves
2012	Byers et al.	Subtropical	North	Only minimum size specified	Macroalgae
2012	Cutajar et al.	Temperate	South	Only minimum size specified	Mangroves
2012	de Juan & Demestre	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2012	Elahi & Sebens	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2012	Gestoso et al.	Temperate	North	Only minimum size specified	Macroalgae
2012	Gullström et al.	Temperate	North	Size range of animals defined	Seagrasses
2012	Gustafsson & Salo	Subtropical	North	Only minimum size specified	Seagrasses
2012	Hamilton et al.	Temperate	South	Only minimum size specified	Seagrasses
2012	Haupt et al.	Subtropical	South	No size definition of epifauna given	Other biogenic habitats
2012	Hepburn et al.	Temperate	South	No size definition of epifauna given	Macroalgae
2012	Janiak & Whitlatch	Temperate	North	No size definition of epifauna given	Macroalgae
2012	Källén et al.	Subtropical	South	No size definition of epifauna given	Seagrasses
2012	Karlson & Osman	Subtropical, temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2012	Lambert et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2012	Lewis & Anderson	Subtropical	North	Only minimum size specified	Seagrasses

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2012	Macias	Tropical, subtropical	North	No size definition of epifauna given	Seagrasses
2012	Martinez et al.	Tropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2012	Marzinelli et al.	Subtropical	South	No size definition of epifauna given	Macroalgae
2012	Mosch et al.	Tropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2012	Nerot et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2012	Pagliosa et al.	Subtropical	South	Only minimum size specified	Macroalgae
2012	Przeslawski et al.	Subtropical	South	No size definition of epifauna given	Other biogenic habitats
2012	Ragnarsson & Burgos	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2012	Riedel et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2012	Spicer & Widdicombe	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2012	Strain et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2012	Tait & Hovel	Subtropical	North	No size definition of epifauna given	Seagrasses
2012	Tyrrell et al.	Temperate	North	Only minimum size specified	Macroalgae
2012	Wilkie et al.	Subtropical	South	Only minimum size specified	Other biogenic habitats
2012	Yorke & Metaxas	Temperate	North	No size definition of epifauna given	Macroalgae
2013	Barnes et al.	Subtropical, temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2013	Bell et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2013	Bilkovic et al.	Temperate	North	Only minimum size specified	Mangroves
2013	Bishop et al.	Subtropical	South	No size definition of epifauna given	Macroalgae, mangroves
2013	Bowden et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2013	Brandt et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	Broszeit et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	Cartes et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2013	Coleman et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	Cook et al.	Temperate	North	Only minimum size specified	Other biogenic habitats

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2013	Dauvin et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	de Juan et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	Delgado et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	Dhib et al.	Temperate	North	Only minimum size specified	Mangroves
2013	Do et al.	Temperate	North	Only minimum size specified	Seagrasses
2013	Ellis et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2013	Engelen et al.	Temperate	North	Only minimum size specified	Macroalgae
2013	Fleddum et al.	Subtropical	South	Only minimum size specified	Benthic & unidentified habitats
2013	Foveau et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2013	Gartner et al.	Subtropical	North, South	No size definition of epifauna given	Seagrasses
2013	Gribben et al.	Temperate	South	No size definition of epifauna given	Macroalgae
2013	Hammerschlag-Peyer et al.	Subtropical	North	Only minimum size specified	Seagrasses
2013	Krone et al.	Temperate	North	Only minimum size specified	Artificial structures
2013	Laboy-Nieves & Muniz-Barretto	Tropical	North	No size definition of epifauna given	Other biogenic habitats
2013	Lambert et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	MacDonald & Weis	Tropical	North	No size definition of epifauna given	Mangroves
2013	Mangano et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	Neumann et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2013	Ortiz et al.	Tropical, subtropical	South	No size definition of epifauna given	Macroalgae, other biogenic habitats
2013	Pascal et al.	Temperate	North	No size definition of epifauna given	Mangroves
2013	Popadić et al.	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
2013	Prato et al.	Temperate	North	Only minimum size specified	Macroalgae
2013	Reinhardt et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	Riera et al.	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats
2013	Roff et al.	Tropical	North	Only minimum size specified	Macroalgae

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2013	Ross et al.	Temperate	South	Only minimum size specified	Other biogenic habitats
2013	Sciberras et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	Sell & Kröncke	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	Smith et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2013	Staszak & Armitage	Subtropical	North	No size definition of epifauna given	Mangroves
2013	Tuya et al.	Subtropical	North	Only minimum size specified	Seagrasses
2013	Urra et al.	Temperate	North	Size range of animals defined	Macroalgae, seagrasses, benthic & unidentified habitats
2013	Vitaliano et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2013	Wolf et al.	Tropical	North	No size definition of epifauna given	Corals, macroalgae
2014	Altieri & Witman	Tropical	South	No size definition of epifauna given	Other biogenic habitats
2014	Bedini et al.	Temperate	North	No size definition of epifauna given	Macroalgae
2014	Bhagirathan et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2014	Blain & Gagnon	Temperate	North	No size definition of epifauna given	Macroalgae
2014	Blake et al.	Temperate	North	Size range of animals defined	Seagrasses
2014	Boulcott et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2014	Brahim et al.	Subtropical	North	No size definition of epifauna given	Seagrasses
2014	Buzá-Jacobucci & Pereira-Leite	Tropical	South	Only minimum size specified	Macroalgae
2014	Carvalho et al.	Temperate	North	Only minimum size specified	Corals
2014	Cebrian et al.	Temperate	North	No size definition of epifauna given	Macroalgae
2014	Corrêa et al.	Tropical	South	Only minimum size specified	Other biogenic habitats
2014	Esqueda-González et al.	Tropical	North	Size range of animals defined	Artificial structures, other biogenic habitats
2014	Fariñas-Franco & Roberts	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2014	Fernandez et al.	Subtropical	South	No size definition of epifauna given	Macroalgae
2014	Fukunaga et al.	Tropical	North	Only maximum size specified	Mangroves
2014	Gatune et al.	Tropical	South	Only minimum size specified	Macroalgae

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2014	Hosono	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2014	Huang et al.	Tropical, subtropical, temperate	North, South	No size definition of epifauna given	Benthic & unidentified habitats
2014	Hughes	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2014	Jones et al.	Tropical	South	No size definition of epifauna given	Artificial structures
2014	Konsulova & Doncheva	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2014	Kornijow	Na	Na	Only minimum size specified	Benthic & unidentified habitats
2014	Lambert et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2014	Lange & Griffiths	Subtropical, temperate	South	No size definition of epifauna given	Seagrasses
2014	Lefcheck et al.	Temperate	North	No size definition of epifauna given	Seagrasses
2014	Leopardas et al.	Tropical	North	Only minimum size specified	Benthic & unidentified habitats
2014	Muntadas et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2014	Navarro-Barranco et al.	Subtropical, temperate	North	Only minimum size specified	Benthic & unidentified habitats
2014	Nordström et al.	Subtropical	North	No size definition of epifauna given	Mangroves
2014	Palardy & Witman	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2014	Pierri-Daunt & Tanaka	Tropical	South	Only minimum size specified	Macroalgae
2014	Png-Gonzalez et al.	Tropical	North	Only minimum size specified	Macroalgae, seagrasses
2014	Reynolds et al.	Temperate	North	Only minimum size specified	Seagrasses
2014	Ronowicz et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2014	Smeulders et al.	Temperate	North	Only minimum size specified	Corals, benthic & unidentified habitats
2014	Smith et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2014	Trave & Sheaves	Subtropical	North	No size definition of epifauna given	Seagrasses
2014	Tuya et al.	Subtropical	North	Only minimum size specified	Macroalgae, seagrasses
2014	Vassallo et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2014	Veiga et al.	Temperate	North	Only minimum size specified	Macroalgae
2014	Vidović et al.	Temperate	North	Size range of animals defined	Benthic & unidentified habitats

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2015	Barry et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2015	Bergman et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2015	Carcedo et al.	Temperate	South	Only minimum size specified	Benthic & unidentified habitats
2015	Chen et al.	Subtropical	North	Only minimum size specified	Mangroves
2015	Coolen et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2015	Cúrdia et al.	Temperate	North	Only minimum size specified	Corals
2015	de Jong et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2015	de Jong et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2015	De Mesel et al.	Temperate	North	Only minimum size specified	Artificial structures
2015	DeAmicis & Foggo	Temperate	North	No size definition of epifauna given	Macroalgae, seagrasses
2015	Dias et al.	Temperate	North	Only minimum size specified	Corals
2015	Eklöf et al.	Temperate	North	Only minimum size specified	Macroalgae, seagrasses, benthic & unidentified habitats
2015	Fernandez et al.	Tropical	South	No size definition of epifauna given	Artificial structures
2015	Green & Fong	Subtropical	North	Only minimum size specified	Macroalgae
2015	Greene	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2015	Gutow et al.	Temperate	North	Only minimum size specified	Macroalgae
2015	Hemery et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2015	Howarth et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2015	Huang et al.	Temperate	North	No size definition of epifauna given	Seagrasses
2015	Knight et al.	Temperate	North	Only minimum size specified	Seagrasses
2015	Kristensen et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2015	Lanham et al.	Subtropical	South	Only minimum size specified	Macroalgae
2015	Lee et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2015	Long et al.	Temperate	North	Only minimum size specified	Seagrasses
2015	McDonald et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2015	McFarlin et al.	Temperate	North	Size range of animals defined	Mangroves
2015	Munari et al.	Temperate	North	Only minimum size specified	Macroalgae
2015	Navarro-Barranco et al.	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats
2015	Nogueira et al.	Tropical	South	Only minimum size specified	Corals
2015	Ortiz et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2015	Ortiz et al.	Tropical	South	No size definition of epifauna given	Corals
2015	Palmer & Montagna	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2015	Sepúlveda et al.	Temperate	South	No size definition of epifauna given	Other biogenic habitats
2015	Sheehan et al.	Temperate	North	No size definition of epifauna given	Corals
2015	Sokołowski et al.	Temperate	North	Only minimum size specified	Macroalgae, seagrasses
2015	Torres et al.	Temperate	North	Only minimum size specified	Macroalgae
2015	Vader & Tandberg	Na	Na	No size definition of epifauna given	Other biogenic habitats
2015	van der Zee et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2015	Veeragurunathan et al.	Tropical	North	No size definition of epifauna given	Macroalgae
2015	Whomersley et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2015	Wong & Dowd	Temperate	North	Only minimum size specified	Seagrasses
2015	Zupo et al.	Temperate	North	Only minimum size specified	Seagrasses
2016	Arnold et al.	Temperate	North	No size definition of epifauna given	Macroalgae
2016	Ba-Akdah et al.	Tropical	North	Only minimum size specified	Macroalgae
2016	Bowden et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2016	Clark et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2016	de Jong et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2016	Demers et al.	Temperate	South	No size definition of epifauna given	Seagrasses
2016	Du Preez et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2016	Figueroa et al.	Subtropical, Temperate	North	No size definition of epifauna given	Macroalgae

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2016	Filimon et al.	Temperate	North	Only minimum size specified	Macroalgae
2016	Fritz	Na	Na	No size definition of epifauna given	Benthic & unidentified habitats
2016	Hemery & Henkel	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2016	Jimenez et al.	Tropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2016	Kollars et al.	Subtropical	North	No size definition of epifauna given	Macroalgae
2016	Lefcheck et al.	Temperate	North	Only minimum size specified	Seagrasses
2016	Leite et al.	Tropical	South	No size definition of epifauna given	Other biogenic habitats
2016	Luckenbach et al.	Temperate	North	Only minimum size specified	Artificial structure, macroalgae
2016	Marzinelli et al.	Subtropical	South	Only minimum size specified	Macroalgae
2016	McDonald et al.	Subtropical	North	Only minimum size specified	Seagrasses
2016	McSkimming et al.	Temperate	South	Only minimum size specified	Seagrasses
2016	Meyer et al.	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
2016	Muntadas et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2016	Murat et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2016	Navarro-Barranco et al.	Subtropical	North	Only minimum size specified	Other biogenic habitats
2016	Neumann et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2016	Piló et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2016	Piras et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2016	Rodrigues et al.	Tropical	South	No size definition of epifauna given	Mangroves
2016	Rodríguez-Zaragoza et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2016	Rosli et al.	Temperate	South	Only minimum size specified	Benthic & unidentified habitats
2016	Tano et al.	Tropical	South	Only minimum size specified	Macroalgae, seagrasses
2016	Theodor et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2016	Vanreusel et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2016	Walls et al.	Temperate	North	No size definition of epifauna given	Macroalgae

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2016	Zharikov & Lysenko	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2017	Agostini et al.	Subtropical	South	Only minimum size specified	Other biogenic habitats
2017	Alfaro-Lucas et al.	Subtropical	South	Only minimum size specified	Other biogenic habitats
2017	Balestra et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2017	Boyé et al.	Temperate	North	Only minimum size specified	Seagrasses
2017	Collie et al.	Na	Na	No size definition of epifauna given	Benthic & unidentified habitats
2017	Cox et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2017	Davoult et al.	Temperate	North	Only minimum size specified	Macroalgae
2017	Donadi et al.	Temperate	North	No size definition of epifauna given	Macroalgae
2017	Eddy et al.	Tropical, subtropical, Temperate	North, South	No size definition of epifauna given	Benthic & unidentified habitats
2017	Fernandez-Gonzalez & Sanchez-Jerez	Temperate	North	Only minimum size specified	Macroalgae, other biogenic habitats
2017	Foveau & Dauvin	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2017	Gribben et al.	Subtropical	South	Only minimum size specified	Seagrasses
2017	Hamilton et al.	Subtropical	North	No size definition of epifauna given	Mangroves
2017	Lambert et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2017	Lavender et al.	Subtropical	South	Only minimum size specified	Artificial structures
2017	Lefcheck et al.	Temperate	North	Only minimum size specified	Macroalgae, seagrasses
2017	Mach et al.	Temperate	North	Only minimum size specified	Seagrasses
2017	Mariani et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2017	Neumann et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2017	O'Carroll et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats, benthic & unidentified habitats
2017	O'Carroll et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2017	Pascal et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2017	Ramalho et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2017	Reynolds et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2017	Salmo et al.	Tropical	North	Only minimum size specified	Mangroves
2017	Sokołowski et al.	Temperate	North	Size range of animals defined	Artificial structures
2017	Suárez-Jiménez et al.	Temperate	South	No size definition of epifauna given	Macroalgae
2017	Taylor et al.	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2017	Vermeij	Tropical	North, South	No size definition of epifauna given	Benthic & unidentified habitats
2017	Winkler et al.	Subtropical	South	Only minimum size specified	Macroalgae
2017	Xu et al.	Temperate	North	No size definition of epifauna given	Artificial structures
2017	Yeager & Hovel	Subtropical	North	No size definition of epifauna given	Seagrasses
2017	Zaabar et al.	Temperate	North	Only minimum size specified	Macroalgae, seagrasses
2018	Alitto et al.	Subtropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2018	Audino & Marian	Subtropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2018	Baker et al.	Tropical	North	Size range of animals defined	Macroalgae
2018	Belattmania et al.	Subtropical	North	Only minimum size specified	Macroalgae, seagrasses
2018	Belattmania et al.	Subtropical	North	Only minimum size specified	Macroalgae
2018	Brix et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2018	Burnett & Koehl	Temperate	North	No size definition of epifauna given	Macroalgae
2018	Coffin et al.	Temperate	North	Only minimum size specified	Macroalgae, seagrasses
2018	Cunha et al.	tropical	South	Only minimum size specified	Macroalgae
2018	das Chagas et al.	Tropical	South	Only minimum size specified	Artificial structures
2018	Desmond et al.	Temperate	South	Only minimum size specified	Macroalgae, macroalgae
2018	dos Santos et al.	Tropical	South	Only minimum size specified	Other biogenic habitats
2018	Douglass et al.	Subtropical	North	Size range of animals defined	Seagrasses
2018	Eggleton et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2018	Esqueda-González et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2018	Fariñas-Franco et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2018	French & Moore	Temperate	North	Only minimum size specified	Seagrasses
2018	Gabara et al.	Subtropical	North	No size definition of epifauna given	Turf algae & microalgae
2018	Gavira-O'Neill et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2018	Glaspie et al.	Subtropical	South	Only minimum size specified	Other biogenic habitats
2018	Ha & Williams	Temperate	North	Only minimum size specified	Seagrasses
2018	Hamoutene et al.	Temperate	North	No size definition of epifauna given	Artificial structures
2018	Hemery et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2018	Hermosillo-Núñez et al.	Tropical	North	No size definition of epifauna given	Macroalgae
2018	Hermosillo-Núñez et al.	Tropical, subtropical, temperate	South	No size definition of epifauna given	Corals
2018	Howarth et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2018	Janiak et al.	Subtropical	North	Only minimum size specified	Artificial structures, mangroves
2018	Kaiser et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2018	Kaminsky et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2018	Kennedy et al.	Temperate	North	No size definition of epifauna given	Seagrasses
2018	Kniesz et al.	Tropical	North	No size definition of epifauna given	Other biogenic habitats
2018	Little et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2018	Lundquist et al.	Temperate	South	Only minimum size specified	Benthic & unidentified habitats
2018	McGann & Conrad	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats
2018	Momota & Nakaoka	Temperate	North	Only minimum size specified	Seagrasses
2018	Monk et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2018	Montereale-Gavazzi et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2018	Moreno et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2018	Morris et al.	Subtropical	South	Size range of animals defined	Benthic & unidentified habitats
2018	Mosbahi et al.	Subtropical	North	No size definition of epifauna given	Seagrasses

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2018	Muntadas et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2018	Nakamoto et al.	Subtropical	North	Only minimum size specified	Macroalgae, seagrasses
2018	Namba & Nakaoka	Temperate	North	Size range of animals defined	Seagrasses
2018	Navarro-Barranco et al.	Temperate	North	Only minimum size specified	Macroalgae
2018	Parameswaran et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2018	Saarinen et al.	Temperate	North	Only minimum size specified	Macroalgae
2018	Scheffel et al.	Subtropical	North	Only minimum size specified	Mangroves
2018	Schweitzer et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2018	Singh et al.	Tropical	North	Only minimum size specified	Benthic & unidentified habitats
2018	Soler-Hurtado et al.	Tropical	South	Only minimum size specified	Corals
2018	Sutherland et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2018	Tanner et al.	Subtropical, temperate	South	Only minimum size specified	Benthic & unidentified habitats
2018	Tilot et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2018	Vaughn & Hoellein	Na	Na	No size definition of epifauna given	Benthic & unidentified habitats
2018	Venturelli et al.	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats
2018	Viola et al.	Subtropical	North	No size definition of epifauna given	Artificial structures
2018	Waters et al.	Temperate	South	No size definition of epifauna given	Macroalgae
2018	Wenger et al.	Tropical	South	Only minimum size specified	Macroalgae
2018	Whippo et al.	Temperate	North	Only minimum size specified	Seagrasses
2018	Williams et al.	Subtropical, temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2018	Yusa et al.	Temperate	North	Only minimum size specified	Seagrasses
2018	Zwerschke et al.	Temperate	North	Only maximum size specified	Other biogenic habitats
2019	Abdelhady et al.	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats
2019	Audino et al.	Na	Na	No size definition of epifauna given	Benthic & unidentified habitats
2019	Barrientos-Lujan et al.	Tropical	North	No size definition of epifauna given	Corals

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2019	Bentley et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Bertolini	Temperate	North	No size definition of epifauna given	Macroalgae
2019	Bonaglia et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2019	Bremec & Schejter	Temperate	South	No size definition of epifauna given	Other biogenic habitats
2019	Brooks & Crowe	Temperate	North	No size definition of epifauna given	Artificial structures, macroalgae
2019	Cadier & Frouws	Tropical	South	Only minimum size specified	Seagrasses
2019	Campanyà-Llovet & Snelgrove	Temperate	North	Only minimum size specified	Macroalgae
2019	Carmen & Grunden	Temperate	North	No size definition of epifauna given	Seagrasses
2019	Casamajor et al.	Temperate	North	No size definition of epifauna given	Macroalgae
2019	Cavalcante et al.	Tropical	South	Only minimum size specified	Seagrasses
2019	Ferreira et al.	Tropical	South	Only minimum size specified	Macroalgae
2019	Fields et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Foster et al.	Tropical	North	No size definition of epifauna given	Macroalgae
2019	Fulton et al.	Tropical, subtropical, Temperate	North, South	No size definition of epifauna given	Macroalgae
2019	Gan et al.	Tropical	North	No size definition of epifauna given	Macroalgae
2019	Gárate et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Garcia et al.	Tropical	South	Only minimum size specified	Macroalgae
2019	Gates et al.	Temperate	North	No size definition of epifauna given	Artificial structures
2019	Githaiga et al.	Tropical	South	Only minimum size specified	Seagrasses
2019	Guillas et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2019	Hayduk et al.	Temperate	North	Only minimum size specified	Macroalgae, seagrasses
2019	Henseler et al.	Temperate	North	Only minimum size specified	Macroalgae
2019	Hossain	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Hossain et al.	Tropical	North	Size range of animals defined	Benthic & unidentified habitats
2019	Iliff et al.	Subtropical	North	Only minimum size specified	Other biogenic habitats

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2019	Ito et al.	Temperate	North	Only minimum size specified	Macroalgae
2019	Jacobucci et al.	Tropical	South	Only minimum size specified	Macroalgae
2019	Janas et al.	Temperate	North	Size range of animals defined	Seagrasses
2019	Lomeli et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Lozano-Cortés et al.	Subtropical	North	Only minimum size specified	Artificial structures
2019	Luff et al.	Temperate	North	No size definition of epifauna given	Seagrasses
2019	Lutz et al.	Subtropical	North	Only minimum size specified	Macroalgae
2019	Meysick et al.	Temperate	North	Only minimum size specified	Seagrasses
2019	Michaelis et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Michaelis et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Navarro-Barranco et al.	Temperate	North	Only minimum size specified	Macroalgae
2019	Olivier et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Outinen et al.	Temperate	North	No size definition of epifauna given	Macroalgae, benthic & unidentified habitats
2019	Piechaud et al.	Na	Na	No size definition of epifauna given	Benthic & unidentified habitats
2019	Powell et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Price et al.	Temperate	North	No size definition of epifauna given	Corals
2019	Salmo et al.	Tropical	North	Only minimum size specified	Mangroves
2019	Seitz et al.	Temperate	North	Only minimum size specified	Artificial structures
2019	Slavik et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Smith et al.	Subtropical	North	Only minimum size specified	Mangroves
2019	Sutherland et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Talbot et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2019	Trannum et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2019	Tuya et al.	Subtropical, temperate	North	Only minimum size specified	Seagrasses
2019	Wee et al.	Tropical	North	Only minimum size specified	Corals

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2019	Yeager et al.	Subtropical	North	Only minimum size specified	Seagrasses
2019	Zhang & Silliman	Subtropical	North	Only minimum size specified	Macroalgae, seagrasses
2020	Babcock et al.	Subtropical	North	No size definition of epifauna given	Artificial structures, macroalgae
2020	Barbosa & Taylor	Subtropical	North	No size definition of epifauna given	Seagrasses
2020	Belattmania et al.	Subtropical	North	Only minimum size specified	Macroalgae
2020	Callaway et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2020	Chen et al.	Tropical	South	Size range of animals defined	Macroalgae
2020	Couce et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2020	Cramer et al.	Tropical	North	Size range of animals defined	Corals
2020	Fraser et al.	Tropical, subtropical, temperate	South	Only minimum size specified	Corals, macroalgae, turf algae & microalgae, other biogenic habitats
2020	Gagnon et al.	Tropical, subtropical, temperate	North, South	No size definition of epifauna given	Mangroves, seagrasses
2020	Ge et al.	Subtropical	North	Only minimum size specified	Mangroves
2020	González-García et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2020	Gracia et al.	Tropical	North	Only minimum size specified	Other biogenic habitats, benthic & unidentified habitats
2020	Kodama et al.	Temperate	North	No size definition of epifauna given	Macroalgae
2020	Lanham et al.	Temperate	South	Only minimum size specified	Macroalgae
2020	Ledbetter & Hovel	Subtropical	North	Only minimum size specified	Seagrasses
2020	López-Garrido et al.	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2020	Ma et al.	Tropical	North	Only minimum size specified	Mangroves
2020	Namba et al.	Temperate	North	Size range of animals defined	Seagrasses
2020	Noble-James et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2020	Pisapia et al.	Tropical	South	Only minimum size specified	Corals
2020	Proudfoot et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2020	Rouse et al.	Temperate	North	No size definition of epifauna given	Artificial structures

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Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
2020	Rowden et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2020	Sedano et al.	Temperate	North	Only minimum size specified	Artificial structures
2020	Sedano et al.	Temperate	North	Only minimum size specified	Artificial structures
2020	Shelamoff et al.	Temperate	South	Only minimum size specified	Macroalgae
2020	Simpson et al.	Subtropical	South	No size definition of epifauna given	Artificial structures
2020	Stelling-Wood et al.	Subtropical	South	Only minimum size specified	Macroalgae
2020	Stevens et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2020	Wei et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats

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