# Oceanography and Marine Biology

## An Annual Review

### Volume 58

**Edited by**

S. J. Hawkins, A. L. Allcock, A. E. Bates, A. J. Evans, L. B. Firth,
C. D. McQuaid, B. D. Russell, I. P. Smith, S. E. Swearer, P. A. Todd

## Chapter 5

### Priority Species to Support the Functional Integrity of Coral Reefs

*Kennedy Wolfe, Ken Anthony, Russell C. Babcock, Line Bay, David G. Bourne, Damien Burrows, Maria Byrne, Dione J. Deaker, Guillermo Diaz-Pulido, Pedro R. Frade, Manuel Gonzalez-Rivero, Andrew Hoey, Mia Hoogenboom, Mark McCormick, Juan-Carlos Ortiz, Tries Razak, Anthony J. Richardson, George Roff, Hannah Sheppard-Brennand, Jessica Stella, Angus Thompson, Sue-Ann Watson, Nicole Webster, Donna Audas, Roger Beeden, Jesseca Carver, Mel Cowlishaw, Michelle Dyer, Paul Groves, Dylan Horne, Lauric Thiault, Jason Vains, David Wachenfeld, Damien Weekers, Genevieve Williams & Peter J. Mumby*

# PRIORITY SPECIES TO SUPPORT THE FUNCTIONAL INTEGRITY OF CORAL REEFS

KENNEDY WOLFE[1], KEN ANTHONY[2], RUSSELL C. BABCOCK[3], LINE BAY[2],
DAVID G. BOURNE[2,4], DAMIEN BURROWS[5], MARIA BYRNE[6], DIONE J. DEAKER[6],
GUILLERMO DIAZ-PULIDO[7], PEDRO R. FRADE[4,8], MANUEL GONZALEZ-
RIVERO[2], ANDREW HOEY[9], MIA HOOGENBOOM[4,9], MARK McCORMICK[9], JUAN-
CARLOS ORTIZ[1,2], TRIES RAZAK[7], ANTHONY J. RICHARDSON[3,10], GEORGE ROFF[1],
HANNAH SHEPPARD-BRENNAND[6], JESSICA STELLA[11], ANGUS THOMPSON[2],
SUE-ANN WATSON[9,12], NICOLE WEBSTER[2,13], DONNA AUDAS[11], ROGER BEEDEN[11],
JESSECA CARVER[11], MEL COWLISHAW[11], MICHELLE DYER[11], PAUL GROVES[11],
DYLAN HORNE[11], LAURIC THIAULT[14], JASON VAINS[11], DAVID WACHENFELD[11],
DAMIEN WEEKERS[11], GENEVIEVE WILLIAMS[11] & PETER J. MUMBY[1]

*[1]Marine Spatial Ecology Lab, School of Biological Sciences and ARC Centre of Excellence
for Coral Reef Studies, University of Queensland, St Lucia, QLD 4072, Australia
[2]Australian Institute of Marine Science (AIMS), Townsville, QLD 4810, Australia
[3]Commonwealth Scientific and Industrial Research Organisation (CSIRO) Oceans and
Atmosphere, Queensland Biosciences Precinct, Brisbane, QLD 4067, Australia
[4]College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia
[5]TropWATER – Centre for Tropical Water and Aquatic Ecosystem Research,
James Cook University, Townsville, QLD 4811, Australia
[6]School of Life and Environmental Sciences, University of Sydney, Sydney, NSW 2006, Australia
[7]School of Environment and Science, Griffith University, Brisbane, Queensland 4111, Australia
[8]Centre of Marine Sciences, University of Algarve, 8005-139 Faro, Portugal
[9]ARC Centre of Excellence for Coral Reef Studies, James Cook
University, Townsville, QLD 4811, Australia
[10]School of Mathematics and Physics, University of Queensland, St Lucia, QLD 4072, Australia
[11]Great Barrier Reef Marine Park Authority (GBRMPA), Townsville, QLD 4810, Australia
[12]Biodiversity and Geosciences Program, Museum of Tropical Queensland,
Queensland Museum, Townsville, QLD 4810, Australia
[13]Australian Centre for Ecogenomics, University of Queensland, St Lucia, QLD 4072, Australia
[14]National Center for Scientific Research, PSL Université Paris, CRIOBE, USR 3278
CNRS-EPHE-UPVD, Maison des Océans, 195 rue Saint-Jacques, 75005, Paris,
France, and Laboratoire d'Excellence CORAIL, 98729 Moorea, French Polynesia*

**Abstract** Ecosystem-based management on coral reefs has historically focussed on biodiversity conservation through the establishment of marine reserves, but it is increasingly recognised that a subset of species can be key to the maintenance of ecosystem processes and functioning. Specific provisions for these key taxa are essential to biodiversity conservation and resilience-based adaptive management. While a wealth of literature addresses ecosystem functioning on coral reefs, available information covers only a subset of specific taxa, ecological processes and environmental

stressors. What is lacking is a comparative assessment across the diverse range of coral reef species to synthesise available knowledge to inform science and management. Here we employed expert elicitation coupled with a literature review to generate the first comprehensive assessment of 70 taxonomically diverse and functionally distinct coral reef species from microbes to top predators to summarise reef functioning. Although our synthesis is largely through the lens of the Great Barrier Reef, Australia, a particularly data-rich system, it is relevant to coral reefs in general. We use this assessment to evaluate which taxa drive processes that maintain a healthy reef and whether management of these taxa is considered a priority (i.e. are they vulnerable?) or is feasible (i.e. can they be managed?). Scientific certainty was scored to weight our recommendations, particularly when certainty was low. We use five case studies to highlight critical gaps in knowledge that limit our understanding of ecosystem functioning. To inform the development of novel management strategies and research objectives, we identify taxa that support positive interactions and enhance ecosystem performance, including those where these roles are currently underappreciated. We conclude that current initiatives effectively capture many priority taxa but that there is significant room to increase opportunities for underappreciated taxa in both science and management to maximally safeguard coral reef functioning.

# Introduction

Coral reefs have changed profoundly over recent decades due to cumulative impacts from local (e.g. fisheries, water quality) and global (i.e. ocean warming) stressors. While continued exposure to extreme events could stimulate some level of adaptive capacity and resilience in surviving cohorts (Maynard et al. 2008, Hughes et al. 2019a, b), reef recovery and persistence will be variable at local and global scales (Guzman & Cortes 2007, Graham et al. 2011b, Glynn et al. 2015, Bento et al. 2016, Mumby et al. 2016, de Bakker et al. 2017, Mellin et al. 2019). It is estimated that up to 90% of coral reefs may disappear as soon as 2050 if global emissions are not curbed in line with improved local management strategies to resolve mounting pressures (Wilkinson 2006, Albright et al. 2016a, Schleussner et al. 2016, van Hooidonk et al. 2016, Harvey et al. 2018, Hughes et al. 2018a).

High-biodiversity systems, like coral reefs, are suggested to have broader systemic resilience to environmental perturbation through increased trait diversity and functional redundancy (Boucher 1997, Bellwood et al. 2004, Hooper et al. 2005, Micheli & Halpern 2005, Ferrigno et al. 2016, McWilliam et al. 2018). Species-poor ecosystems, in contrast, may be particularly susceptible to collapse following the loss of just a few key species (Mumby et al. 2008). One of the foremost examples of this exists for Caribbean reefs, where loss of a predominant grazing herbivore (a diadematid sea urchin) resulted in undesirable algal growth and catastrophic, largely irreversible, phase shifts towards macroalgal and cyanobacterial reefs (Hughes 1994, Gardner et al. 2003, Mumby et al. 2006a, Brocke et al. 2015, de Bakker et al. 2017). Even in high-diversity ecosystems, the loss of key species can result in ecological changes that impair critical processes and services, including resource use, fisheries productivity and carbonate accretion (McClanahan et al. 2002, Kennedy et al. 2013, Holbrook et al. 2015, Rogers et al. 2015, 2018a, Mora et al. 2016, Harborne et al. 2017, Mumby 2017, Clements & Hay 2019).

Coral reefs are complex ecosystems with a great diversity of players, including microbes, algae, sponges, corals, other invertebrates and fishes (Reaka-Kudla 1997, Fisher et al. 2015). While high biodiversity is considered the hallmark of healthy and productive ecosystems, many studies highlight the critical importance of a small subset of species in maintaining ecosystem functioning through a range of positive interactions (Halpern et al. 2007, Naeem et al. 2012, Shaver & Silliman 2017, Renzi et al. 2019), their broad distributions and high abundances or high degree of specialisation with limited functional redundancy (Power et al. 1996, Piraino et al. 2002, Bellwood et al. 2004, Hooper et al. 2005, Mouillot et al. 2013). Corals, for

example, are major contributors to calcification and reef building, but some species contribute disproportionately to coral recovery and coverage (e.g. *Acropora*) (Johns et al. 2014, Ortiz et al. 2014, 2018), while others contribute more to rates of reef building in high-sediment regions (e.g. *Turbinaria*) (Browne 2012, Morgan et al. 2016). Beyond corals, microbial organisms underpin many ecosystem processes (Glasl et al. 2018a), benthic invertebrates and cryptobenthic fishes are at the foundation of fisheries productivity (tertiary production) (Depczynski & Bellwood 2003, Kramer et al. 2015, Brandl et al. 2018, 2019), planktivorous fishes partition their feeding activity into different reef zones (Hamner et al. 1988, Holzman et al. 2005, Motro et al. 2005, Yahel et al. 2005), some herbivorous fishes are more important in controlling fouling macroalgae (Bellwood et al. 2004, Mumby et al. 2006a, 2014, Hoey & Bellwood 2009, 2010b, Loffler et al. 2015a) and predatory fishes can alter reef community structure (Almany & Webster 2004, Rizzari et al. 2014, Stier & White 2014, Palacios et al. 2016b, Stier et al. 2017). As biodiversity conservation is often based on broad-scale habitat protection through marine reserves (Maynard et al. 2016, Mellin et al. 2016), ensuring that specific provisions for key species are incorporated could enhance effectiveness of management strategies (Halpern et al. 2007, Naeem et al. 2012, Shaver & Silliman 2017, Richards & Day 2018).

The biology and ecology of coral reef species are generally well understood, but information on reef ecosystem functioning is largely weighted towards hard (scleractinian) corals and reef fishes (Bellwood & Choat 1990, Bellwood et al. 2004, 2017, 2019, Munday et al. 2009b, Stuart-Smith et al. 2013, McClanahan et al. 2014, Pratchett et al. 2015, Bourne et al. 2016, Konow et al. 2017, Bierwagen et al. 2018, Brandl et al. 2018, McWilliam et al. 2018), overlooking many other species important to a functioning ecosystem. A growing number of studies provide comprehensive reviews of the significance of alternative groups to reef functioning, including for microorganisms (Mouchka et al. 2010, Charpy et al. 2012, Garren & Azam 2012b, Thompson et al. 2015, Hernandez-Agreda et al. 2017), sponges (Wulff 2006, Bell 2008, Maldonado et al. 2015, Pawlik et al. 2018), algae (McCook et al. 2001, Tribollet 2008, Nelson 2009, Connell et al. 2014), phyto- and zoo-plankton (McKinnon et al. 2007, Ferrier-Pages et al. 2011), echinoderms (Birkeland 1989, Pratchett et al. 2014, Purcell et al. 2016a) and coral-associated invertebrates (Castro 1976, Stella et al. 2011b). Some also review specific ecological processes on coral reefs, such as bioerosion (Hutchings & Kiene 1986, Sammarco 1996, Tribollet 2008), calcification and carbonate accretion (Allemand et al. 2011, Tambutte et al. 2011, Bertucci et al. 2013, Kennedy et al. 2013), herbivory (Cvitanovic et al. 2007, Mumby 2009a, Bonaldo et al. 2014, Puk et al. 2016), foraging associations (Lukoschek & McCormick 2000), cleaning symbioses (Cote 2000, Vaughan et al. 2017) and certain modes of predation like corallivory (Cole et al. 2008, Rotjan & Lewis 2008, Konow et al. 2017, Rice et al. 2019). As coral reefs degrade, a growing body of literature also draws focus on the environmental stressors threatening biological processes and reef functioning, including climate change (Hoegh-Guldberg et al. 2007, Atkinson & Cuet 2008, Baker et al. 2008, Pratchett et al. 2008b, Przeslawski et al. 2008, Graham et al. 2011b, Harley et al. 2012, Andersson & Gledhill 2013, Munday et al. 2013b, Albright et al. 2016a, Anthony 2016, Hoey et al. 2016a, Camp et al. 2018a, Espinel-Velasco et al. 2018, Harvey et al. 2018), storms and cyclones (Harmelin-Vivien 1994), water quality (Fabricius 2005, McKinley & Johnston 2010, Brodie et al. 2012, Browne et al. 2012, Erftemeijer et al. 2012, Wear & Thurber 2015, Hairsine 2017) and anthropogenic stressors more generally (Wilkinson 1999, Brodie & Waterhouse 2012, Ban et al. 2014b, Uthicke et al. 2016, Harborne et al. 2017, Richards & Day 2018). However, the majority of these studies are still focussed on corals and fishes.

While a wealth of empirical data and literature reviews address ecosystem functioning on coral reefs, they are typically targeted at specific taxa, processes and/or stressors. What is lacking is a comparative assessment across the diverse range of taxonomic and functional groups of coral reef species to synthesise available knowledge to inform science and management. Given global degradation of many coral reefs, it is not only timely but imperative to ask whether key species that

support ecosystem functioning are being adequately protected. To date, the paradigm in ecosystem restoration has been to reduce the negative effects of physical stress, human impacts and/or species interactions (e.g. invasions), but explicit recognition of positive species interactions is critical to conservation success (Halpern et al. 2007, He et al. 2013, Shaver & Silliman 2017, Thomsen et al. 2018, Renzi et al. 2019, Zhang & Silliman 2019). Identifying and protecting species of particular importance is essential for the conservation of coral reefs and in providing targeted information to safeguard species, biodiversity and functioning in a future ocean (McClanahan et al. 2014, Rogers et al. 2015, Richards & Day 2018).

Here we employed expert elicitation coupled with an extensive compilation of the literature to create a hierarchy of key coral reef taxa – from microbes to top predators – that support reef functioning. As a particularly data-rich system, our synthesis is focussed on the Great Barrier Reef (GBR), Australia, but is relevant for coral reefs globally. We assessed taxa based on their contributions to ecosystem processes and functioning and examined their perceived vulnerability and manageability to improve the holistic management of GBR species, values and processes. Specifically, we assessed which taxa drive processes that maintain a healthy reef and address whether management is considered a priority (i.e. are they vulnerable?) or feasible (i.e. can they be managed?). Elicitation results were used to guide compilations of the literature for key taxa outlined at various levels of ecosystem processes, functioning and stressors. This includes case-specific compilations for key species (tabular corals, branching corals, microorganisms, crustose coralline algae [CCA], turf algae, herbivorous parrotfishes, crown-of-thorns starfish [CoTS]) and novel candidates (chemoautotrophic microbes, cleaner wrasse, bivalves, coral-associated decapods, detritivorous fishes).

Scientific certainty was addressed so that data-deficient groups were not overlooked in our analysis with the objective to highlight novel cases. We also present five case studies to address current gaps in knowledge that limit our understanding at various levels of ecosystem functioning on the GBR. Case study themes were nominated by our expert panel during workshop discussions, and consensus decisions were made to reflect the multidisciplinary expert assemblage, including 1) invertivory, 2) the carbonate budget, 3) microbial links to water quality, 4) recreational spearfishing and 5) the CoTS juvenile life stage. We conclude by outlining the desired outcomes for both science and management to support and protect priority species regarding ecosystem functioning on coral reefs using a framework that can be expanded to guide future integrated and holistic management.

## Defining 'key' species

There is some confusion and debate regarding the definition of 'key' versus 'keystone' species (Piraino & Fanelli 1999, Valls et al. 2015). Keystone species (Paine 1969) are those that have a large, disproportionate effect on their community relative to their abundance (Power et al. 1996). The 'keystone' archetype was applied to an intertidal marine predator that shaped community assemblages despite their low relative abundance (Paine 1969) but is not exclusive to top-down processes (Mills et al. 1993). Yet notably, species that drive ecosystem processes, energy flows and/ or functioning can be abundant and dominant and thus should not be included in the 'keystone' typology (Paine 1995, Piraino & Fanelli 1999). Here, we refer to 'key' species as those with explicit roles in ecosystem functioning regardless of their relative abundance This facilitated our analysis across a diverse range of coral reef species at various levels of taxonomy and functioning, whether comparatively rare or abundant. This is particularly important given the challenges associated with identifying key species and quantifying their roles in high-diversity ecosystems (Gotelli et al. 2011, Pigot et al. 2016), including coral reefs (Maire et al. 2018). Critically, species' roles in ecosystem functioning are dynamic, and species and their interactions have variable inputs and outputs over space and time (Piraino et al. 2002, Bellwood et al. 2019, Williams & Graham 2019).

## *Ecosystem functioning on coral reefs*

Ecosystem functioning (Jax 2005) refers to the range of natural processes and components that contribute to the production and exchange of energy and materials (Srivastava & Vellend 2005, Pacala & Kinzig 2013, Bellwood et al. 2019), sustain and fulfil life (Daily et al. 1997) and provide goods and services for human use (de Groot et al. 2002). Despite the diversity of interpretations in the literature, the overarching typology of ecosystem functioning considers the natural properties and processes that work to support an ecosystem and their direct or indirect anthropogenic benefits (de Groot et al. 2002, Jax 2005, Srivastava & Vellend 2005, Farnsworth et al. 2017). In the marine environment, ecosystem functioning depends on interactive physical (e.g. waves, currents, sediment, light), chemical (e.g. nutrient cycling, ocean pH, salinity) and ecological (e.g. primary production, herbivory, predation, calcification) processes. While we recognise that physical and chemical processes are essential components of coral reefs, a species' contribution to ecosystem functioning is inextricably linked to its ability to perform ecological processes (Figure 1). To identify species – or functional groups of species – that are disproportionately important to the maintenance of coral reef functioning, this review focussed on key ecological processes.

We examined species' contributions to a range of ecological process that scale up to support habitat (e.g. reef accretion) and production (e.g. fisheries) functioning (Figure 1). Together, these form the foundations of coral reefs through 1) habitat provisioning and the stocks of energy and material (e.g. calcification, bioerosion) and 2) the production and fluxes of energy and materials across ecosystem networks (e.g. trophic transfers, photosynthesis, nutrient uptake) (de Groot et al. 2002, Srivastava & Vellend 2005, Kennedy et al. 2013, Harborne et al. 2017, Bellwood et al. 2019). These effectively incorporate the construction (and destruction) of the biogenic reef structure – the fundamental framework of coral reefs (Wild et al. 2011) – and trophic pathways and interactions across the food web (Figure 1). Habitat and production functioning encapsulate the most important goods and services provided by coral reefs, scaling up to benefit coastal protection and fisheries production (Moberg & Folke 1999, Harborne et al. 2017). They are fundamental attributes of outstanding universal value (OUV) and contribute to the values and integrity of coral reefs, including for the World Heritage property of the GBR (GBRMPA 2014c).

Due to a growing number of local and global stressors, irreversible shifts in the ecological processes that maintain coral reefs are already measurable, including for those that support habitat
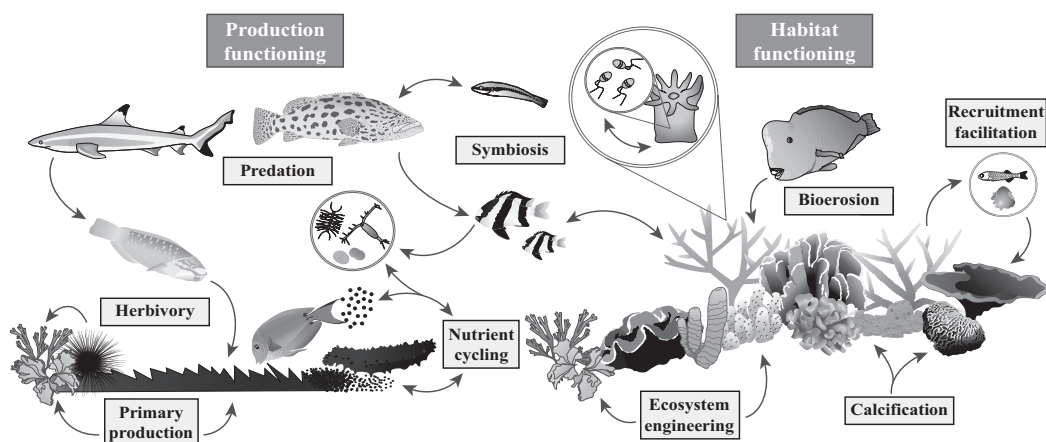


**Figure 1** Simplistic representation of the nine key ecological processes considered here in support of habitat and production functioning on coral reefs.

and production functioning (De'ath et al. 2012, Cinner et al. 2016, 2018, Hughes et al. 2018b, Richardson et al. 2018, Rogers et al. 2018a). Some examples include changes to processes that support: 1) calcification and bioerosion rates, which impact reef community composition, reef accretion and the net carbonate budget (Silverman et al. 2012, 2014, De'ath et al. 2013, Dove et al. 2013, DeCarlo et al. 2015, Albright et al. 2016b, 2018, Perry & Harborne 2016, Manzello et al. 2017, Schönberg et al. 2017, Cyronak et al. 2018); 2) herbivory and algal growth that results in phase shifts away from coral towards algal-dominated reefs (Ceccarelli et al. 2006, Hughes et al. 2007b, Mumby 2009b, Burkepile & Hay 2010, Cheal et al. 2010, Hoey & Bellwood 2011, Bellwood et al. 2012b, Adam et al. 2015a); 3) impaired recruitment opportunity and success, which limits reef growth and persistence across generations (Doropoulos et al. 2012b, Doropoulos & Diaz-Pulido 2013, Hughes et al. 2019a) and 4) antagonistic population outbreaks of predatory species with impacts on live coral cover (Endean 1982, Brodie & Waterhouse 2012, De'ath et al. 2012, Baird et al. 2013, Pratchett et al. 2014, Hoey et al. 2016b). Such shifts in the coral reef archetype will continue to have serious repercussions on ecosystem resilience and recovery and in how we shape current and future management practises (Knowlton 2012, Uthicke et al. 2016, van de Leemput et al. 2016, Osborne et al. 2017, Stuart-Smith et al. 2018). With this in mind, we provide a framework to rationalise priority species and processes that work to support coral reefs at their highest levels of functioning in a changing environment.

# Methods

## *Expert elicitation*

Quantifying the importance of species to ecosystem functioning is challenging and complex, especially for high-diversity ecosystems like rainforests and coral reefs. A number of studies have addressed this at specific levels of taxonomy and functioning, including for lichen assemblages within soil ecosystems (Gotelli et al. 2011), avian traits regarding plant-frugivore interactions (Pigot et al. 2016) and the influence of coral reef fishes on live coral cover and socio-environmental services (Maire et al. 2018). Yet for coral reefs, functional ecology lacks a clear definition and empirical evidence on the assumed links between reef taxa and processes (Williams & Graham 2019). Further, knowledge of reef functioning is largely weighted towards certain taxonomic and functional groups (e.g. corals and fishes; Bellwood et al. 2004, 2017, 2019, Stuart-Smith et al. 2013, Bierwagen et al. 2018, McWilliam et al. 2018). Given the breadth of our analysis, we employed expert elicitation to facilitate a comparative assessment of the ecological roles of a diverse array of coral reef taxa – from microbes to top predators – and broad spectrum of ecosystem processes and functioning.

Expert elicitation can provide valuable insight and data to inform science and decision-making, particularly when there are significant limitations and inconsistencies in scientific knowledge (Morgan et al. 2001, Knol et al. 2010, O'Leary et al. 2011, Polasky et al. 2011, Runge et al. 2011, Martin et al. 2012, Ban et al. 2014b, Morgan 2014, Rogers et al. 2015). Experts were selected from a literature search and using background knowledge of coral reef ecologists currently involved in research in the focal region, the GBR, Australia. Using a snowball approach, experts were invited to participate in the project, ensuring a multidisciplinary assemblage with expertise across taxonomic groups, levels of ecosystem functioning and environmental stressors. A total of 18 experts were directly involved in project development, scientific workshops and/or the elicitation process. This size pool is within the lower ($n = 3$; Clemen & Winkler 1999) and upper ($n = 60$; de Franca Doria et al. 2009) ranges for the expert elicitation process (Ban et al. 2014b). Given the level of involvement and knowledge provided through the elicitation process, experts were included as co-authors.

Our expert elicitation process conformed to the Investigate, Discuss, Estimate, Aggregate (IDEA) protocol, which was designed to improve the accuracy of expert judgement (Burgman 2016, Hemming et al. 2018). In short, in a two-day workshop, we convened our panel of GBR experts, where they were first asked to *Investigate* knowledge and information on key coral reef

taxa across a range of processes, functioning and threats. Attempts at compiling and formulating this information into questions and evidence were then open to feedback. Experts were encouraged to *Discuss* interpretations and results to promote critical thinking and reduce ambiguity. These two stages provided the framework of further project and survey development before experts completed an official independent *Estimate* scoring stage. Expert responses and scores were then *Aggregated* to produce mean data across responses. Specific details on project and survey development, and data handling and aggregation, can be found in the following sections.

## *Project and survey development*

In the two-day workshop with our expert panel, we identified 70 functionally and taxonomically distinct groups of marine species common on the GBR (Figure 2). Functional groups remained broadly defined but were occasionally refined to individual species with explicit and well-documented roles (e.g. CoTS). Subsequent in-depth examination was intended for high-ranking groups at later stages of the project through targeted literature searches. Some taxa were excluded (e.g. marine reptiles, mammals, seabirds), as these groups are often rare on the GBR and/or already intensively addressed and managed (see: Stoeckl et al. 2010b, Birtles et al. 2014, GBRMPA 2014b,c, Richards & Day 2018, Risch et al. 2019). Many species within these taxa are of OUV and are critical to the way the World Heritage Convention is implemented on the GBR (GBRMPA 2014c), with key social and economic value, particularly regarding tourism (Stoeckl et al. 2010a,b, Marshall et al. 2018, Curnock et al. 2019). The exclusion of these species does not devalue their contributions to a functioning ecosystem (e.g. Graham et al. 2018, Savage 2019, Tavares et al. 2019) or their necessity to be considered in context of social, cultural and economic values for holistic management (GBRMPA 2014a,c).

As the world's largest coral reef ecosystem, the GBR is an amalgamation of bioregions with their own, often unique, dynamics (McCook et al. 2010, Day 2016) and governance (Day 2002, Brodie & Waterhouse 2012, Morrison 2017). Due to the sheer size and diversity of the GBR, our expert panel chose to focus attention on the functioning of classical reef slope and reef crest habitats, as these are typically the most diverse and coral-rich ecosystems that support the greatest range of services (Mumby et al. 2008, Harborne et al. 2017). This refined approach acknowledges the exclusion of other important and interconnected biomes of coral reefs (e.g. mangroves, seagrass meadows, interreefal areas) (GBRMPA 2004, 2014b,c, van de Koppel et al. 2015, Sievers et al. 2019), including deep (or mesophotic) reefs (Bridge et al. 2012, Harris et al. 2013, Turner et al. 2017), but was employed to ensure a targeted research design to inform the holistic management of GBR species, values and processes. There is the opportunity to build on the current framework of biological functioning in future work to include other important coral reef biomes and give greater consideration to social, cultural and economic values.

A methodology to assess functionally important species was developed by our scientific panel during the workshop (Figure 3; Table 1) in a series of stages framed by the IDEA protocol for expert elicitation (as previously) (Burgman 2016, Hemming et al. 2018). Outcomes were used to construct annotated online surveys that operated under three main criteria:

1. Functional importance: a process-based assessment of species' contributions to ecosystem processes and functioning.
   *Question: Who contributes most to ecosystem functioning on the GBR?*
2. Vulnerability: an assessment of the sensitivity and exposure of species to current and near-future stressors and their likely recoverability.
   *Question: What species are most vulnerable on the GBR, and do they require protection?*
3. Manageability: an assessment of the probable effectiveness and feasibility of a management intervention in the context of biological functioning.
   *Question: Is management feasible for important species?*

Microbes
- Phototrophic (Synechococcus, Prochlorococcus)
- Heterotrophic (Bacteroidetes, Proteobacteria)
- Chemoautotrophic (Archaea)
- Host-associated (Symbiodinium)

Algae
- Phytoplankton (Coccolithophores, *Trichodesmium*)
- Algal turfs (*Cladophora*, *Lyngbya*, *Oscillatoria*)
- Leathery (*Sargassum*)
- Foliose (*Dictyota*, *Lobophora*, *Ulva*)
- Calcareous (*Amphiroa*, *Halimeda*)
- Crustose coralline (CCA) (*Hydrolithon*, *Porolithon*)

Sponges
- Phototrophic (*Carteriospongia*, *Cymbastella*, *Stylissa*)
- Heterotrophic (*Xetospongia*, *Rhopaloeides*)
- Boring (*Aka*, *Cliona*)
- Cryptic

Corals
- Tabular (*Acropora hyacinthus*)
- Staghorn (*Acropora muricata*)
- Other branching (*Acropora*, *Pocillopora*)
- Massive (*Porites*)
- Encrusting (*Montipora*)
- Free-living (*Fungia*)
- Soft corals (*Dendronephthya*, *Sinularia*, *Xenia*)
- Benthic foraminifera

Worms
- Nematodes
- Other worms (Nemertea, Plathyhelminthes)
- Polychaetes
- *Spirobranchus*

Crustaceans
- Decapods (herbivores; Diogenidae, Xanthidae)
- Decapods (predatory)
- Coral associates (Trapeziidae, Tetraliidae)
- Sessile (barnacles)
- Stomatopods (mantis shrimp, *Odontodactylus*)
- Cleaner shrimp (*Lysmata*)
- Zooplankton (copepods, larvaceans)
- Infauna (harpacticoid copepods, amphipods)
- Parasitic (gnathiid isopods)

Molluscs
- Gastropods (herbivores; turbo snails, *Aplysia*)
- Gastropods (predators; nudibranchs, *Conus*)
- Triton snails (*Charonia*)
- Corallivores (*Drupella*)
- Giant clams (*Tridacna*)
- Bivalves (oysters, mussels)
- Chitons (Polyplacophora)
- Cephalopods (octopus, squid, cuttlefish)

Echinoderms
- Starfish (herbivores; *Linckia*)
- Starfish (predators; *Culcita*)
- Crown-of-thorns (*Acanthaster*)
- Sea cucumbers (deposit-feeders; stichopodids)
- Sea cucumbers (suspension feeders; *Cucumaria*)
- Sea urchins (regular; *Diadema*, *Echinometra*)
- Sea urchins (irregular; sand dollars, heart urchins)
- Brittle stars (ophiuroids)
- Feather stars (crinoids)

Fishes
- Cryptobenthic fishes (gobies)
- Herbivores - farmers (damselfishes; pomacentrids)
- Herbivores - scrapers (parrotfishes; scarids)
- Herbivores - browsers (surgeonfishes; *Naso*)
- Herbivores - browsers (rabbitfishes; siganids)
- Herbivores - browsers (other; chubs)
- Herbivores - excavators (*Bolbometopon*)
- Herbivores - excavators (other; scarids)
- Detritivores (mullids, blennies, *Ctenochaetus*)
- Planktivores (*Chromis*)
- Corallivores (butterflyfishes)
- Invertivores (wrasses; labrids)
- Invertivores (lutjanids)
- Invertivores (other; pufferfishes, triggerfishes)
- Piscivores (resident; emperors, *Plectropomus*)
- Piscivores (transient; sharks, barracuda)
- Eels (morays; muraenids)
- Cleaner fishes (*Labroides*)

**Figure 2**  Taxonomic and functional groups partitioned in this assessment with examples in parentheses. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/) and Hutson et al. (2018). Note: 1) dinoflagellate Zooxanthellae are not considered part of the 'phytoplankton'; 2) it is understood that foraminifera are not corals; 3) zooplankton includes groups outside of the Crustacea (e.g. larvaceans, chaetognaths, salps).
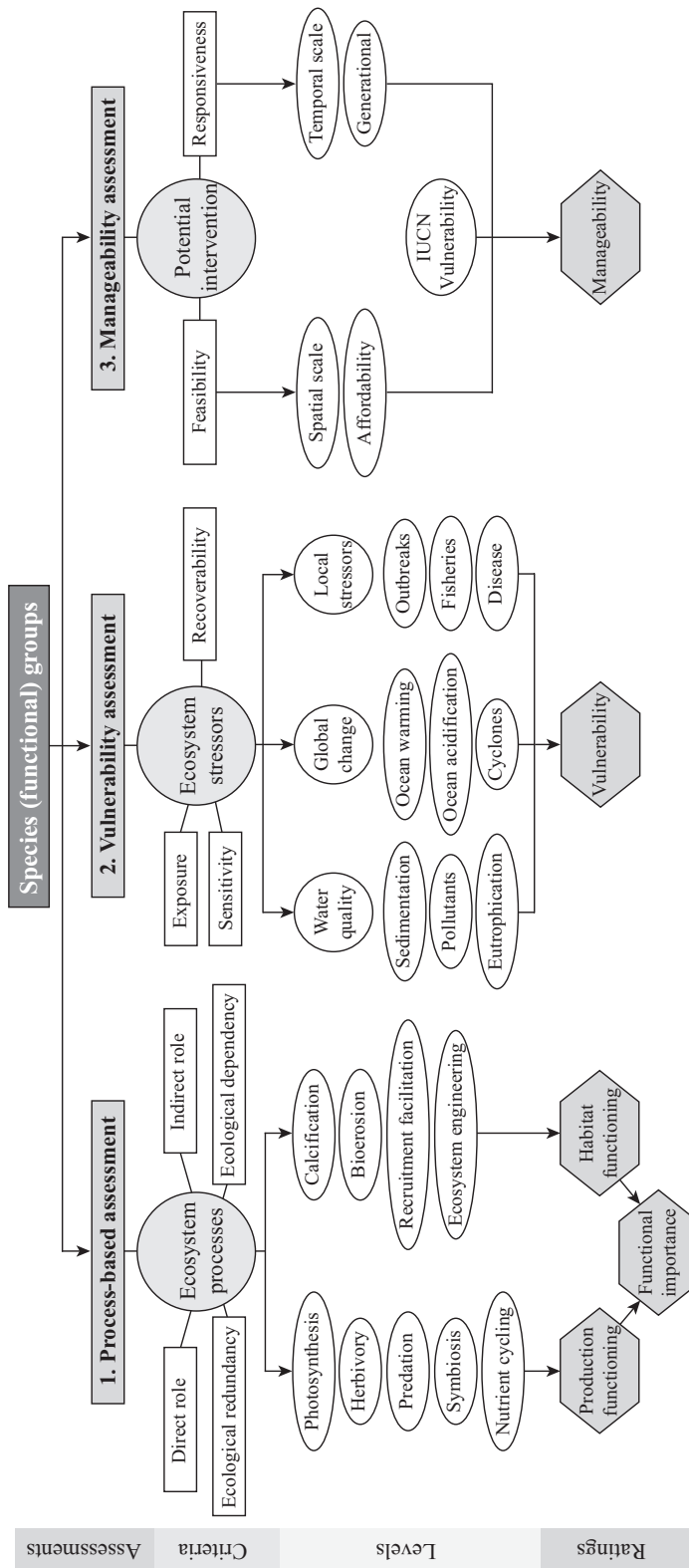
**Figure 3** Framework outlining the assessment criteria employed to identify and rank priority species in support of ecosystem functioning based on their 1) functional importance (process-based assessment), 2) vulnerability and 3) manageability.

**Table 1**  Criteria used to score 70 functional groups on their (A) functional importance, (B) vulnerability and (C) manageability on the GBR.

| Dynamic | Category | Score | Notes |
|---|---|---|---|
| **A. Functional importance** | | | |
| Direct contribution | None | 0 | No direct role performing the process |
| | Low | 1 | Directly contributes to the process but is not a key player |
| | High | 2 | Ecologically significant contribution to the process |
| Indirect facilitator/mediator | None | 0 | No real indirect effect on others performing the process |
| | Low | 1 | Some level of impact on the process; competition, mutualism |
| | High | 2 | Specific impact; key predator, top-down/bottom-up control |
| Redundancy | None | 0 | Critical and specific performing the process or in mediating it |
| | Low | 1 | Some level of replaceability, similar species performing the process |
| | High | 2 | Replaceable in its role performing the process |
| Dependency | None | 0 | Self-sufficient in performing the process |
| | Low | 1 | Some level of dependence to perform the process |
| | High | 2 | Reliant on other organisms to complete the process |
| Certainty | Low | 0.25 | Little empirical work and expert knowledge |
| | Medium | 0.50 | Some empirical work and expert experience |
| | High | 0.75 | Extensive work and/or experience |
| **B. Vulnerability** | | | |
| Sensitivity (S) | Sensitive | −2 | Highly sensitive to the stressor |
| | Slight impact | −1 | Partial negative impacts |
| | No impact | 0 | Not affected |
| | Slight gain | 1 | Partial benefit from stressor |
| | Beneficial | 2 | Stressor is highly beneficial |
| Exposure (E) | None | 0 | Not exposed to the stressor |
| | Low | 1 | Low exposure, low likelihood of exposure |
| | High | 2 | Highly exposed, highly likely to be exposed |
| Potential Recoverability (PR) | Low | 0.25 | Unlikely to recover before next event |
| | Medium | 0.50 | Some level of recoverability |
| | High | 0.75 | Highly likely to recover before next event |
| Certainty | Low | 0.25 | Little empirical work and expert knowledge |
| | Medium | 0.50 | Some empirical work and expert experience |
| | High | 0.75 | Extensive work and/or experience |
| **C. Manageability** | | | |
| Responsiveness | None | 0 | Species/populations unlikely to change following intervention |
| | Low | 1 | Some response predicted through action |
| | High | 2 | Action is likely to have a strong effect on populations |
| Feasibility | None | 0 | Broad scale, not affordable, inefficient, impossible |
| | Low | 1 | Plausible but likely restricted to some locations/populations |
| | High | 2 | Very possible, with good scope-cost benefits |
| Information | None | 0 | Little existing work, hard to monitor |
| | Low | 1 | Some work exists, monitoring possible (but patchy) |
| | High | 2 | Extensive work exists, easy to monitor |

Surveys to address these criteria were developed online using the Surveymonkey platform and were open for several weeks (July–August 2018). Surveys were targeted at our expert panel, but responses remained anonymous. A low-range scoring system (e.g. none/low/high) was employed to reduce ambiguity in responses (see Table 1), as qualitative words and broad scoring ranges are prone to subjectivity and uncertainty (Morgan et al. 2001, Morgan 2014). Space for comments and

feedback was provided throughout the surveys, which is outlined as a critical elicitation process to ensure expert knowledge is accurately captured and interpreted (Martin et al. 2012, Hemming et al. 2018). A total of 16 survey responses were completed across our taxonomic and functional groups, with equal-weighted averages taken across expert responses. Group averages are simple but can be effective in producing estimates of elicitation (Martin et al. 2012). Scores were checked and calibrated against the literature and empirical data (where possible) to reduce subjectivity and bias. This proved particularly effective during the *Discuss* stage of the IDEA framework (Hemming et al. 2018). Scoring criteria are explicitly outlined for each assessment (Figure 3; Table 1).

Extensive literature searches were conducted by the primary author between March 2018 and June 2019 using online databases, including Web of Science and Google Scholar. Experts involved in the elicitation process had the opportunity to recommend relevant literature through the IDEA framework, but the review process remained largely independent of the expert panel. Peer-reviewed research and review articles pertaining to the 70 species groups and various levels of ecosystem processes, functioning and/or environmental stressors, as addressed in this review, were of focus. As a particularly data-rich system, literature explicitly related to the GBR was targeted, although we included relevant information for coral reefs more generally. Particular attention was given to species groups that scored highly at specific levels of ecosystem processes, functioning and/or stressors to benchmark results against peer-reviewed literature. This process aided in the interpretation of expert results and response accuracy (Hemming et al. 2018). We outline discrepancies between expert responses and the literature when evident, particularly for groups that scored highly despite receiving comparatively marginal representation in the literature. Independent literature searches were also conducted for each of the five case studies integrated in this review.

## *Scoring criteria*

### *Functional importance: A process-based assessment*

Contributions of organisms to ecosystem processes (e.g. calcification, bioerosion, herbivory, predation; Figure 1) drive and support ecosystem functioning (e.g. reef accretion, habitat complexity, energy/trophic transfers) and services (e.g. coastal protection, fisheries, tourism). The first stage of our surveys elicited experts to score the contribution of 70 taxonomic and functional groups of coral reef species (Figure 2) to nine ecosystem processes considered critical to ecosystem functioning (Figures 1 and 3). These processes were selected due to their broad representation in the literature and current consideration in management reports for the GBR (GBRMPA 2014b). These nine processes scale up to support habitat and production functioning, which are fundamental to the future of coral reefs in terms of reef construction, trophic pathways and ecosystem services (de Groot et al. 2002, Harborne et al. 2017). All ecosystem processes were considered equally important to ensure that all were represented at their highest levels; that is, no process was weighted as more important to a functioning ecosystem.

Species groups were scored based on their direct and indirect contributions to each process (Figure 3; Table 1A). This was intended to capture both the immediate contribution of an individual to a process (e.g. hard corals to calcification) and, equally important, their indirect facilitation and/or mediation of the process (e.g. algae to herbivory), as indirect effects are fundamental to the complexity of ecosystem functioning and to conservation outcomes (Wootton 1994, 2002, Dulvy et al. 2004, Jordán et al. 2008, Bergstrom et al. 2009, Ritchie & Johnson 2009). Species groups were also scored based on their ecological redundancy and dependency on a per-process basis (Figure 3; Table 1A), as species interactions and functional diversity can highlight critically important taxa (Petchey & Gaston 2002, Mouillot et al. 2013, 2014). Expert scores were compiled and average scores calculated for each functional group–ecosystem process combination. Finally, experts were elicited to rate the level of confidence (i.e. certainty; Table 1A) in their scores for each functional group. These scores were used *post hoc* to weight final scores for management recommendations.

Scores for direct ($D$) and indirect ($I$) contributions were combined as a measure of the magnitude ($M$) of the role of each functional group to each ecosystem process, using the equation:

$$M = (D + I)^2$$

This equation worked under the assumption that direct and indirect effects were equally important to ecosystem processes and functioning. Scores were squared to elevate organisms that scored highly for any given process and to amplify even the slightest differences among expert responses. Scores for magnitude, redundancy and dependency were then categorised and ranked for each species–process combination (Table 2). For magnitude, the top and bottom 33rd percentile of scores were classed as 'high' and 'low', respectively, with the remaining scores classed as 'intermediate' (Table 2). Thus, rankings were relative to the range of scores within each process. We worked under the assumption that magnitude was the most important score for determining the importance of species groups; that is, how much they contribute (directly or indirectly) to the process outweighed their ecological redundancy and/or dependency (Table 2). Examples of 'high' magnitude scores existed in algal turfs to primary production, branching and tabular corals to calcification and piscivorous fishes to predation. Examples of 'low' magnitude scores were worms to primary production and piscivorous fishes to calcification.

Redundancy and dependency were used as mediators of scores for magnitude. Species with 'low' (or no) ecological redundancy (average scores ≤1) were considered more important for targeted management (Table 2), as this suggests specialisation and irreplaceability in their roles (Hooper et al. 2005, Jain et al. 2014, McWilliam et al. 2018). Species with 'high' redundancy (average scores >1) were deemed replaceable and were down-weighted (Table 2). For example, triton snails had low redundancy for the predation process, as they are essential predators of CoTS, while other predatory molluscs were considered to have higher redundancy in this process. Species groups with 'low' dependency (average scores ≤1) were considered more important than those with 'high' dependency (Table 2), under the assumption that they can effectively perform their roles exclusive of others and are thus better candidates for targeted management. Conversely, dependent species were down-weighted (Table 2), as their ecological performance requires inclusion of other species with implications for management efficacy.

**Table 2**  Ranking scheme for functional groups based on their magnitude, redundancy and dependency in the context of nine key ecosystem processes on the GBR

| Rank | Magnitude | Redundancy | Dependency |
|------|-----------|------------|------------|
| 1 | H | L | L |
| 2 | H | L | H |
| 3 | H | H | L |
| 4 | H | H | H |
| 5 | M | L | L |
| 6 | M | L | H |
| 7 | M | H | L |
| 8 | M | H | H |
| 9 | L | L | L |
| 10 | L | L | H |
| 11 | L | H | L |
| 12 | L | H | H |

*Abbreviations:*  H, high; M, intermediate; L, low.

Ranks were determined on a per-process basis. Within this scoring scheme, a functional group with the highest magnitude of contribution to an ecosystem process but the lowest ecological redundancy and dependency would rank the highest: an 'essential provider'. Conversely, a low-contributing group with high redundancy and dependency would rank the lowest; a 'leech'. Total functional importance (FI) was then calculated across the $i = 9$ process rankings using a sum of squares equation:

$$FI = \sum_{i=1}^{9} (13 - x)^2$$

where $x$ is the rank score for each process. This ensured that highly ranked groups (i.e. $x = 1$) received higher final scores, and that those ranked highly for just one process were recognised. This also ensured that no species scored a complete zero (i.e. when $x = 12$). Final values for FI were square root transformed to normalise data. FI was calculated in the same manner for habitat and production functioning separately. Scores for expert scientific certainty were examined *post hoc*. Final values for FI with high certainty were considered top priority, while scores that were largely uncertain were up-weighted under precautionary principles.

*Assessing the vulnerability of coral reef species*

Ecosystems are considered healthy if they are able to maintain (or recover) structure and functioning in the face of external pressures (Costanza & Mageau 1999). To understand potential threats to functioning on the GBR, pertinent current and near-future (2050 outlook; [DEE 2015, GBRMPA 2018b]) stressors were workshopped (Figure 3). Parallel to scoring functional importance, experts were elicited to score the 70 functional groups (Figure 2) based on their vulnerability to nine critical stressors (Figure 3) in line with previous projects, elicitation processes and reviews (Ban et al. 2014a,b, Uthicke et al. 2016, Harborne et al. 2017). The Intergovernmental Panel on Climate Change (IPCC) Vulnerability Framework (IPCC 2007) formed the basis of this assessment, which uses the sensitivity and exposure of an individual, as well as its potential to recover, to calculate its total vulnerability (Figure 3; Table 1B).

Experts scored species groups based on their known (and anticipated) sensitivity, exposure and recoverability to each of the nine pertinent stressors (Figure 3). Sensitivity ($S$) was scored across a range of positive to negative scores (Table 1B), as some species may benefit from a particular stressor (e.g. ocean warming on algal growth, herbivore abundance due to overfishing of predators), while others may be severely impacted (e.g. calcification due to ocean change, sea cucumbers due to overfishing). However, since our focus was to identify vulnerable species for management, scores that suggested positive effects from a stressor ($S > 0$) were counted to have no effect (i.e. not sensitive; $S = 0$). Exposure ($E$) was considered generally for typical reef habitats (e.g. reef crest, reef slope) but was assessed differently for inner reefs and offshore regions on the GBR, as some stressors, such as those related to water quality, are often more significant on inshore reefs proximal to terrestrial influence (Devlin & Brodie 2005, Wooldridge et al. 2006, Brodie & Waterhouse 2012, Brodie et al. 2012, Kroon et al. 2012, Waterhouse et al. 2012, Fabricius et al. 2014, Lam et al. 2018, MacNeil et al. 2019, Mellin et al. 2019).

Potential impact (PI) was calculated from average expert scores for each stressor–functional group combination, using the equation:

$$PI = (S \times E)^2$$

This calculation assumes that sensitive groups that are not exposed to a stressor ($E = 0$) are not vulnerable, as for groups that are exposed but not at all sensitive ($S = 0$). *PI* was calculated for each

of $i = 9$ stressors, and total vulnerability ($V$) was then calculated across all stressor values, using the equation:

$$V = \frac{\sqrt{\sum_{i=1}^{9} PI}}{PR}$$

This framework ensured that species with high potential recovery ($PR$) were down-weighted under the assumption that management would be less necessary for species likely to recover. Conversely, $V$ would be greater for species with low $PR$ under the assumption that they would require greater management attention to improve recovery chances. Experts also scored the certainty of their scores for each functional group here (Table 1B), which was used *post hoc* to address the validity of vulnerability scores. Final rankings suggesting high vulnerability with high certainty were considered the most critical to address. Vulnerable species groups with a low-rated level of certainty could also be examined under precautionary principles so that data-deficient groups were not overlooked.

Final scores for $V$ and $FI$ were combined to identify key species where both factors were high. The relative impact ($Imp$) of our nine stressors was also calculated by multiplying $V$ and $FI$ for each species-process-stressor combination:

$$Imp_{species} = V_{stressor} \times FI_{process}$$

From this template, we could determine the proportional impact that each stressor was considered to have on each functional group at their highest level of functioning. This was also calculated for each ecosystem process-stressor combination. The proportional impact of a given stressor would be weighted higher by taxa scored to be more functionally important. Conversely, the proportional impact of a stressor would be less driven by species with marginal importance. This information could be used to identify combinations of species, stressor and/or processes that may be most critical to address and protect.

*Assessing the manageability of coral reef species*

Each functional group was assessed in context of its relative manageability on the GBR. This assessment was in context of the biological roles of each species group and was not an assessment of other attributes such as social, cultural and economic values. These additional attributes would be important to consider if building out from the current framework. Experts were elicited to score groups based on their likely 1) responsiveness to management intervention, 2) feasibility of implementation (affordability, geographic scale, etc.) (Figure 3) and 3) availability and attainability of information (i.e. monitorability) (Table 1C). Conservation status (e.g. IUCN Red List species) was also considered *post hoc* to address 'at risk' populations (Richards & Day 2018) (Figure 3).

Manageability ($Mg$) was calculated using average expert scores for responsiveness ($R$) and feasibility ($F$), using the equation:

$$Mg = (R + F)^2$$

Scores for information/monitorability were not included in this calculation under the assumption that functionally important and vulnerable species should be a priority regardless of their ability to be monitored. Thus, the predicted ability for species to respond to management ($R$) and feasibility ($F$) of implementation formed the foundations of our $Mg$ calculation (Figure 3). Groups were categorised as a high priority for management if they were in the top 66th percentile of scores for $Mg$,

while those in the bottom 33rd percentile were deemed lower management priorities. Top-scoring organisms for functional importance, vulnerability and management priority were considered top candidates overall. High scoring groups that were considered lower priority for management would be highlighted as groups that may require innovative approaches.

### Incorporating uncertainty

Experts were elicited to score the certainty of their scores for functional importance and vulnerability. Certainty was scored categorically as low (0.25), medium (0.50) or high (0.75) (Table 1A, B). These scores were used *post hoc* to support our recommendations, particularly when scientific certainty was comparatively high or low. High certainty solidified the merit of our recommendations, particularly for highly ranking functional groups. Under precautionary principles, scores that were uncertain were highlighted so that functional groups that 'slipped through the cracks' in our ranking system due to data deficiencies were not missed. Thus, low-ranked functional groups had the potential to be elevated in their importance and/or vulnerability if certainty was low.

### Knowledge gaps in ecosystem functioning on the Great Barrier Reef

Formal expert elicitation is a structured and transparent methodology that effectively addresses uncertainties in scientific knowledge (Knol et al. 2010, Polasky et al. 2011). In addition to the scoring criteria previously, critical knowledge gaps in our understanding of reef functioning were made evident by our expert panel. Consensus decisions on the most logical, feasible and important knowledge gap themes were made, which were developed into five subprojects that reflect our multidisciplinary expert assemblage across taxonomic groups, levels of ecosystem functioning and environmental stressors on the GBR. Within the lifetime of this project, teams of researchers addressed these knowledge gaps, which are presented here as case studies that highlight pivotal species (and groups of species) at specific levels of ecosystem functioning to directly inform this project and future research;

1. Invertivory on the GBR: a poorly understood link in the trophic chain.
2. Addressing the carbonate budget for the GBR.
3. Microbial communities as indicators of water quality on the GBR.
4. Functional impacts of recreational spearfishing on the GBR.
5. Juvenile CoTS 'in waiting': the missing link in population and connectivity models.

## Results and discussion

Species of particular functional importance on the GBR are outlined subsequently using an ecosystem process-based assessment for 70 distinct groups (Figure 2). Rankings for functional importance are provided at various levels of ecosystem functioning, 1) for each ecosystem process, 2) for habitat and production functioning and 3) combined overall (Figure 3). Additional rankings are outlined for species groups based on their perceived vulnerability to nine key environmental stressors on the GBR and for their relative manageability (Figure 3). Final scores are presented across these three components and weighted to scientific certainty. Note that all levels of ecosystem processes were considered equally important to a functioning reef to reflect all species and processes at their highest level of functioning.

### Process-based assessment

Top-ranked species groups within each process are outlined in Table 3. Scores are discussed, interpreted and/or supported in the following sections through case-specific reviews of the literature available for coral reefs, primarily the GBR, at various levels of ecosystem processes and

**Table 3** Functional importance (FI) rankings for 70 functional groups per process on the GBR

| Taxa | Functional group | Primary production | Herbivory | Predation | Nutrient cycling | Symbiosis | Calcification | Bioerosion | Ecosystem engineering | Recruitment facilitation |
|---|---|---|---|---|---|---|---|---|---|---|
| Microbes | Phototrophic | 4 | 7 | 7 | 4 | 4 | 7 | 4 | 4 | 7 |
| | Host-associated | 2 | 7 | 7 | 4 | 2 | 2 | 2 | 2 | 4 |
| | Chemoautotrophic | 4 | 7 | 7 | 4 | 4 | 6 | 4 | 4 | 4 |
| | Heterotrophic | 4 | 7 | 7 | 4 | 4 | 8 | 4 | 4 | 4 |
| Algae | Phytoplankton | 2 | 7 | 7 | 2 | 7 | 7 | 5 | 11 | 5 |
| | Algal turfs | 2 | 3 | 7 | 2 | 7 | 7 | 2 | 8 | 2 |
| | Leathery | 8 | 3 | 7 | 8 | 7 | 5 | 11 | 4 | 11 |
| | Foliose | 4 | 3 | 7 | 8 | 7 | 5 | 11 | 4 | 2 |
| | Calcareous | 6 | 3 | 7 | 6 | 7 | 2 | 11 | 8 | 5 |
| | CCA | 2 | 5 | 7 | 6 | 7 | 2 | 11 | 4 | 2 |
| Sponges | Heterotrophic | 7 | 7 | 7 | 6 | 4 | 7 | 7 | 3 | 3 |
| | Phototrophic | 3 | 7 | 7 | 6 | 4 | 7 | 7 | 3 | 3 |
| | Boring | 3 | 7 | 7 | 10 | 4 | 4 | 2 | 6 | 4 |
| | Cryptic | 7 | 7 | 7 | 6 | 4 | 3 | 3 | 5 | 3 |
| Coral | Tabular | 4 | 7 | 7 | 2 | 2 | 2 | 7 | 2 | 2 |
| | Staghorn | 4 | 7 | 7 | 4 | 4 | 4 | 7 | 2 | 2 |
| | Branching (other) | 4 | 7 | 7 | 8 | 4 | 4 | 11 | 4 | 2 |
| | Massive | 4 | 7 | 7 | 8 | 2 | 4 | 11 | 2 | 4 |
| | Encrusting | 4 | 11 | 7 | 8 | 4 | 4 | 7 | 4 | 4 |
| | Free-living | 8 | 11 | 7 | 8 | 4 | 8 | 11 | 8 | 8 |
| | Soft corals | 4 | 7 | 7 | 4 | 2 | 7 | 11 | 4 | 8 |
| | Foraminifera | 8 | 11 | 11 | 8 | 4 | 4 | 7 | 12 | 12 |
| Worms | Nematodes | 11 | 11 | 7 | 7 | 8 | 7 | 3 | 7 | 11 |
| | Nemertea | 11 | 11 | 7 | 7 | 8 | 7 | 3 | 7 | 11 |
| | Polychaetes | 11 | 11 | 3 | 7 | 8 | 7 | 3 | 7 | 7 |

(*Continued*)

**Table 3 (*Continued*)**  Functional importance (FI) rankings for 70 functional groups per process on the GBR

| Taxa | Functional group | Primary production | Herbivory | Predation | Nutrient cycling | Symbiosis | Calcification | Bioerosion | Ecosystem engineering | Recruitment facilitation |
|---|---|---|---|---|---|---|---|---|---|---|
| | *Spirobranchus* | 11 | 11 | 8 | 11 | 4 | 7 | 3 | 7 | 5 |
| Crustaceans | Decapods (H) | 7 | 3 | 7 | 7 | 8 | 7 | 7 | 7 | 7 |
| | Decapods (P) | 11 | 11 | 3 | 7 | 7 | 7 | 7 | 7 | 11 |
| | Coral-associated | 7 | 11 | 4 | 6 | 2 | 2 | 3 | 8 | 7 |
| | Barnacles | 11 | 11 | 7 | 11 | 8 | 7 | 7 | 7 | 7 |
| | Stomatopods | 11 | 11 | 3 | 7 | 8 | 7 | 3 | 7 | 7 |
| | Cleaner shrimp | 7 | 11 | 8 | 10 | 6 | 5 | 11 | 7 | 5 |
| | Infauna | 7 | 7 | 3 | 7 | 8 | 7 | 7 | 7 | 7 |
| | Zooplankton | 7 | 3 | 3 | 2 | 7 | 7 | 11 | 11 | 11 |
| | Parasitic | 11 | 11 | 7 | 7 | 8 | 7 | 11 | 11 | 11 |
| Molluscs | Gastropods (H) | 7 | 3 | 7 | 7 | 7 | 3 | 7 | 7 | 7 |
| | Gastropods (P) | 11 | 7 | 3 | 7 | 7 | 3 | 7 | 7 | 11 |
| | Triton snails | 7 | 7 | 1 | 7 | 5 | 3 | 7 | 5 | 11 |
| | *Drupella* | 7 | 11 | 7 | 7 | 7 | 3 | 7 | 7 | 7 |
| | Tridacnidae | 7 | 7 | 7 | 7 | 8 | 3 | 7 | 7 | 3 |
| | Bivalves | 7 | 7 | 7 | 8 | 7 | 3 | 7 | 7 | 3 |
| | Chitons | 7 | 7 | 7 | 7 | 7 | 3 | 7 | 7 | 7 |
| | Cephalopods | 11 | 7 | 1 | 7 | 8 | 7 | 7 | 7 | 11 |
| Echinoderms | Seastars (H) | 7 | 3 | 7 | 7 | 7 | 7 | 7 | 7 | 11 |
| | Seastars (P) | 11 | 11 | 7 | 7 | 7 | 7 | 7 | 7 | 7 |
| | CoTS | 7 | 3 | 3 | 7 | 7 | 3 | 3 | 7 | 7 |
| | Sea cucumbers (DF) | 7 | 7 | 7 | 5 | 8 | 5 | 7 | 7 | 11 |
| | Sea cucumbers (SF) | 7 | 11 | 7 | 11 | 7 | 11 | 7 | 11 | 11 |
| | Sea urchins (regular) | 7 | 3 | 7 | 7 | 7 | 3 | 3 | 7 | 7 |
| | Sea urchins (irregular) | 7 | 7 | 7 | 11 | 7 | 7 | 7 | 7 | 11 |
| | Brittle stars | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 11 |

(*Continued*)

**Table 3 (*Continued*)** Functional importance (FI) rankings for 70 functional groups per process on the GBR

| Taxa | Functional group | Primary production | Herbivory | Predation | Nutrient cycling | Symbiosis | Calcification | Bioerosion | Ecosystem engineering | Recruitment facilitation |
|---|---|---|---|---|---|---|---|---|---|---|
| Fishes | Feather stars | 7 | 11 | 11 | 11 | 7 | 7 | 7 | 7 | 11 |
| | Cryptobenthic | 7 | 7 | 3 | 2 | 8 | 11 | 11 | 7 | 7 |
| | Farmers | 7 | 2 | 9 | 8 | 7 | 5 | 9 | 3 | 2 |
| | Scrapers (scarids) | 7 | 4 | 9 | 4 | 11 | 5 | 3 | 3 | 1 |
| | Browsers (nasos) | 7 | 4 | 9 | 8 | 11 | 5 | 11 | 7 | 3 |
| | Browsers (siganids) | 7 | 4 | 9 | 8 | 11 | 5 | 11 | 7 | 3 |
| | Browsers (other) | 7 | 4 | 9 | 8 | 11 | 5 | 11 | 7 | 3 |
| | *Bolbometopon* | 7 | 2 | 7 | 6 | 11 | 5 | 3 | 1 | 3 |
| | Excavators (other) | 7 | 2 | 5 | 8 | 11 | 5 | 3 | 3 | 3 |
| | Detritivores | 7 | 2 | 9 | 1 | 11 | 7 | 11 | 7 | 5 |
| | Planktivores | 11 | 9 | 7 | 7 | 11 | 11 | 11 | 11 | 5 |
| | Corallivores | 11 | 9 | 7 | 11 | 11 | 7 | 11 | 7 | 9 |
| | Invertivores (labrids) | 7 | 11 | 4 | 7 | 11 | 11 | 7 | 7 | 9 |
| | Invertivores (other) | 7 | 7 | 7 | 7 | 11 | 11 | 5 | 7 | 11 |
| | Invertivores (lutjanids) | 7 | 5 | 7 | 11 | 11 | 11 | 5 | 7 | 9 |
| | Eels | 11 | 6 | 5 | 5 | 11 | 11 | 11 | 7 | 7 |
| | Piscivores (residents) | 11 | 8 | 4 | 7 | 11 | 11 | 11 | 7 | 7 |
| | Piscivores (transients) | 11 | 7 | 3 | 7 | 11 | 11 | 11 | 7 | 9 |
| | Cleaner wrasse | 7 | 5 | 5 | 10 | 2 | 5 | 9 | 6 | 5 |

*Note*: Shading denotes highest scores; 1st = dark, 2nd = mid, 3rd = light.

*Abbreviations*: H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders.

functioning. Results met expectations in many cases, but due to our assessment of both direct and indirect effects, and ecological redundancy and dependency, we highlight novel and sometimes unexpected players. This interpretation was supported through the evaluation of peer-reviewed literature, outlined for groups that received high scores despite comparatively marginal attention in the literature.

### *Primary production*

Algal turfs, phytoplankton, CCA and host-associated phototrophic microbes were the top-ranked groups for primary production (Table 3). Approximately 70% of the carbon fixed by primary producers on the GBR originates from phytoplankton (Furnas & Mitchell 1987, 1988, McKinnon et al. 2007). Typical of tropical ecosystems, phytoplankton communities on the GBR are diverse, including a range of diatoms, dinoflagellates, cyanobacteria and picophytoplankton, which form the baseline of pelagic food webs (Revelante & Gilmartin 1982, Revelante et al. 1982, McKinnon et al. 2007, Davies et al. 2016). Microbial metabolic pathways are involved with 59%–100% of the net primary production on coral reefs, including within the phytoplankton (Arias-Gonzalez et al. 1997, Silveira et al. 2017). This sweeping contribution to primary production is captured here for all microbial groups (FI ≥ 4). Host-associated phototrophic groups (e.g. Symbiodiniaceae) ranked highest, owing to their niche role facilitating productivity and organic carbon cycling in corals (and other hosts) (Silveira et al. 2017) and supporting the physiology, ecology and evolution of coral reefs (LaJeunesse et al. 2018).

Turf algae are critical primary producers in oligotrophic coral reef waters, exhibiting high mass-specific rates of productivity (Adey & Goertemiller 1987), though we acknowledge the high diversity and ubiquitous nature of this group. Turf growth and productivity can be enhanced by high wave energy (Roff et al. 2019) and nutrient enrichment with links to water quality (Vermeij et al. 2010, Gordon et al. 2016a), particularly on inshore reefs of the GBR (Lam et al. 2018). Turf algae are rapid colonisers of bare substrates on coral reefs, particularly in degraded systems (Roth et al. 2018). Although they have a relatively low biomass per unit area and typically only reach heights of ~1 cm, algal turfs have a rapid turnover and can shape coral reef communities from cryptic species diversity (Carpenter 1985, 1986, Klumpp et al. 1988, Klumpp & McKinnon 1989, Klumpp & Pulfrich 1989, Enochs 2012, Enochs & Manzello 2012) to herbivore assemblages on reef flats (Bellwood et al. 2018). The contribution of algal turfs to net primary production on the GBR is 100–500 g.C.m$^{-2}$.yr$^{-1}$ for both inshore and offshore habitats (Klumpp & McKinnon 1992, Russ 2003), lower than estimates for fleshy macroalgae (e.g. *Sargassum*; 1000 g.C.m$^{-2}$.yr$^{-1}$) (Schaffelke & Klumpp 1997). Turfs often persist as constant grazing by herbivores prevents overgrowth by larger, fleshy seaweeds (e.g. *Sargassum*) (Diaz-Pulido & McCook 2008). However, once established, species such as *Sargassum* are highly resilient to physical and biological removal with implications for altered trophodynamics and production functioning on degraded reefs (Loffler & Hoey 2018). The contradiction in ranks between turf and macroalgal groups here may reflect the relatively low biomass of fleshy macroalgae across much of the offshore area of the GBR.

Primary production by CCA is similar to that by turf algae (Chisholm 2003, Diaz-Pulido & McCook 2008, Lewis et al. 2017). Despite lower direct contributions to primary production, algal turfs and CCA ranked higher than fleshy macroalgae due to a suggested lower redundancy with expansive assemblages at scales from centimetres to kilometres (Harris et al. 2015). Turfs and CCA dominate the epilithic algal matrix (EAM) across the GBR, with direct links to total benthic and grazer (i.e. fisheries) productivity (Klumpp & McKinnon 1992, Russ 2003, Littler & Littler 2007, Arnold et al. 2010), and recruitment dynamics (Doropoulos et al. 2017a,b).

Interestingly, no group scored the top ranking (FI = 1; Table 3), attributing to the broad ecological redundancy in primary production across and within functional groups, and/or dependency of some species on others to complete this role (i.e. host-associated phototrophic microbes). Corals are active primary producers through their association with their microbial partners (Zooxanthellae;

Symbiodiniaceae, and endolithic algae) but scored lower here (FI ≤ 4), as they have high levels of dependency and generally lower rates of production than most algae. Experts noted that the contribution of corals to photosynthesis was considered largely redundant, as it would be readily replaced by algal productivity.

## *Herbivory*

Farming (e.g. damselfishes) and excavating (e.g. parrotfishes) fishes were the highest-rated groups for herbivory (FI = 2; Table 3). Farming damselfishes are well recognised for their role regulating the growth and composition of algal assemblages within their territories (Ceccarelli et al. 2001, 2011, Hata & Kato 2004, Hoey & Bellwood 2010c), where they shape benthic coral reef communities (Ceccarelli et al. 2001, Ceccarelli 2007, Casey et al. 2015a) and reef fish behaviour and assemblages (Eurich et al. 2018). Densities of herbivorous fishes and intensity of herbivory can be influenced by proximity to reef structure. Distinct grazing halos around reef structures are a physical indication of top-down behavioural interactions between herbivores and predators (Sweatman & Robertson 1994, Madin et al. 2011, Downie et al. 2013, Ollivier et al. 2018), particularly for species that are closely associated with reef refugia, including farming damselfishes.

Nominally herbivorous parrotfishes are typically attracted to the endolithic algal growth on dead coral surfaces, and their scraping and excavating feeding behaviour promotes reef bioerosion (Clements et al. 2017). The green humphead parrotfish, *Bolbometopon muricatum*, is one of the largest roaming herbivores on coral reefs. Its high score for herbivory here is likely a reflection of its functionally explicit contribution to reef bioerosion through its feeding ecology. Despite being a nominal herbivore, each individual ingests around 5 tonnes of structural carbonate per year (around half is living coral) (Bonaldo et al. 2014). Replacement of the functional roles of *B. muricatum* by other species is unlikely (i.e. low ecological redundancy), as observed on some coral reefs where this species has experienced extreme population declines from overfishing (Myers 1999, Donaldson & Dulvy 2004).

All nominally herbivorous reef fishes scored highly for their magnitude of contribution to the herbivory process (FI ≥ 4). Certain species of scrapers (e.g. parrotfishes) and browsers (e.g. rabbitfishes, unicornfishes) are considered particularly important herbivores at various scales across the GBR, with several key species highlighted in the literature: *Naso lituratus*, *N. unicornis*, *Siganus canaliculatus*, *S. doliatus*, *Calotomus carolinus*, *Kyphosus vaigiensis* (Hoey & Bellwood 2009, 2010a, Hoey et al. 2013, Loffler et al. 2015a,b, Streit et al. 2015). Their slightly lower-ranked importance for herbivory here (Table 3) may reflect an arguably broader level of ecological redundancy in the scrapers and browsers compared to excavators on the GBR. However, dietary groupings of nominal herbivores do not necessarily reflect taxonomy (Choat et al. 2002), and key herbivorous species appear to have specialised traits in their feeding ecology that can have specific and dynamic influences on algal communities at local and regional scales (Bellwood et al. 2006a, Hoey & Bellwood 2009, Wismer et al. 2009, Johansson et al. 2013, Loffler et al. 2015a, Streit et al. 2015, Loffler & Hoey 2018). Caution must be taken when assuming functional redundancy among herbivorous fishes, particularly when generalising within the common nominal feeding modes (Bejarano et al. 2017).

Interestingly, detritivorous fishes, including blennies and surgeonfishes, ranked among the highest for herbivory despite having a lower magnitude of contribution (direct and indirect) than nominally herbivorous groups (Table 3). As scored by experts, this may be an artefact of the low functional redundancy of detritivores, which are outlined in the literature as fundamental components of nutrient pathways and the transfer of energy from the EAM (i.e. algal turfs) to secondary consumers (Crossman et al. 2001, 2005, Wilson et al. 2003, Bellwood et al. 2014). Regardless, this group represents ∼40% of the biomass of EAM-grazing assemblages on the GBR (Wilson et al. 2003). The surgeonfish *Ctenochaetus striatus* was highlighted by experts as particularly important. This is supported in the literature, which describes the active role of *C. striatus* in removing sediment and

detritus from the EAM, indirectly facilitating herbivory by other species (Goatley & Bellwood 2010, Marshell & Mumby 2012, 2015). Detritivores can be key nuclear species that affect the behaviour and distribution of other species and provide high contributions to the export of nutrients across reefs from sand flats to hard reef structure (Lukoschek & McCormick 2000, Crossman et al. 2001, Goatley & Bellwood 2010, Marshell & Mumby 2012). Interestingly, detritivores and other functional groups (including herbivores) can supplement their diet with a range of other food sources (e.g. invertebrates, microbes, diatoms), which have a higher protein, fatty acid and/or total energy content than their primary food source (Montgomery & Galzin 1993, Choat et al. 2002, 2004, Clements et al. 2009, 2017, Hernaman et al. 2009, Kramer et al. 2013). Notably, diet partitioning and selectivity are currently underestimated for many nominal detritovores and herbivores (Choat & Clements 1998, Clements et al. 2017).

Most benthic algal groups scored highly for herbivory (FI = 3) due to their role as food for herbivores, demonstrating the importance of assessing indirect effects in ecosystem functioning. This was not captured in expert responses for phytoplankton, which are ubiquitously important for grazers in the plankton, including early life stages of most marine invertebrates and fishes (Hamner et al. 1988, Furnas et al. 2005, McKinnon et al. 2005, 2015). Zooplankton, and a range of other invertebrates (sea urchins, decapods, gastropods, seastars), scored highly for herbivory (FI = 3; Table 3). Pelagic grazers, such as copepods, larvaceans and salps, provide the fundamental links in production and energy flow to higher order consumers. Mesozooplankton (the medium-sized zooplankton) can graze ~40% of the production by phytoplankton in oligotrophic regions (Calbet 2001), including essentially all production in certain size classes, yet zooplankton may still be food limited in the oligotrophic waters of the GBR (McKinnon & Thorrold 1993, McKinnon et al. 2005, Skerratt et al. 2019).

Many micro- and macro-invertebrates occupy specific functional space, but since they typically have a lower magnitude of herbivory compared to reef fishes, their roles often go unappreciated (Brawley & Adey 1981, Klumpp & Pulfrich 1989, Altman-Kurosaki et al. 2018). Sea urchins are top herbivores on some coral reefs, usually after populations of herbivorous fishes and/or urchin predators are depleted through fishing (Ogden & Lobel 1978, Carpenter 1986, McClanahan 1988). Echinoids are often considered keystone species, with a range of contributions to reef ecosystem functioning (Birkeland 1989). Detrimental coral-algal phase shifts can occur in their absence, as documented in the Caribbean (Carpenter 1990, Mumby 2006, Mumby et al. 2006b). Some sea urchin species are also outplanted as biocontrol (e.g. *Tripneustes*) to maintain invasive algal growth on some reefs (Conklin & Smith 2005, Stimson et al. 2007, Westbrook et al. 2015, Neilson et al. 2018). Other benthic herbivores (e.g. trochus snails, diogenid hermit crabs, amphipods) can be active in areas not accessible to reef fishes, particularly in the cryptic reef framework, limiting algal growth and facilitating coral recruitment in refugia from higher order grazers (Brawley & Adey 1981, Coen 1988, Klumpp & Pulfrich 1989, Doropoulos et al. 2012b, 2016). Conversely, grazing by some herbivorous invertebrates may disrupt coral recruitment and regeneration, as posited for the blue starfish, *Linckia laevigata* (Laxton 1974b), but there is surprisingly little information available on the ecology of this vibrant well-known species.

## Predation

Somewhat unexpectedly, the top-ranked groups for the predation process were triton snails and cephalopods (FI = 1; Table 3). Triton snails, specifically the giant triton, *Charonia tritonis*, are among the largest mobile predatory invertebrates on the GBR and are a key predator of adult CoTS (Endean 1969, Pratchett et al. 2014, Cowan et al. 2017, Hall et al. 2017). Expert scores for triton snails are likely a reflection of this niche role in predation, especially as CoTS population control is a prime management focus on the GBR (Pratchett et al. 2014, Babcock et al. 2016a, Hoey et al. 2016b). CoTS population outbreaks have been attributed to the removal of *C. tritonis* from the GBR in the mid-1900s (the 'predator removal hypothesis'), although controlled laboratory experiments suggest they

only consume ~0.7 CoTS ind$^{-1}$ week$^{-1}$ and that they also target a range of other marine invertebrates (Pearson & Endean 1969). Regardless, their ranking here reflects this important predatory niche, which has been addressed for the GBR in depth previously in the context of conservation and CoTS outbreak management (Hall et al. 2017).

Interestingly, invertivorous fishes did not score highly in the predation process (Table 3), including those that target CoTS at various life stages (e.g. emperors, pufferfishes, triggerfishes) (Cowan et al. 2017). It has been estimated that ~70% of fishes on the GBR feed predominantly on invertebrates (Kramer et al. 2015), including many with specialised feeding mechanisms and roles, such as tuskfishes (*Choerodon*) (Jones et al. 2011), cleaner wrasses (*Labroides*) (Grutter 1997) and rockmover wrasses (*Novaculichthys*) (Wainwright et al. 2002). The lack of consideration of invertivores by experts here may reflect the broad ecological redundancy of this group at this level of functioning and, importantly, the data gaps regarding empirical observations of invertivory on the GBR (Case Study 1).

Cephalopods also received the top score for the predation process (FI = 1), despite the literature being largely restricted to their taxonomy and diversity (Roper & Hochberg 1987, Norman 1992, Norman & Finn 2001, Rosa et al. 2019). Surprisingly little information exists on their functional ecology on the GBR and in general (Ponder et al. 2002). The ecological importance of cephalopods is perhaps mostly presumed from their fast growth rates (Pecl & Jackson 2008), broad cross-shelf distributions occupying cryptobenthic to pelagic habitats (Moltschaniwskyj & Doherty 1995) and their contributions to fisheries productivity as both predators and prey (Connell 1998, Beukers-Stewart & Jones 2004, Taylor & Bennett 2008). The relatively high feeding rates and densities of squid and other cephalopods have the potential to control recruitment dynamics of many commercially and ecologically important fishes (Hunsicker & Essington 2008). Changes to predatory-prey dynamics of cephalopods could have ecosystem-level implications (Pecl & Jackson 2008, Spady et al. 2014, 2018, Rosa et al. 2019). Benthic shallow-water octopuses are likely key predators within the reef matrix where large predatory fishes cannot access. Their behaviours are complex for an invertebrate and can involve interesting mutualistic hunting relationships with predatory fishes such as coral trout (Vail et al. 2013). Moray eels (muranids) occupy a similar niche in the reef matrix and demonstrate the same hunting mutualism (Vail et al. 2013) but were rated slightly lower for the predation process by experts here (FI = 5). Overall, trophic interactions in cryptic habitats are difficult to quantify and are poorly characterised.

Cryptobenthic fishes, which also occupy the reef matrix, rated highly for predation (FI = 3), despite the lack of empirical information on their taxonomy and ecological roles (Bellwood et al. 2019, Brandl et al. 2019). This group, which includes the gobies, represent around half the total number of reef fishes on the GBR, with around 8% of this population consumed daily (Depczynski & Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018), producing almost 60% of the consumed reef fish biomass (Brandl et al. 2019). Representing some of the smallest marine vertebrates, cryptobenthic fishes are fundamental to predation processes and production functioning as prey. They are also important crypto-invertebrate predators in the reef framework (Goatley et al. 2017), particularly of microcrustaceans (e.g. copepods) (Case Study 1).

Copepods are the most speciose group in the zooplankton on the GBR and are at the base of marine food webs that directly and indirectly support fisheries production (McKinnon & Thorrold 1993, McKinnon et al. 2005). It is estimated that the flux of zooplankton to the coral reef 'wall of mouths' is ~0.5 kg m$^{-1}$ d$^{-1}$ (Hamner et al. 1988), with extrapolations that suggest copepod production across the entire GBR is >630,000 tonnes carbon yr$^{-1}$ (McKinnon & Thorrold 1993, McKinnon et al. 2005, 2007). Zooplankton scored high within the predation process (FI = 3), given their fundamental contribution to reef trophodynamics. Plankton occupy the largest coral reef habitat – the pelagic ecosystem – and are key to ecosystem functioning (McKinnon et al. 2007). It should be noted that this broad-scale pelagic context stretches beyond the typical reef habitat examined here for targeted management recommendations.

## CASE STUDY 1: INVERTIVORY ON THE GREAT BARRIER REEF: A POORLY UNDERSTOOD LINK IN THE TROPHIC CHAIN

*Hannah Sheppard-Brennand, Maria Byrne, Jessica Stella, Kennedy Wolfe*

It has been estimated that ~70% of fishes on the GBR feed predominantly on invertebrates (Kramer et al. 2015), but data gaps remain regarding invertivory on benthic mobile invertebrates (BMIs) including crustaceans, gastropods, worms and echinoderms. In this case-specific review of over 550 studies, only 35 reported nominally invertivorous fishes to incorporate BMIs in their diet on the GBR. This included 174 species from 20 families (Figure CS1.1; Appendix 1), ~10% of the total known number of fish species on the GBR. This diversity spans a range of life stages, sizes, morphologies and feeding modes and exceeds that of herbivorous (178 species from 9 families; Cvitanovic et al. 2007), detritivorous (24 species from 5 families; Wilson et al. 2003) and corallivorous (128 species from 11 families; Cole et al. 2008) fishes on the GBR. Quantitative measures of invertivory on BMIs were only found for 18 families in 33 studies, including three families that consumed <10% invertebrates (Acanthuridae, Blenniidae, Siganidae). This highlights the paucity of direct observations and quantification of fish invertivory on BMIs. It should be noted that this does not include fishes that target CoTS, as this has already received considerable attention (see Cowan et al. 2017). Targeted research is imperative to quantify predator-prey dynamics for invertivores on the GBR, including a focus on quantifying direct measures of invertivory, prey availability and trophic transfers from the benthos to higher order taxa to enhance production functioning.
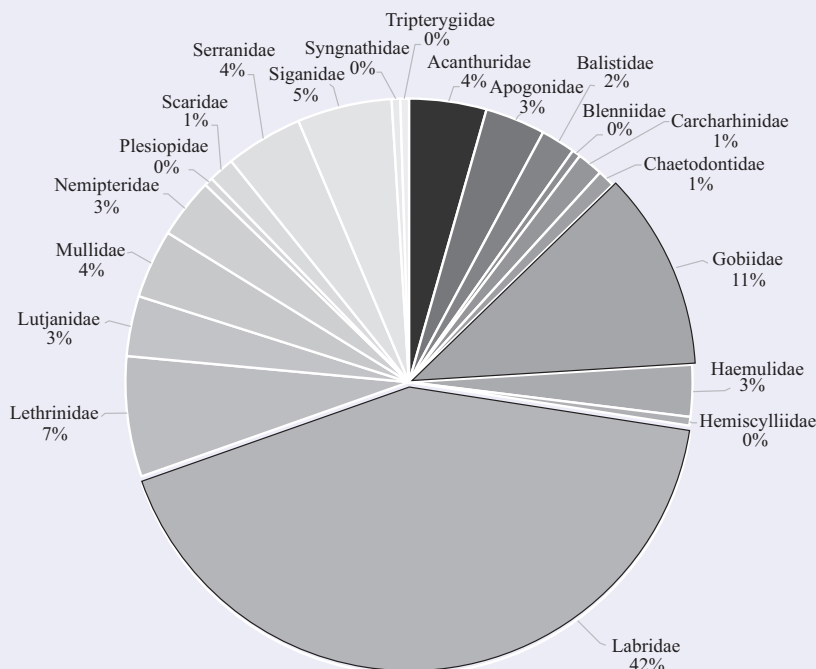


**Figure CS1.1** Proportion of coral reef fishes and sharks (by family) that are reported to consume benthic mobile invertebrates on the GBR.

The greatest diversity of invertivores came from the Labridae (wrasses), followed by the Gobiidae (gobies) (Figure CS1.1). Labrids are one of the most functionally and ecologically diverse groups of fishes on coral reefs and account for the highest biomass of invertivores on the GBR (Williams & Hatcher 1983, Bellwood et al. 2006b, Kramer et al. 2015). While this may suggest high functional redundancy (Bellwood et al. 2006b), labrids exhibit the greatest range of specialised feeding mechanisms and species with key roles; for example, tuskfishes (*Choerodon*) use tools to break open mollusc shells (Jones et al. 2011), cleaner wrasses (*Labroides*) target gnathiid isopods over other parasites (Grutter 1997), rockmover wrasse (*Novaculichthys*) overturn the benthos to access hidden prey (Wainwright et al. 2002). Cryptobenthic fishes (e.g. gobies) represent around half the total number of reef fishes on the GBR, are particularly important predators of microcrustaceans (e.g. copepods) and themselves provide direct trophic pathways to higher order consumers (Depczynski & Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018, 2019). Apogonids (cardinalfishes) and a range of other nocturnally active species (e.g. reef sharks, epaulette sharks, sweetlips and emperors) are functionally significant invertivores at night, particularly regarding larger crustaceans (e.g. Malacostraca) (Marnane & Bellwood 2002, Boaden & Kingsford 2012).

For species where invertivory was quantified (Figure CS1.2), ~40% were obligate consumers of invertebrates. Crustaceans were the predominant prey across all families of invertivorous fishes (Figure CS1.2). Annelid worms represented the greatest proportion of the diet of the Hemiscylliidae (epaulette sharks) and Mullidae (goatfishes) (Figure CS1.2), but this was only quantified for one species in each family. Many species not classified as nominal invertivores in the literature are documented to ingest significant amounts of benthic invertebrates (e.g. carnivores: *Cheilodipterus quinquelineatus* and *Carcharhinus melanopterus*, >35% of stomach contents; herbivores and detritivores: *Amblygobius phalaena* and *Bathygobius fuscus*, >15%; carnivores/piscivores: *Lethrinus nebulosus*, >50%) (Appendix 1). Detritivores and other functional groups may supplement their diet with invertebrates to avail of the higher protein and energy content (Hernaman et al. 2009, Kramer et al. 2013).
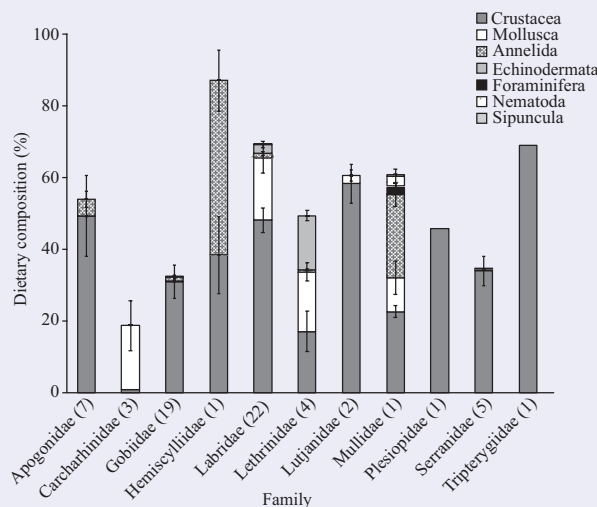


**Figure CS1.2** Mean proportion (±SE) of invertebrates (by phyla) in the diet of nominally invertivorous fishes (by Family). Number of species are indicated in parentheses after family name. Note only 11 of 18 families are presented as other data were not comparable.

Notably, the zooplankton group also comprises the macro- and mega-plankton, which includes the larger-bodied (>200 mm) cnidarian and ctenophoran jellyfishes. This group has explicit roles in ecosystem functioning through their typically carnivorous predation on smaller zooplankton groups (Hutchings et al. 2019) and as an important food source themselves (Ates 1988, 1991, Purcell & Arai 2001). Jellyfish blooms are increasingly documented around the world, including on the GBR, with impacts on ecosystem stability and functioning (Hutchings et al. 2019). Cubozoans (box jellyfish and *Irukandji*) are a particularly important group on the GBR resulting from their socioeconomic impacts on inshore reefs through their sometimes fatal envenomation (Huynh et al. 2003, Kingsford et al. 2012, Gershwin et al. 2014).

In context of the 'wall of mouths' (Hamner et al. 1988), planktivorous fishes (e.g. damselfishes, fusiliers, anthias) scored surprisingly low (FI = 7), despite their well-appreciated roles transferring carbon (in plankton) from the water column into trophic networks, especially within close proximity of reef structure and refugia (Holzman et al. 2005, Motro et al. 2005, Yahel et al. 2005) and their contribution as prey to a multitude of species (Hamner et al. 1988, 2007, Johansen & Jones 2013). The unexpectedly low score for planktivorous fishes may, in part, reflect their broad ecological redundancy, as they represent >20% of all coral reef fishes and account for >60% of the total fish biomass (Bellwood & Hughes 2001, Bellwood et al. 2004). It is also possible that experts scored the predation process from a top-down perspective, resulting in lower scores for many intermediate-level predators, including the planktivores and invertivores. Similarly, corals did not score highly for predation (FI ≥ 7), likely due to their broad redundancy regarding this process and propensity to switch between autotrophy and heterotrophy to meet energy requirements (Anthony & Fabricius 2000, Grottoli et al. 2006, Ferrier-Pages et al. 2011, Hoogenboom et al. 2015). This ability is highly dynamic depending on species and location, with some corals on turbid inshore reefs 10–20 times more heterotrophic than their counterparts in oligotrophic waters (Anthony 2000, 2006).

Other invertebrates, including predatory polychaete worms, crustaceans (decapods, stomatopods, infauna) and molluscs (e.g. *Conus*, nudibranchs), ranked highly (FI = 3). Both pelagic and benthic micro- and cryptopredators provide the foundations of energy transfer to higher trophic levels (Goatley et al. 2017). This includes impressive cases for key benthic predators like mantis shrimp (*Odontodactylus*) (deVries et al. 2016, Goatley et al. 2017) and cone snails (*Conus*) (Kohn 2015), which can be highly specialised physically and/or chemically to target larger vertebrate prey. Harlequin shrimp (*Hymenocera*) and a number of other predatory invertebrates may be important cryptic predators, including of the juvenile life stage of CoTS hidden in the reef and rubble framework (Glynn 1984, Cowan et al. 2017, Keesing et al. 2018). Nudibranchs can influence benthic cyanobacterial productivity through top-down effects on key herbivores (Geange & Stier 2010), and sponge-feeding nudibranchs sequester chemical defences that can alter fish feeding behaviour (Proksch 1994, Becerro et al. 1998, Ritson-Williams & Paul 2007). Nudibranchs are among the most abundant spongivores on coral reefs, but their low relative densities limit their ability to shape sponge abundance and distributions (Powell et al. 2015).

CoTS also ranked among these invertebrates for the predation process (Table 3), as top corallivores with extreme predatory potential during population outbreaks (Pratchett et al. 2014). Outbreaks aside, CoTS adults can consume up to 250 cm$^2$ of live coral per day (Chesher 1969, Glynn 1973), around 2–5 times the rate of other similarly sized corallivorous starfish, such as *Culcita novaeguineae* (Glynn & Krupp 1986, Birkeland 1989). Non-*Acanthaster* predatory asteroids scored lower for predation (FI = 7), although their selective feeding habits can influence the relative abundance of some coral species (Glynn & Krupp 1986). A recent (but rare) outbreak of *Culcita schmideliana* in the Maldives was associated with 24% mortality of juvenile acroporid and pocilloporid corals, hindering postbleaching reef recovery (Bruckner & Coward 2019). The boom-and-bust population characteristic typical of echinoderms attributes to the ephemeral nature of their ecological roles and impacts (Birkeland 1989, Uthicke et al. 2009). Even the nominally herbivorous sea star, *Linckia*

*laevigata*, is reported to feed on live coral, but this behaviour is rare, with little documented impact as their stomachs are relatively small (Laxton 1974b).

Large predatory reef fishes (transients and residents) were among the highest scoring fishes within the predation process but were rated lower by experts than a range of other taxa (Table 3). This is in line with suggestions in the literature that top-down forces on the GBR are weak (Rizzari et al. 2015, Casey et al. 2017). While top-down effects of predatory reef fishes can alter reef fish recruitment and community structure (Webster & Almany 2002, Almany 2004b, Almany & Webster 2004, Rizzari et al. 2014, Palacios et al. 2016a,b), their relative rarity and limited links across trophic networks can reduce their overall functional importance (Roff et al. 2016, Casey et al. 2017). In contrast to common ecological theory, there is a degree of ecological redundancy in the mesopredator group on the GBR, which includes the sharks (Rizzari et al. 2015, Frisch et al. 2016b). Most reef-associated sharks do not act as apex predators but instead function as mesopredators along with a diverse group of coral reef fishes (Roff et al. 2016). Interestingly, resident fishes (e.g. coral trout) scored lower (FI = 4) than transient predatory fishes (e.g. sharks, barracudas) (FI = 3). As reflected in expert scores, this may be associated with the dependency of resident predators on habitat refugia (Rogers et al. 2014, 2018b). Hunting regularity and success are typically greater in resident reef fishes, but transient predators can be the primary source of mortality for non-reef associated fishes (Hixon & Carr 1997, Almany 2004a).

## Nutrient cycling

Detritivorous fishes were the highest-ranked group regarding nutrient cycling (FI = 1; Table 3). They are outlined in the literature as fundamental components of nutrient pathways transferring energy from the EAM (i.e. algal turfs) to secondary consumers (Crossman et al. 2001, 2005, Wilson et al. 2003, Bellwood et al. 2014) and in the export of nutrients and detritus from sand patches across the calcified reef structure (Lukoschek & McCormick 2000, Crossman et al. 2001, Goatley & Bellwood 2010, Marshell & Mumby 2012). Blennies are considered key detritivores on the GBR, representing ∼60% of this trophic group's density in some habitats (Wilson 2001) and exhibiting incredible population productivity with estimates that <1% survive for more than one year (Wilson 2004). This is similar for cryptobenthic fishes (e.g. gobies) (FI = 2), which are super abundant and highly productive and provide direct links from the hidden and largely inaccessible reef matrix to higher consumers (Depczynski & Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018). The small size (<50 mm length) and rapid population turnover of cryptobenthic fishes reflect their niche roles in top-down trophodynamics within the reef matrix and bottom-up pathways that support fisheries productivity (Depczynski & Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018, 2019). The high scores for blennies and gobies here capture their critical roles in coral reef trophodynamics.

Phytoplankton and turf algae also scored highly for nutrient cycling (FI = 2) at the baselines of pelagic and benthic productivity, respectively (Furnas & Mitchell 1987, 1988, Klumpp & McKinnon 1992, Russ 2003, Littler & Littler 2007, McKinnon et al. 2007). In the context of productivity, *in situ* growth rates of dominant phytoplankton species range from one to several doublings per day, resulting in fast growth rates and substantial contributions to nutrient cycling. Phytoplankton species are important in nitrogen fixation, particularly *Trichodesmium*, which form extensive cyanobacterial rafts (Revelante & Gilmartin 1982, Revelante et al. 1982, Furnas 1992). Similarly, turf algae are particularly important in the fixation of nitrogen on coral reefs. Much of the nitrogen in coral reefs is 'fixed' (made biologically available) by blue-green algae within the EAM, which have rapid growth rates and are intensively grazed, distributing nitrogen and other nutrients throughout the reef (Borowitzka et al. 1977, Borowitzka 1981, Wilkinson et al. 1984, Hatcher 1988, Larkum et al. 1988). On turf and macroalgal-rich reefs, microbial community density and diversity increase with the potential to shape nutrient pathways and reef health (Haas et al. 2016, Brown et al. 2019).

All four functional groups of microbes, as nominally partitioned here, also scored highly (FI = 4). Microbial communities are key drivers of large-scale biogeochemical processes in the

oceans (Falkowski et al. 2008), with fundamental roles in mediating nutrient cycling (e.g. phosphorus, nitrogen) (Charpy et al. 2012, Tout et al. 2014, Ferrier-Pages et al. 2016) and influencing water quality (Glasl et al. 2017, 2018a). Impressively, host-associated microbes (the 'coral microbiome') (FI = 2) can provide >90% of a coral's nutritional requirements (Muscatine & Porter 1977, Bourne et al. 2016). While the ecological contribution of the coral microbiome is poorly understood, it appears to be inextricably linked to the passage and cycling of nutrients (carbon, nitrogen, sulphur, phosphorus, vitamins) and overall reef productivity (Bourne et al. 2016).

Tabular corals (FI = 2) were ranked higher than the remaining coral groups (FI = 4–8) by our expert panel. Based on the literature, this is likely a result of the broader importance of tabular corals regarding rapid reef growth and post disturbance recovery (Connolly & Muko 2003, Ortiz et al. 2014, 2018). In the context of nutrient cycling, the relative contribution of autotrophy and heterotrophy in corals is variable, dynamic and plastic (Grottoli et al. 2006, Ferrier-Pages et al. 2011, Hoogenboom et al. 2015). A range of coral species, including some acroporids and pocilloporids, exhibit higher rates of heterotrophy in turbid environments near shore compared to the same species in oligotrophic waters offshore (Anthony 2000, Anthony & Fabricius 2000). Soft corals tend to dominate the turbid waters typical of nearshore reefs on the GBR, suggesting regional specificity in functional importance between coral taxa (Fabricius 1997, Fabricius & De'ath 2001a). Some soft coral species are even herbivorous, feeding predominantly on phytoplankton – an important consideration that can shape community structure on eutrophic inshore reefs (Fabricius et al. 1995, Fabricius & De'ath 2008).

Interestingly, sponges rated fairly low (FI ≤ 6), despite their well-documented roles in benthic-pelagic coupling and detrital pathways (de Goeij et al. 2013, Mumby & Steneck 2018). This discrepancy between expert scores and peer-reviewed evidence is important to note. This may be a result of the lack of information available for sponges (particularly cryptic species) on Pacific reefs, as most information on the trophic ecology of sponges is derived from the Caribbean (Wilkinson 1983, 1987, Mumby & Steneck 2018).

The highest-scoring mobile invertebrates to nutrient cycling were the zooplankton (FI = 2; Table 3), which include a diversity of pelagic crustaceans (e.g. copepods and mysids), doliolids, salps, larvaceans (Appendicularia) and chaetognaths. Zooplankton are intermediate trophic levels in pelagic food webs, linking primary production by phytoplankton with higher-order taxa, and thus support oceanic and coastal fisheries. Zooplankton are also key players in benthic-pelagic coupling, as they are consumed by benthic fishes and invertebrates, including corals (Bishop & Greenwood 1994, Marnane & Bellwood 2002, Holzman & Genin 2003, Holzman et al. 2005). An estimated 25%–100% of particulates in the water column fall to the benthos each day, making planktonic groups and the faeces and marine snow they produce, important components of benthic functioning (i.e. benthic-pelagic coupling) (McKinnon et al. 2007, Alongi et al. 2015, Lonborg et al. 2017). There are also demersal zooplankton that migrate between the benthos and water column daily with important roles in nocturnal trophodynamics (Jacoby & Greenwood 1988). Zooplankton can be highly abundant with distinct cross-shelf community assemblages (Sammarco & Crenshaw 1984, Williams et al. 1988, McKinnon & Thorrold 1993, McKinnon et al. 2005). Their biomass is greatest inshore and around shallow reef areas in the southern and central GBR and is greater in summer months (Russell 1935, Skerratt et al. 2019). Appendicularia have been found to grow faster than any other multicellular organism (Hopcroft & Roff 1995) and can be nearly as abundant as copepods on coral reefs, where they are important food source for planktivores and fish larvae (Noda et al. 1992, Llopiz 2013, Carrillo-Baltodano & Morales-Ramirez 2016, Dupuy et al. 2016).

Most benthic mobile invertebrate groups scored low, with deposit-feeding sea cucumbers (FI = 5) and coral-associated decapods (FI = 6) among the highest ranked groups (Table 3). As reflected by expert scores here, these groups are commonly underappreciated in their roles compared to reef fishes and corals. Sea cucumbers have been coined the 'vacuum cleaners' of the reef (Samyn & Tallon 2005), with functionally important roles in bioturbation, carbonate chemistry and nutrient cycling and a

strong influence on benthic productivity and infaunal community structure (Uthicke & Klumpp 1998, Uthicke 1999, 2001, Wolkenhauer et al. 2010, Schneider et al. 2011, 2013, Purcell et al. 2016a, Lee et al. 2017, Wolfe & Byrne 2017a, Wolfe et al. 2018). In terms of ecosystem functioning, the relative importance of sea cucumbers would likely be greater in lagoon systems, outside of the focal coral reef habitat here. Coral-associated decapods (e.g. Tetraliidae, Trapeziidae) have direct relationships with their hosts, typically acroporid and pocilloporid corals (Stella et al. 2011b, Gonzalez-Gomez et al. 2018). They play important roles utilising large amounts of coral mucus, recycling detritus and organic matter (Glynn 1983, Hutchings 1983, Stimson 1990), and even physically defending their coral host from predators (e.g. CoTS, *Drupella*) (Pratchett 2001, Stella et al. 2011b). Their high dependency on their coral host (and thus highly localised benefits) worked to lower their overall score here.

## Symbiosis

As organismal symbioses are defined by interactions and interdependency, it was not possible to receive the highest score for this process within our scoring scheme. Top-rated (FI = 2) functional groups for symbiosis were microbes (host-associated phototrophic), corals (tabular, massive, soft), decapods (coral-associated) and fishes (cleaner wrasse) (Table 3). The coral microbiome (i.e. coral-associated microbes) can exist at densities exceeding one million cells per $cm^2$ of host tissue (Garren & Azam 2012a), with diversities in the thousands in some host species (Mouchka et al. 2010, Blackall et al. 2015, Bourne et al. 2016). The best-known coral symbionts are photosynthetic dinoflagellates within the Symbiodiniaceae, which can reach densities $>10^6$ $cm^{-2}$ of host tissue (Garren & Azam 2012a, Bourne et al. 2016). These microbes are at the foundation of coral reefs, particularly in their relationships with benthos-dominating species such as corals, sponges and algae, where they are pivotal to host fitness through nutrient provisioning and waste removal pathways (Egan et al. 2013, Blackall et al. 2015, Bourne et al. 2016, Ferrier-Pages et al. 2016, Glasl et al. 2016, 2018b, Ramsby et al. 2018b). Coral holobionts are at the core of a healthy coral animal – and coral reef – sometimes providing corals with almost all of their nutritional requirements (Muscatine & Porter 1977, Bourne et al. 2016), including up to 100% of their carbon requirements (Falkowski et al. 1993, Palardy et al. 2008). The relative abundance of particular *Symbiodinium* cells (e.g. Clade D) can increase thermal tolerance in their coral hosts (Howells et al. 2012, 2013, Stat et al. 2013, Bay et al. 2016). All corals scored highly (FI ≥ 4), reflecting their important symbioses, not only with microbial communities, but also their diverse and fundamental associations with a range of reef taxa spanning from worms to fishes that depend on corals as habitat. Recent observations suggest that soft corals (FI = 2) may be particularly important in providing reef structure post disturbance (i.e. bleaching), with potential to promote fish diversity and density at a critical time of recovery (Ferrari 2017).

Corals co-exist with a great diversity of symbiotic reef biota. Coral-associated decapods are strongly bound to their coral hosts, where they can increase coral growth, deter predators, and even reduce disease in their coral host (e.g. *Cymo*, *Tetralia*, *Trapezia*) (Glynn 1980, 1983, Pratchett 2001, Stella et al. 2011b, Pollock et al. 2013). Christmas tree worms (*Spirobranchus*) also scored highly (FI = 4), with similar coral-host associations, enhancing water circulation across coral polyps, influencing coral nutrition, growth and recovery (Strathmann et al. 1984, Dai & Yang 1995, Ben-Tzvi et al. 2006), and aiding in the protection of corals from predators (e.g. CoTS) (DeVantier et al. 1986, Rowley 2008). However, corals exist in the absence of these associates, meaning they may not be functionally imperative. Similar to corals, giant clams (Tridacnidae) host symbiotic autotrophs that can provide >50% of the individual's carbon needs for both respiration and growth, superseding their need for heterotrophy through filter-feeding as they grow (Klumpp et al. 1992). This symbiotic association was not captured for giant clams here (FI = 8), which may reflect the coral-centric interpretation of symbioses in expert scores.

For the reef fishes, cleaner wrasses (*Labroides*) scored highest (FI = 2). Cleaners, particularly *L. dimidiatus* on the GBR, have highly developed interspecies communication and 'cleaning' services, removing ectoparasites, dead skin and mucus from their clients (Grutter & Poulin 1998, Bshary &

Grutter 2002). Ranging from small fishes to charismatic megafauna, clients frequent cleaning stations to ensure their bodies are well maintained and parasite free. This service has been documented to reduce stress hormones in the client (Soares et al. 2011) and increase fish density, diversity, size (Grutter et al. 2003, Clague et al. 2011, Waldie et al. 2011), recruitment (Sun et al. 2015) and cognitive performance (Binning et al. 2018). Cleaner wrasses may also be self aware – a hallmark of cognition and intelligence (Kohda et al. 2019). Cleaner wrasses appear to fill an ecological niche with little ecological redundancy, but more information is needed on other cleaning species (e.g. *Lysmata* shrimp, other fishes) (Cote 2000, Vaughan et al. 2017) and how their symbioses scale up to support greater reef functioning.

## *Calcification*

Microbes (host-associated phototrophic), calcifying algae (CCA, calcareous species) and corals (tabular) scored highest for their roles in calcification (Table 3). The influence of the coral microbiome on coral health and functioning is widely appreciated in the literature (Egan et al. 2013, Blackall et al. 2015, Bourne et al. 2016, Glasl et al. 2016, 2018b), and their functional ranks by experts here even outweighed some coral species. Corals are largely dependent on their microbiome for their carbon requirements (Falkowski et al. 1993, Palardy et al. 2008), and restructuring of reef communities occurs when this symbiotic relationship breaks down (i.e. coral bleaching) (Fitt et al. 2001, Bourne et al. 2016, Hughes et al. 2018b, Stuart-Smith et al. 2018). Coral calcification provides the framework and complexity of the reef, so not surprisingly, most corals scored highly (FI ≥ 4). Tabular corals were considered the most functionally significant contributors to calcification on the GBR, owing to the rapid growth characteristic of acroporids (Pratchett et al. 2015, Anderson et al. 2017, 2018), including those on turbid inshore reefs (Thompson & Dolman 2010, Browne 2012, Browne et al. 2013, Rocker et al. 2017). Acroporids (including tabular corals) generally exhibit the highest calcification rates, with the greatest influence on the carbonate budget (Case Study 2). In addition, the redundancy of key tabular corals could be considered relatively low, with just three species considered common on the GBR: *Acropora hyacinthus*, *A. cytherea* and *A. clathrata*.

Calcification by CCA can be particularly fast in shallow-water habitats (up to 10 kg $CaCO_3$ $m^{-2}$ $yr^{-1}$) (Kinsey 1983, Chisholm 2000), where they can completely dominate benthic cover (90%–100%) (Atkinson & Grigg 1984, Glynn et al. 1996). CCA calcification in deeper (≥6 m) reef slope habitats (as focused on here) is likely to be slower (≤ 5 kg $CaCO_3$ $m^{-2}$ $yr^{-1}$) (Chisholm 2000, Lewis et al. 2017). Calcareous algae (e.g. *Halimeda*) contribute to the production of marine sediments and can be major contributors to beach and lagoonal sediments (Marshall & Davies 1988, Delaney et al. 1996), with carbonate production around 2.2 kg $CaCO_3$ $m^{-2}$ $yr^{-1}$ (Drew 1983). While this is lower in comparison to calcification by scleractinian corals (Case Study 2), such as *Porites* (>10 kg $CaCO_3$ $m^{-2}$ $yr^{-1}$) (Cooper et al. 2008, De'ath et al. 2009), the breakdown of calcareous alga can be much faster and can rapidly fill interreefal space. Overall, hard scleractinian corals are calculated to be responsible for ~95% of carbonate production on the GBR, with CCA accounting for the remaining 5% (Case Study 2).

The contribution of non-coral, non-algal species to reef carbonate production (i.e. calcification) was not captured in Case Study 2, as other calcifiers are not captured in the long-term monitoring programme, and/or their contributions are often comparatively marginal. Little is known of the contribution of very small but highly abundant calcifying invertebrate groups (e.g. micro-molluscs and foraminiferans), many of which are yet to be named. For many of these taxa, their contributions to calcification are often overlooked but can be presumed from their presence in carbonate sands. For example, benthic and pelagic Foraminifera can make considerable contributions to the carbonate budget of coral reefs (Langer et al. 1997, McKinnon et al. 2007, Fujita et al. 2009, Doo et al. 2017, Hamylton et al. 2017) and are particularly important attributes in lagoon and reef sediment facies (Yamano et al. 2002, 2015, Wilson & Vecsei 2005, Sarkar et al. 2016, Schmitt & Gischler 2017). Large benthic foraminiferans (e.g. *Marginopora*, *Baculogypsina*) can be the single most important contributors to mass sediment production on

**CASE STUDY 2:  ADDRESSING THE CARBONATE
BUDGET OF THE GREAT BARRIER REEF**

*Tries Razak, Guillermo Diaz-Pulido, Kennedy Wolfe, George Roff, Peter J Mumby*

Coral reefs exist in a dynamic state between reef construction (calcification) and destruction (erosion). The balance between these processes (i.e. the carbonate budget) can be used as a key metric to assess reef health and forecast the ability of reefs to cope with environmental change (Perry et al. 2008, 2018, Kennedy et al. 2013, Mace et al. 2014). Some studies have quantified the rates of carbonate production (e.g. Kinsey 1983, Browne et al. 2012, Silverman et al. 2012) and bioerosion (Kiene & Hutchings 1994, Osorno et al. 2005, Hoey & Bellwood 2008) in specific taxa and/or locations on the GBR. Variability in these rates is the result of complex interactions between these processes and terrestrial influences (e.g. water quality) (Mallela & Perry 2007), reef metabolism (e.g. calcification and dissolution, and photosynthesis and respiration) (DeCarlo et al. 2017, Woodroffe et al. 2017), reef topography and hydrodynamics (Vargas-Ángel et al. 2015) and ocean change (Kennedy et al. 2013, Shaw et al. 2016, Manzello et al. 2018, McMahon et al. 2019). For example, net ecosystem calcification dropped by 46% on a reef flat at Lizard Island, GBR, between 2009 and 2016, immediately after a mass-bleaching event (McMahon et al. 2019). Such dramatic changes in reef-scale calcification rates would impact reef functioning. Ocean change stressors are likely to retard reef carbonate systems at the global scale (Dove et al. 2013, Kennedy et al. 2013, Manzello et al. 2017, Albright et al. 2018, Cyronak et al. 2018), though examples of resilience and recovery at local scales are promising (Manzello et al. 2018). Critically, current carbonate budget estimates are largely restricted to specific regions (Yamano et al. 2000, Suzuki et al. 2001, Browne et al. 2013, Hamylton et al. 2013, 2014, 2017), making it imperative to upscale this information to establish a baseline carbonate budget at the whole-of-reef scale in the face of global change.

Carbonate production and bioerosion rates were calculated from coral cover reported for 37 reefs across the southern GBR between 2017 and 2019 using the long-term monitoring programme (LTMP) data provided by the Australian Institute of Marine Science (AIMS) (Jonker et al., 2008). Southern reefs were selected as this analysis spanned a period of time when coral cover was in serious decline on the northern GBR (Hughes et al., 2017b, 2018b). This is an important consideration with regard to spatial and temporal changes in the carbonate budget of the GBR in future work. Data for coral cover were combined with published extension, production or erosion rates sourced from the ReefBudget website (http://www.exeter.ac.uk/geography/reefbudget) and other publications for the GBR (Drew, 1983; Musso, 1994; Osorno et al., 2005; Hoey & Bellwood, 2008; Pratchett et al., 2015; Anderson et al., 2017; Razak et al., 2017; Rocker et al., 2017). Total carbonate production of each reef was calculated with a model derived from geometric growth forms of corals. Estimates were derived from rates of carbonate production (or accretion) by hard corals and calcareous algae (CCA, articulated calcareous red algae, *Halimeda* and *Peyssonnelia*). Carbonate removal (bioerosion) by parrotfishes (*Bolbometopon*, *Cetoscarus*, *Chlorurus*, *Hipposcarus* and *Scarus*) was calculated using density and size records in the AIMS LTMP fish transect dataset. Secondary bioerosion by micro- and macro-borers (including polychaetes, sipunculans, sponges [e.g. *Cliona*] and molluscs) was estimated using experimental data from the GBR (Kiene & Hutchings, 1994; Osorno et al., 2005; Chazottes et al., 2017).

Hard coral assemblages contributed to approximately 95.5% of the total reef carbonate production (calcification) across all reefs on the GBR, with the remaining 4.5% contributed by calcareous algae, including CCA, *Halimeda* spp., *Peyssonnelia* spp. and calcareous red algae

**Table CS2.1**  Mean rates (±SE) of carbonate production, bioerosion and carbonate budget in the southern GBR

|  |  | kg m$^{-2}$ yr$^{-1}$ |
| --- | --- | --- |
| **Production** | Primary (corals) | 6.36 ± 0.52 |
|  | Secondary (algae) | 0.30 ± 0.03 |
|  | Total | 6.66 ± 0.54 |
| **Bioerosion** | Primary (parrotfish) | −4.18 ± 0.53 |
|  | Secondary (micro/macroborers) | −0.42 ± 0.02 |
|  | Total | −4.60 ± 0.53 |
| **Carbonate budget** |  | 2.07 ± 0.77 |

(Table CS2.1). *Acropora* species exhibit the greatest calcification rates on the GBR compared to other carbonate producers (i.e. non-*Acropora* corals and calcareous algae) (Figure CS2.1). Total carbonate production ranged between 0.49 and 12.97 kg m$^{-2}$ yr$^{-1}$ in the southern GBR (Table CS2.1). Mean bioerosion rates, driven almost entirely by grazing parrotfishes (Figure CS2.1), ranged between 0.69 and 19.0 kg m$^{-2}$ yr$^{-1}$) (Table CS2.1). Overall, the total carbonate budget ranged from −14.9 to 12.05 kg m$^{-2}$ yr$^{-1}$ with a mean of 2.1 ± 0.8 kg m$^{-2}$ yr$^{-1}$, suggesting a positive carbonate budget in the southern GBR (Table CS2.1). How the relative abundance of different coral taxa contributed to the observed variability in the carbonate budget will be important to differentiate in order to determine potential thresholds in coral cover to maintain reef resilience and recovery in a future ocean.
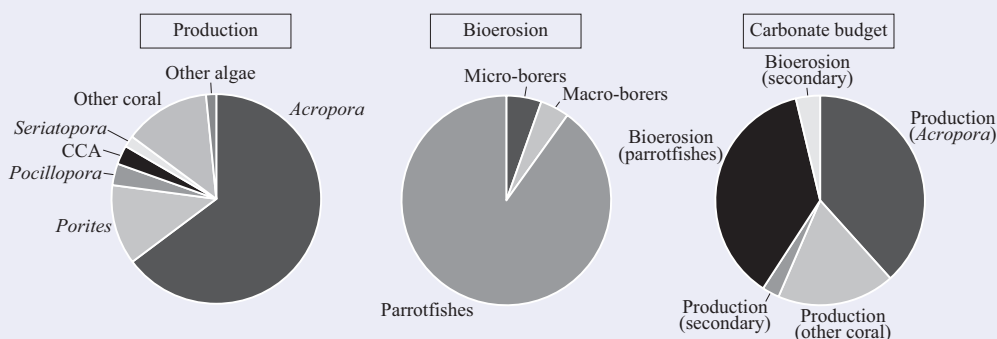


**Figure CS2.1**  Proportional mean rates of production (calcification), bioerosion and the total carbonate budget by key groups in the southern GBR between 2017 and 2019 (AIMS LTMP).

the GBR where they can make up >60% of biogenic sediment (Yamano et al. 2000, Dawson & Smithers 2014, Dawson et al. 2014). As such, foraminiferans received their highest score across all processes for calcification (FI = 4).

Coral-associated decapods scored highly for the calcification process (FI = 2), which emphasises the importance of looking beyond direct roles when evaluating ecosystem functioning. While the direct magnitude of calcification by decapods is likely to be minimal at best, the influence of coral-associated crabs in regulating coral mucus can enhance the growth and survival of their coral hosts

(Glynn 1983, Hutchings 1983, Stimson 1990). They can also have pronounced effects on corals by reducing fouling algal epibionts (Coen 1988). These symbiotic benefits, which facilitate coral calcification, upregulated coral associates within this process compared to other crustaceans.

Molluscs generally scored highly (FI = 3), but as for crustaceans, they have lower direct contributions to calcification compared to corals. Calcification in Mollusca is perhaps greatest for giant clams (Tridacnidae), with some species reaching >120 cm across and weighing >200 kg (Rosewater 1965). Calcifying zooplankton such as pteropods and heteropods (molluscs) are relatively uncommon in GBR waters, although the pteropod *Cavolinia longirostris* can form aggregations in summer (Russell 1935). Corallivorous molluscs (e.g. *Drupella*) have indirect impacts on calcification through coral predation (Cumming 1999, 2009, Glynn & Enochs 2011), as for CoTS (FI = 3), which have been attributed to >40% of the decline in coral cover on the GBR (De'ath et al. 2012). Sea urchins (e.g. *Diadema*) scored similarly due to their indirect role in the balance between reef accretion and erosion through their herbivorous grazing (Birkeland 1989, Alvarado et al. 2016), as well as the direct calcification of their tests and spines. In addition, during winter when algal production slows down on Caribbean reefs, up to 25% of the diet of *Diadema antillarum* can be derived from living scleractinian corals (Carpenter 1981), an unsuspected coral predator.

## Bioerosion

No group received the top ranking for bioerosion, reflecting the high redundancy within this process (Table 3). Host-associated phototrophic microbes, algal turfs and boring sponges scored highest (FI = 2). A diversity of bacteria, fungi and endolithic algae ('microborers') biochemically penetrate live and dead coral and CCA substrates (Golubic et al. 1981, 2005, Tribollet 2008, Hutchings 2011, Diaz-Pulido et al. 2014, Reyes-Nivia et al. 2014). These groups represent somewhat hidden bioerosion pathways operating on micro-biological scales on and within the reef matrix (Hutchings 1986, Glynn & Manzello 2015). All groups of microbes scored highly (FI ≥ 4), with significant roles in carbonate dissolution–calcification processes. Cyanobacteria are estimated to be responsible for 18%–30% of sediment dissolution of coral reef and lagoon sediments on the GBR (Tudhope & Risk 1985). Epilithic (surface) microfloral (e.g. algal turfs) and microbial communities can shape bioerosion pathways and biological community structure (Chazottes et al. 2002). Microborers are often the primary agents of bioerosion in the first year following coral mortality, which promotes larger bioeroding grazers (e.g. parrotfishes) to dominate in the years to follow (Tribollet et al. 2002, Tribollet & Golubic 2005). However, the contributions of microborers to net reef erosion are difficult to quantify, and large knowledge gaps remain (Case Study 2) (Hutchings 1986, Glynn & Manzello 2015). Likewise, there is a need to quantify and distinguish the contribution of microbial metabolic processes from that of purely thermodynamic and chemical processes (e.g. low saturation of interstitial seawater with respect to calcium carbonates, e.g. omega undersaturation) to the rates of internal biological carbonate erosion (e.g. Reyes-Nivia et al. 2014). Both biological and chemically driven processes are fundamental for an accurate quantification of erosion rates of reef cements.

Boring and cryptic sponges ranked as important bioeroders (FI = 3). The most important genera of siliceous sponges to bioerosion are *Cliona*, *Anthosigmella* and *Spheciospongia* (Wilkinson 1983, Schönberg 2000, Fang et al. 2017). Sponges can be the most significant invertebrate bioeroders on coral reefs, with *Cliona* species reported to contribute up to 23 kg $CaCO_3$ $m^{-2}$ $yr^{-1}$ (Neumann 1966, Glynn & Manzello 2015). Around 2%–3% of the carbonate skeleton is dissolved in this process, with the remainder passed on as sediments (Glynn & Manzello 2015). In extreme cases, sponges can also infest and kill live coral colonies (Lopez-Victoria et al. 2006, Marulanda-Gomez et al. 2017). *Cliona* and non-*Cliona* sponges are the only bioeroding invertebrates captured in the AIMS LTMP dataset, as densities of other cryptic bioeroding invertebrate species are hard to quantify. The lack of spatially explicit data on these groups makes it difficult to upscale their contributions to bioerosion and reef carbonate budgets (Case Study 2). This might explain why bioeroding molluscs (e.g.

lithophagid bivalves, boring clams) scored low for bioerosion here (FI = 7) despite their documented contribution to bioerosive and biocorrosive processes (Hutchings 1986, Lazar & Loya 1991, Krumm 1999, Londono-Cruz et al. 2003, Chen et al. 2013, Schönberg et al. 2017).

All groups of worms ('macroborers') scored highly for bioerosion (FI = 3), but as an incredibly diverse assemblage, they are likely to have diversity and redundancy in their biological and ecological roles. The first suite of macroeroders to proliferate in dead coral substrate are typically short-lived polychaetes (e.g. *Polydora*, fabriciniids), which can be extremely abundant, followed by longer-lived polychaetes (e.g. Cirratulidae, Eunicidae, Sabellidae) (Hutchings et al. 1992, Hutchings 2011). In high densities (up to 80,000 ind. m$^{-2}$), these worms can contribute to erosional losses around 0.7–1.8 kg CaCO$_3$ m$^{-2}$ yr$^{-1}$ (Davies & Hutchings 1983). *Spirobranchus* (Serpulidae) scored highly among the other worm groups, but, importantly, they do not bore into live coral directly. Instead, these worms stimulate corals to grow around their thinly calcified tubes, where they can have significant indirect effects on calcification, bioerosion and the deterrence of some corallivores (DeVantier et al. 1986, Rowley 2008, Hutchings et al. 2019).

A range of other mobile invertebrates also scored highly (FI = 3; Table 3). Mean bioerosion rates of chitons on One Tree Island, southern GBR, were 0.16 kg CaCO$_3$ ind$^{-1}$ yr$^{-1}$ (Barbosa et al. 2008). At high densities, chitons may have an equivocal role in carbonate erosion budgets as other macroeroders like sea urchins and parrotfishes, namely in the intertidal. Regular sea urchins (e.g. diadematids, echinometrids) contribute to erosion rates >10 kg CaCO$_3$ m$^{-2}$ yr$^{-1}$ on some reefs (Glynn & Manzello 2015, Alvarado et al. 2016), but rates on the GBR are comparatively low, perhaps due to comparatively healthy fish populations regulating urchin densities (Sammarco 1985). CoTS scored among these invertebrates, possibly as its consumption of live coral promotes colonisation by bioeroders on dead coral surfaces altering the biological character of the reef (Glynn & Manzello 2015).

Scraping and excavating parrotfishes scored highly for bioerosion (FI = 3). Most of these nominally herbivorous fishes are attracted to the endolithic algal growth on dead corals, with substantial bioerosion resulting from their feeding behaviour (Clements et al. 2017). Some species also target live coral in >50% of the diet (e.g. *Bolbometopon muricatum*) (Bonaldo et al. 2014). Parrotfishes are generally the greatest contributors to bioerosion on coral reefs and are key drivers in total reef carbonate budgets (Case Study 2) (Perry et al. 2012a). Calculations in Case Study 2 suggest that 25 species of parrotfishes from five genera (*Bolbometopon*, *Cetoscarus*, *Chlorurus*, *Hipposcarus* and *Scarus*) are responsible for almost all of the bioerosion in the southern GBR. Excavating parrotfishes (*Bolbometopon* and *Chlorurus* spp.) are typically the most significant external bioeroders on coral reefs, contributing to erosion rates over 32 kg CaCO$_3$ m$^{-2}$ yr$^{-1}$ on the GBR (Hoey & Bellwood 2008), with significant contributions to sediment production (Bellwood & Choat 1990, Bellwood et al. 2003). *Bolbometopon muricatum* alone accounts for around 87.5% of the erosive processes and almost all of the live coral predation by parrotfishes on outer-shelf reefs of the GBR (Bellwood et al. 2003, Hoey & Bellwood 2008).

## *Ecosystem engineering*

*Bolbometopon* scored highest by experts regarding ecosystem engineering (FI = 1; Table 3). This was influenced by the low redundancy of this species, which is supported in the literature, given its functionally explicit role as a mass excavator of live and dead coral, particularly on outer-shelf reefs (Hoey & Bellwood 2008, Bonaldo et al. 2014). Other parrotfishes also scored highly for this role (FI = 3) but were down-weighted due to a comparatively higher redundancy across the group. In healthy systems on the GBR, parrotfish bioerosion can balance net reef accretion (calcification) (Hoey & Bellwood 2008) and has the potential to drive a negative carbonate budget (Case Study 2), especially following disturbance Farming damselfishes scored along with the parrotfishes for their roles in shaping algal communities and coral reef growth within their territories (Ceccarelli et al. 2001, 2011, Hata & Kato 2004, Ceccarelli 2007, Casey et al. 2015a). This can further impact reef fish behaviour and community structure (Eurich et al. 2018). Damselfishes seem to exhibit a positive

association with both coral habitat and predators (e.g. coral trout) across the GBR (Emslie et al. 2019), with impacts on coral growth, resilience and recovery (Chase et al. 2014, 2018).

Corals (tabular, staghorn, massive) and host-associated phototrophic microbes scored highly (FI = 2). This reflects the symbiotic relationship between the coral and its microbiome and the fundamental importance of both to the construction of the reef (Bourne et al. 2016). The rugosity and complexity of branching and tabular corals, including acroporids and pocilloporids, provide critical refugia that support the diversity of coral reefs (Hixon & Menge 1991, Cheal et al. 2008, Harborne et al. 2012, Rogers et al. 2014, 2018a,b). Different coral species support different fish communities (Holbrook et al. 2008, 2015, Messmer et al. 2011), suggesting that coral and fish biodiversity are tightly linked. For example, tabular coral formations provide particularly important shelter for larger predatory fishes, which inspires competition, predation and community dynamics and scales up to support fisheries productivity (Pratchett et al. 2008a, Kerry & Bellwood 2012, 2015a,b, 2016, 2017). However, tabular and branching corals typically have ephemeral life history traits (Tanner et al. 1996), and the loss of particular coral species can have disproportionate impacts on reef fish assemblages and biodiversity (Messmer et al. 2011, Holbrook et al. 2015). The influence and importance of specific functional and morphological coral groups is dynamic over time and space (McWilliam et al. 2018, Bellwood et al. 2019).

Exhibiting high recruitment rates, tabular corals (e.g. *Acropora hyacinthus*) are key to the growth, maintenance and recovery of coral reefs (Connolly & Muko 2003, Ortiz et al. 2014, 2018, Yadav et al. 2016). Staghorn corals (e.g. *Acropora muricata*) are commonly regarded as fast-growing 'weedy' species, as they have greater calcification rates but exhibit disturbance-prone 'boom-and-bust' characteristics (Knowlton 2001, Graham et al. 2014, Anderson et al. 2017). Massive corals (e.g. *Porites*) are slow growing, but their broader resilience and longevity are important characteristics regarding long-term reef accretion, persistence and recovery (Baldock et al. 2014, Ortiz et al. 2014, 2018, Yadav et al. 2016). Some corals (e.g. *Turbinaria*) may be more resilient to turbid conditions on inshore reefs, where their functional importance is likely to be comparatively greater in the absence of other groups (Anthony 2006, Browne 2012, Browne et al. 2013). In response to mass coral bleaching and mortality on the GBR (Hughes et al. 2018b), brooding *Pocillopora* (grouped here within 'other branching corals') replaced broadcast spawning acroporids as the predominant recruitment taxon for the first time recorded (Hughes et al. 2019a) and may emerge as key features in the current reef recovery trajectory owing to transgenerational plasticity and adaptation through local retention of brooding reproductive modes (Torda et al. 2013a,b, 2017).

Sponges also scored highly for ecosystem engineering, particularly larger conspicuous groups (heterotrophs, phototrophs) (Table 3). In addition to providing structural complexity to a reef (Maldonado et al. 2015), marine sponges host a diverse microbiome, which can occupy up to 35% of sponge volume and impact host defence, metabolism and resilience to perturbation (Simister et al. 2012, Webster & Taylor 2012, Taylor et al. 2013). It is not surprising that all microbe groups also scored highly (FI ≥ 4). Although scoring lower for ecosystem engineering than other sponge groups (Table 3), the role of cryptic and boring sponges to reef and rubble consolidation is well appreciated (Wulff & Buss 1979, Wilkinson 1983, Hutchings 2011), with important inferences for settlement, recruitment and recovery on coral reefs (Biggs 2013). This is similar for CCA (Matsuda 1989, Diaz-Pulido & McCook 2008, Arnold et al. 2010, Doropoulos et al. 2012a), which scored among the highest algal groups (FI = 4). The role of a range of taxa (e.g. CCA, algae, sponges and microbes) in the biogenic cementation and consolidation of degraded reef rubble habitat is likely to be critical to reef functioning and recovery in a future ocean (Johns et al. 2018), but this remains poorly characterised.

### Recruitment facilitation

Parrotfishes scored highest for recruitment facilitation (FI ≥ 3; Table 3). As previously, the bulk excavation of both live and dead coral by scraping and excavating parrotfishes is an important process for bioerosion and ecosystem engineering. Parrotfish feeding scars are hypothesised to

facilitate settlement of corals and a range of other species through the excavation of live coral polyps and/or removal of epilithic algae from hard surfaces (Bellwood & Choat 1990, Bonaldo & Bellwood 2009, Bonaldo et al. 2014). This may also be true for grazing invertebrates like sea urchins (Dart 1972). Farming damselfishes also scored highly (FI = 2), due to their territorial behaviour that influences coral recruitment and juvenile survival (Gleason 1996, Gochfeld 2010, Doropoulos et al. 2013, Casey et al. 2015a), as well as community dynamics of larger reef fishes (Ceccarelli et al. 2001). Generally, herbivores play functionally diverse roles in recruitment facilitation owing to their diet, behaviour and distribution on the reef (Dart 1972, Doropoulos et al. 2013).

The roles of algae in recruitment facilitation are diverse, including indirect pathways through herbivory and feeding scars (Dart 1972), adding structural complexity free from the coral polyp 'wall of mouths' (Hamner et al. 1988) and/or biochemical settlement cues (e.g. CCA, macroalgae) (Heyward & Negri 1999, Harrington et al. 2004, Birrell et al. 2008b, Arnold et al. 2010, Doropoulos et al. 2012a, 2013, Brooker et al. 2016b). While turf and macroalgal growth can impair the recruitment of coral reef species (Birrell et al. 2008a, Diaz-Pulido & McCook 2008, Arnold et al. 2010, Johns et al. 2018), it has been posited that the benefits of macroalgae in protecting juvenile corals from predation by species such as parrotfishes may outweigh the negative impacts of algal growth on coral settlement and coral-algal competition (Venera-Ponton et al. 2011). Interestingly, the presence of CCA can prevent such undesirable algal growth to facilitate recruitment processes (Vermeij et al. 2011, Gomez-Lemos & Diaz-Pulido 2017).

Tabular and branching corals scored highly (FI = 2), as increased complexity provides refugia on coral reefs, facilitating the settlement, recruitment and survival of corals, fishes and other marine species (Patton 1994, Ohman et al. 1998, Pratchett et al. 2008a, Shima et al. 2008, Wilson et al. 2008, Coker et al. 2014, Yadav et al. 2016, Gallagher & Doropoulos 2017). Shading by tabular corals can reduce the settlement success of autotrophic species (e.g. corals, algae) and alter benthic community compositions towards heterotrophs (e.g. bryozoans, other invertebrates) (Baird & Hughes 2000). Sponges (FI ≥ 4) also influence settlement and recruitment, perhaps most importantly in their ability to consolidate benthic habitat (e.g. rubble). Coral rubble is an important settlement and recruitment habitat, and unconsolidated rubble can reduce coral settlement and recruit survival, hindering reef recovery (Wulff & Buss 1979, Fox et al. 2003, Fox & Caldwell 2006, Biggs 2013, Johns et al. 2018).

Interestingly, bivalves including giant clams and bed-forming species like oysters scored highly (FI = 3). The structural refugia they provide can facilitate settlement of juvenile fishes and a diversity of other organisms, increasing their protection and survival post settlement, particularly when coral cover is low (Beukers & Jones 1998, Lecchini et al. 2007, Cabaitan et al. 2008, Neo et al. 2015). Shell and 'bed' construction by giant clams and other bivalves offers structural complexity to the reef that provides substrate for colonisation by a diversity of holobionts, epibionts, commensal and ectoparasitic organisms (Neo et al. 2017). In this context, the low scores for bivalves regarding symbiosis (FI = 8) and ecosystem engineering (FI = 7) are surprising but may be considered marginal in terms of reef construction compared to corals. Further, the functional roles of bed-forming species are likely to be greater in intertidal and estuarine habitats (e.g. oysters), beyond the target habitat explored here.

## *Functional importance rankings*

In this section, we provide a ranking across our 70 functionally and taxonomically distinct groups, creating a hierarchy of species in terms of their total functional importance from our ecosystem process-based assessment. Using the scores elicited by experts on a per-process basis (as previously), we produced three sets of ranks for each group's relative importance to: 1) production functioning (i.e. primary production, herbivory, predation, nutrient cycling and symbioses), 2) habitat functioning (i.e. calcification, bioerosion, ecosystem engineering and recruitment facilitation) and 3) total ecosystem functioning (i.e. all nine processes combined) (greater detail can be found in the methods). These ranks are presented in Table 4.

**Table 4**  Functional importance (FI) rankings for functional groups on the GBR, calculated for production and habitat functioning and overall

| Taxa | Functional group | Production functioning | Habitat functioning | Total functioning |
|---|---|---|---|---|
| Microbes | Phototrophic | 10 | 27 | 17 |
| | Host-associated | 2 | 1 | 1 |
| | Chemoautotrophic | 11 | 12 | 9 |
| | Heterotrophic | 12 | 25 | 13 |
| Algae | Phytoplankton | 6 | 41 | 22 |
| | Algal turfs | 1 | 10 | 3 |
| | Leathery | 36 | 43 | 41 |
| | Foliose | 20 | 24 | 18 |
| | Calcareous | 21 | 28 | 28 |
| | CCA | 15 | 9 | 6 |
| Sponges | Heterotrophic | 30 | 17 | 24 |
| | Phototrophic | 16 | 18 | 15 |
| | Boring | 22 | 8 | 11 |
| | Cryptic | 31 | 5 | 10 |
| Coral | Tabular | 3 | 4 | 2 |
| | Staghorn | 13 | 7 | 4 |
| | Branching (other) | 23 | 13 | 19 |
| | Massive | 17 | 14 | 12 |
| | Encrusting | 35 | 16 | 25 |
| | Free-living | 45 | 65 | 62 |
| | Soft corals | 5 | 44 | 26 |
| | Foraminifera | 59 | 52 | 59 |
| Worms | Nematodes | 64 | 38 | 54 |
| | Nemertea | 65 | 39 | 53 |
| | Polychaetes | 46 | 29 | 40 |
| | *Spirobranchus* | 61 | 26 | 48 |
| Crustaceans | Decapods (H) | 33 | 45 | 38 |
| | Decapods (P) | 41 | 53 | 51 |
| | Coral-associated | 19 | 15 | 16 |
| | Barnacles | 69 | 46 | 65 |
| | Stomatopods | 47 | 30 | 39 |
| | Cleaner shrimp | 60 | 42 | 52 |
| | Infauna | 34 | 47 | 37 |
| | Zooplankton | 4 | 68 | 34 |
| | Parasitic | 66 | 69 | 70 |
| Molluscs | Gastropods (H) | 27 | 31 | 30 |
| | Gastropods (P) | 38 | 40 | 36 |
| | Triton snails | 9 | 33 | 21 |
| | *Drupella* | 55 | 32 | 47 |
| | Tridacnidae | 48 | 19 | 33 |
| | Bivalves | 49 | 20 | 32 |
| | Chitons | 42 | 21 | 31 |
| | Cephalopods | 26 | 54 | 45 |
| Echinoderms | Seastars (H) | 28 | 55 | 46 |
| | Seastars (P) | 62 | 48 | 58 |
| | CoTS | 14 | 22 | 14 |

(*Continued*)

**Table 4 (*Continued*)**   Functional importance (FI) rankings for functional groups on the GBR, calculated for production and habitat functioning and overall

| Taxa | Functional group | Production functioning | Habitat functioning | Total functioning |
|------|------------------|------------------------|---------------------|-------------------|
| | Sea cucumbers (DF) | 39 | 49 | 49 |
| | Sea cucumbers (SF) | 63 | 70 | 68 |
| | Sea urchins (regular) | 29 | 23 | 23 |
| | Sea urchins (irregular) | 56 | 56 | 57 |
| | Brittle stars | 43 | 57 | 50 |
| | Feather stars | 68 | 58 | 66 |
| Fishes | Cryptobenthic | 8 | 62 | 35 |
| | Farmers | 32 | 11 | 20 |
| | Scrapers (scarids) | 37 | 2 | 7 |
| | Browsers (nasos) | 50 | 34 | 44 |
| | Browsers (siganids) | 51 | 35 | 43 |
| | Browsers (other) | 52 | 36 | 42 |
| | *Bolbometopon* | 25 | 3 | 5 |
| | Excavators (other) | 24 | 6 | 8 |
| | Detritivores | 7 | 50 | 29 |
| | Planktivores | 67 | 66 | 67 |
| | Corallivores | 70 | 60 | 69 |
| | Invertivores (labrids) | 53 | 61 | 61 |
| | Invertivores (other) | 57 | 59 | 60 |
| | Invertivores (lutjanids) | 58 | 51 | 56 |
| | Eels | 40 | 63 | 55 |
| | Piscivores (residents) | 54 | 64 | 64 |
| | Piscivores (transients) | 44 | 67 | 63 |
| | Cleaner wrasse | 18 | 37 | 27 |

*Note:* Shading denotes ranks; 1st = dark, 2nd = mid, 3rd = light.

*Abbreviations:*   H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders.

Species that scored highly within just one ecosystem process were not necessarily ranked highly in terms of total functional importance (e.g. cephalopods) (Table 4). Similarly, species that scored well within either production or habitat functioning separately may not have ranked highly overall (e.g. zooplankton, cryptobenthic fishes, detritivorous fishes) (Table 4). Only those that scored highly across multiple processes, and those contributing to both production and habitat functioning, would achieve a high final rank (Table 4). For specific details within each process with support from the literature, refer to the sections previously.

## *Vulnerability rankings*

Vulnerability of our 70 functional groups was assessed in context of their biological functioning in the typical reef slope and reef crest habitats on the GBR, with a primary focus on offshore reef regions (Table 5). Inner-reef regions were assessed separately, as exposure to some stressors (particularly those related to water quality) is most significant inshore (Devlin & Brodie 2005, Wooldridge et al. 2006, Brodie & Waterhouse 2012, Brodie et al. 2012, Kroon et al. 2012, Waterhouse et al. 2012, Fabricius et al. 2014, Lam et al. 2018, Mellin et al. 2019), where recovery rates are impaired (MacNeil et al. 2019). Thus, we specifically contrast results for water quality stressors between inshore and offshore regions (Table 6). Vulnerabilities to each of our nine key stressors were considered equal, though we note that some stressors are likely to have greater and broader impacts at local and global

scales and that all stressors will occur in synergy with cumulative and multifaceted impacts (Halpern et al. 2008, Brown et al. 2014, McClanahan et al. 2015, Uthicke et al. 2016, Harborne et al. 2017, Wolff et al. 2018).

*Climate change*    Changes in the global climate are occurring faster than anticipated (IPCC 2018, Xu et al. 2018). The greatest potential impacts across our 70 functional groups were suggested for ocean warming and ocean acidification, followed by cyclones (Table 5). This indicates that climate-related stressors were the primary concern of GBR experts, as demonstrated previously (Ban et al. 2014b). This is in line with the widespread coral bleaching events documented across the GBR over recent years (Hughes et al. 2017b, 2018b,c), with alterations to reef community assemblage and structure (Stuart-Smith et al. 2018), trophodynamics (Hempson et al. 2018a,b), reproduction (Hughes et al. 2019a), community calcification (McMahon et al. 2019) and reduced recovery rates (Osborne et al. 2017, MacNeil et al. 2019) already observed, including for deep (or mesophotic) reefs (Frade et al. 2018). Rates of change in ocean chemistry are also likely to be steeper on the GBR than currently projected by the IPCC (Mongin et al. 2016b), perhaps even more so for inshore reefs (Uthicke et al. 2014). Further, cyclones will have significant spatial and temporal impacts across the GBR (Wolff et al. 2016, Cheal et al. 2017, Mellin et al. 2019). The only comprehensive solution to reduce the impact of global change on coral reefs, and globally, is to rapidly decrease anthropogenic emissions of $CO_2$, but the future of coral reefs is dependent on both local and global action on local and global stressors (Kennedy et al. 2013, Albright et al. 2016a, Hoey et al. 2016a).

There will be spatial variability in the responses of reef organisms to climate change stressors, owing to thermal histories, local adaptation and regional disparities in exposure (Uthicke et al. 2014, Siboni et al. 2015, Hughes et al. 2018b, Stuart-Smith et al. 2018). Intertidal and coastal organisms may be less susceptible to future conditions owing to their current exposure to diel fluctuations (e.g. pH, temperature, oxygen), while offshore and open-ocean organisms may be most vulnerable, as they typically experience the most constant conditions (Byrne 2011, Jarrold et al. 2017, Jarrold & Munday 2018, Wolfe et al. 2020). Transgenerational plasticity may enable some marine organisms to acclimatise over several generations, enhancing adaptive responses, poleward migration and reef resilience in the face of climate change (Byrne et al. 2020, Torda et al. 2017).

Host-associated microbes scored among the most vulnerable to climate change stressors, particularly for ocean warming (Table 5). The sensitivities and responses of free-living microbes (independent of a host organism) are often starkly different and can be important bioindicators of reef health regarding temperature, nutrients and sedimentation (Case Study 4) (Hansen et al. 1992, Falkowski et al. 2008, Glasl et al. 2017, 2018a). Biota permanently in the plankton (e.g. copepods, pteropods), which typically have short generation times, may have resilience in their ability to respond to changes in ocean conditions compared to species with longer generational turnover (McKinnon et al. 2007). Zooplankton were considered more vulnerable to climate change stressors than phytoplankton (Table 5), but impacts will be highly variable across the diversity of these two groups. Anthropogenic stressors and their interactions will impact phyto- and zooplankton growth, development, physiology, abundance and distribution, altering blooms, benthic-pelagic coupling and functioning (Huntley & Lopez 1992, Edwards & Richardson 2004, Richardson & Schoeman 2004, Kirby et al. 2007, Gao et al. 2012, Häder & Gao 2015, Carrillo-Baltodano & Morales-Ramirez 2016, Dupuy et al. 2016). Indirect influences of climate change on oceanographic processes (e.g. currents, upwelling, etc.) are suggested to drive vulnerabilities in the plankton across the GBR region, as reviewed by McKinnon et al. (2007). Any alteration to phytoplankton or zooplankton abundance, composition, productivity and timing of occurrence is likely to have a cascading effect on higher trophic levels and functioning of the GBR (McKinnon et al. 2007).

For coral reef fishes, current evidence suggests that increased water temperature will be a major determinant of future assemblages through habitat degradation and direct effects on larval dispersal, recruitment, physiology and behaviour (Munday et al. 2009b, Hoey et al. 2016a). The

**Table 5**  Potential impact (PI) of six pertinent stressors on 70 functional groups on the GBR

| Taxa | Functional group | Warming | Acidification | Cyclones | Fisheries | Disease | Outbreaks |
|------|------------------|---------|---------------|----------|-----------|---------|-----------|
| Microbes | Phototrophic | 9.0 | 1.0 | | | | |
| | Host-associated | 16.0 | 4.0 | | | 1.0 | |
| | Chemoautotrophic | 4.0 | 1.0 | | | | |
| | Heterotrophic | 9.0 | 1.0 | | | | |
| Algae | Phytoplankton | | | | | | |
| | Algal turfs | 1.0 | | | | | |
| | Leathery | 1.0 | | 2.3 | | | |
| | Foliose | | | 0.3 | | | |
| | Calcareous | 4.0 | 4.0 | 2.3 | | | |
| | CCA | 9.0 | 9.0 | | | | |
| Sponges | Heterotrophic | 1.0 | 7.1 | 16.0 | 1.0 | 1.0 | |
| | Phototrophic | 1.0 | 1.0 | 16.0 | 1.0 | 1.0 | |
| | Boring | 0.4 | | 0.3 | | 1.0 | |
| | Cryptic | 1.0 | 1.0 | 1.0 | | 1.0 | |
| Coral | Tabular | 16.0 | 9.0 | 16.0 | 0.1 | 2.8 | 16.0 |
| | Staghorn | 16.0 | 9.0 | 16.0 | 0.4 | 2.8 | 16.0 |
| | Branching (other) | 16.0 | 9.0 | 16.0 | 0.1 | 1.8 | 16.0 |
| | Massive | 16.0 | 6.3 | 1.8 | 0.1 | 1.8 | 1.8 |
| | Encrusting | 16.0 | 6.3 | 1.8 | 0.1 | 1.8 | 2.8 |
| | Free-living | 12.3 | 6.3 | 4.0 | | 1.8 | 1.8 |
| | Soft corals | 12.3 | 4.0 | 11.1 | 0.1 | 1.0 | |
| | Foraminifera | 4.0 | 6.3 | 7.1 | | 0.4 | |
| Worms | Nematodes | | | | | | |
| | Nemertea | | | 0.3 | | | |
| | Polychaetes | | | 0.3 | | | |
| | *Spirobranchus* | 9.0 | 4.0 | 1.0 | | 1.0 | |
| Crustaceans | Decapods (H) | 9.0 | 16.0 | | | | |
| | Decapods (P) | 16.0 | 16.0 | 0.3 | | | |
| | Coral-associated | 16.0 | 16.0 | 9.0 | | | 0.3 |
| | Barnacles | 9.0 | 9.0 | | | | |
| | Stomatopods | 9.0 | 9.0 | 0.3 | | | |
| | Cleaner shrimp | 9.0 | 16.0 | 1.0 | | | |
| | Infauna | 1.0 | 9.0 | 0.3 | | | |
| | Zooplankton | 9.0 | 16.0 | 0.3 | | | |
| | Parasitic | 4.0 | 9.0 | 0.3 | | | |
| Molluscs | Gastropods (H) | 16.0 | 16.0 | | | | |
| | Gastropods (P) | 9.0 | 7.1 | 1.0 | | | |
| | Triton snails | 9.0 | 7.1 | 1.0 | 0.3 | | |
| | *Drupella* | 16.0 | 16.0 | 0.3 | | | |
| | Tridacnidae | 16.0 | 16.0 | 16.0 | 1.0 | | |
| | Bivalves | 16.0 | 16.0 | 4.0 | 1.0 | 1.0 | |
| | Chitons | 9.0 | 9.0 | 1.0 | | | |
| | Cephalopods | 1.0 | 4.0 | 0.3 | 2.3 | | |
| Echinoderms | Seastars (H) | 9.0 | 4.0 | | | | |
| | Seastars (P) | 9.0 | 1.0 | 1.0 | | | |
| | CoTS | 1.0 | 9.0 | 1.0 | | | |
| | Sea cucumbers (DF) | 9.0 | 4.0 | 2.3 | 16.0 | | |
| | Sea cucumbers (SF) | 9.0 | 1.0 | 1.0 | 1.0 | | |

(*Continued*)

**Table 5 (*Continued*)**    Potential impact (PI) of six pertinent stressors on 70 functional groups on the GBR

| Taxa | Functional group | Warming | Acidification | Cyclones | Fisheries | Disease | Outbreaks |
|------|------------------|---------|---------------|----------|-----------|---------|-----------|
| | Sea urchins (regular) | 9.0 | 16.0 | | | | |
| | Sea urchins (irregular) | 9.0 | 16.0 | 0.3 | | | |
| | Brittle stars | 9.0 | 4.0 | 0.3 | | | |
| | Feather stars | 9.0 | 4.0 | 1.0 | | | |
| Fishes | Cryptobenthic | 11.1 | 4.0 | 11.1 | | | 1.8 |
| | Farmers | | 1.8 | 7.1 | | | |
| | Scrapers (scarids) | | 1.8 | 0.1 | 0.1 | | |
| | Browsers (nasos) | | 1.8 | 0.4 | 0.1 | | |
| | Browsers (siganids) | | 1.8 | 0.4 | 0.4 | | |
| | Browsers (other) | | 1.8 | 0.4 | 0.4 | | |
| | *Bolbometopon* | 1.8 | 4.0 | 1.8 | 0.4 | | |
| | Excavators (other) | | 1.8 | 1.8 | 0.1 | | |
| | Detritivores | 0.4 | 1.8 | 7.1 | | | |
| | Planktivores | 11.1 | 4.0 | 11.1 | | | 2.8 |
| | Corallivores | 16.0 | 11.1 | 2.8 | | | 4.0 |
| | Invertivores (labrids) | 4.0 | 4.0 | 1.8 | 0.1 | | |
| | Invertivores (other) | 4.0 | 4.0 | 1.8 | 1.8 | | |
| | Invertivores (lutjanids) | 4.0 | 4.0 | 1.0 | 0.4 | | |
| | Eels | 7.1 | 4.0 | 1.0 | | | |
| | Piscivores (residents) | 11.1 | 4.0 | 2.8 | 16.0 | | |
| | Piscivores (transients) | 7.1 | 4.0 | 1.8 | 16.0 | | |
| | Cleaner wrasse | 7.1 | 1.8 | 11.1 | | | |

*Note:* Exposure was considered in context of offshore reefs. Shading denotes highest scores; maximum PI = 16 (dark); high PI ≥ 10 (mid); medium PI ≥ 7 (light); blank cells denote PI = 0.

*Abbreviations:*    H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders.

positive associations between a great diversity of reef fishes and their coral habitat exemplifies the fundamental importance of coral as the foundation of healthy reef communities (Coker et al. 2014, Pratchett et al. 2018, Emslie et al. 2019). Thus, there are specific concerns for species that depend on corals as a food source and/or for shelter, including coral-associated decapods (Stella et al. 2011a,b), and corallivorous, planktivorous and cryptobenthic fishes (Munday 2004, Pratchett et al. 2004, 2008b, Wilson et al., 2006 2014, Cole et al. 2010, Bellwood et al. 2012a, Hempson et al. 2018c, Rice et al. 2019) (Table 5). Specialist and obligate corallivorous fishes (e.g. butterflyfishes and tubelip wrasses) are likely to be highly impacted by the combined impacts of global change through prey depletion, starvation and even reduced sociality and reproductive potential (Pratchett et al. 2004, Berumen & Pratchett 2006, Cole et al. 2008, 2010, Graham et al. 2009, Thompson et al. 2019), while their feeding adds further pressure on coral condition (Cole et al. 2009). Butterflyfish (Chaetodontidae) abundance and species richness seem to be primarily influenced by bottom-up drivers making physical changes to their coral habitat a significant concern (Brooker et al. 2016a, Leahy et al. 2016). Yet, trophic and foraging plasticity as documented for a range of coral reef fishes, including some considered to be specialist obligate feeders, will likely offer some resilience in a degraded reef setting (Wen et al. 2016, Hempson et al. 2017, Karkarey et al. 2017, Letourneur et al. 2017, Feary et al. 2018, Zambre & Arthur 2018). The close contact relationships

**Table 6**   Potential impact (PI) of three water quality stressors on 70 functional groups on the GBR

| Taxa | Functional group | Inshore | | | Offshore | | |
| --- | --- | --- | --- | --- | --- | --- | --- |
| | | Nutrients | Sediments | Pollutants | Nutrients | Sediments | Pollutants |
| Microbes | Phototrophic | | 4.0 | 16.0 | | 1.0 | |
| | Host-associated | 16.0 | 9.0 | 16.0 | 4.0 | 2.3 | |
| | Chemoautotrophic | | | 9.0 | | | |
| | Heterotrophic | | | 9.0 | | | |
| Algae | Phytoplankton | | 1.0 | 9.0 | | 0.3 | |
| | Algal turfs | | 1.0 | 9.0 | | 0.3 | |
| | Leathery | | 1.0 | 4.0 | | 0.3 | |
| | Foliose | | 9.0 | 4.0 | | 2.3 | |
| | Calcareous | | 9.0 | 4.0 | | 2.3 | |
| | CCA | 4.0 | 16.0 | 9.0 | 1.0 | 4.0 | |
| Sponges | Heterotrophic | | 7.1 | 11.1 | | 1.8 | |
| | Phototrophic | | 16.0 | 11.1 | | 4.0 | |
| | Boring | | 7.1 | 9.0 | | 1.8 | |
| | Cryptic | | 9.0 | 16.0 | | 2.3 | |
| Coral | Tabular | 12.3 | 9.0 | 1.6 | 3.1 | 2.3 | |
| | Staghorn | 12.3 | 9.0 | 1.6 | 3.1 | 2.3 | |
| | Branching (other) | 12.3 | 7.1 | 1.6 | 3.1 | 1.8 | |
| | Massive | 6.3 | 6.3 | 1.6 | 1.6 | 1.6 | |
| | Encrusting | 6.3 | 9.0 | 1.6 | 1.6 | 2.3 | |
| | Free-living | 4.0 | 6.3 | 1.6 | 1.0 | 1.6 | |
| | Soft corals | 4.0 | 9.0 | 1.6 | 1.0 | 2.3 | |
| | Foraminifera | | 6.3 | 2.3 | | 1.6 | |
| Worms | Nematodes | | | | | | |
| | Nemertea | | | | | | |
| | Polychaetes | | | | | | |
| | *Spirobranchus* | | 4.0 | 9.0 | | 1.0 | |
| Crustaceans | Decapods (H) | | | 4.0 | | | |
| | Decapods (P) | | | 4.0 | | | |
| | Coral-associated | | 4.0 | 9.0 | | 1.0 | |
| | Barnacles | | 4.0 | 4.0 | | 1.0 | |
| | Stomatopods | | | 4.0 | | | |
| | Cleaner shrimp | | | 4.0 | | | |
| | Infauna | | | 1.0 | | | |
| | Zooplankton | | 1.0 | 4.0 | | 0.3 | |
| | Parasitic | | | 1.0 | | | |
| Molluscs | Gastropods (H) | | 1.0 | 4.0 | | 0.3 | |
| | Gastropods (P) | | | 4.0 | | | |
| | Triton snails | | | 4.0 | | | |
| | *Drupella* | | | 4.0 | | | |
| | Tridacnidae | | 9.0 | 4.0 | | 2.3 | |
| | Bivalves | | 1.0 | 4.0 | | 0.3 | |
| | Chitons | | | | | | |
| | Cephalopods | 1.0 | | 4.0 | 0.3 | | |
| Echinoderms | Seastars (H) | | 1.0 | 4.0 | | 0.3 | |
| | Seastars (P) | | | 4.0 | | | |
| | CoTS | | | 1.0 | | | |
| | Sea cucumbers (DF) | | | 4.0 | | | |

(*Continued*)

**Table 6 (*Continued*)**   Potential impact (PI) of three water quality stressors on 70 functional groups on the GBR

| Taxa | Functional group | Inshore | | | Offshore | | |
|------|------------------|---------|---------|-----------|----------|---------|-----------|
| | | Nutrients | Sediments | Pollutants | Nutrients | Sediments | Pollutants |
| | Sea cucumbers (SF) | | 1.0 | 4.0 | | 0.3 | |
| | Sea urchins (regular) | | 1.0 | 4.0 | | 0.3 | |
| | Sea urchins (irregular) | | | 1.0 | | | |
| | Brittle stars | | | 1.0 | | | |
| | Feather stars | | | 4.0 | | | |
| Fishes | Cryptobenthic | 0.4 | 4.0 | 7.1 | 0.1 | 1.0 | |
| | Farmers | | 11.1 | 7.1 | | 2.8 | |
| | Scrapers (scarids) | | 16.0 | 4.0 | | 4.0 | |
| | Browsers (nasos) | | 7.1 | 4.0 | | 1.8 | |
| | Browsers (siganids) | | 7.1 | 4.0 | | 1.8 | |
| | Browsers (other) | | 7.1 | 4.0 | | 1.8 | |
| | *Bolbometopon* | 0.4 | 11.1 | 4.0 | 0.1 | 2.8 | |
| | Excavators (other) | | 16.0 | 4.0 | | 4.0 | |
| | Detritivores | 1.8 | 7.1 | 4.0 | 0.4 | 1.8 | |
| | Planktivores | 0.4 | 4.0 | 7.1 | 0.1 | 1.0 | |
| | Corallivores | 7.1 | 11.1 | 4.0 | 1.8 | 2.8 | |
| | Invertivores (labrids) | | 7.1 | 7.1 | | 1.8 | |
| | Invertivores (other) | | 7.1 | 7.1 | | 1.8 | |
| | Invertivores (lutjanids) | | 4.0 | 4.0 | | 1.0 | |
| | Eels | 1.8 | 7.1 | 4.0 | 0.4 | 1.8 | |
| | Piscivores (residents) | 4.0 | 7.1 | 7.1 | 1.0 | 1.8 | |
| | Piscivores (transients) | 1.8 | 7.1 | 7.1 | 0.4 | 1.8 | |
| | Cleaner wrasse | 0.4 | 1.8 | 4.0 | 0.1 | 0.4 | |

*Note:* Exposure was considered in context of inshore and offshore reefs. Shading denotes highest scores; maximum PI = 16 (dark); high PI ≥ 10 (mid); medium PI ≥ 7 (light); blank cells denote PI = 0.

*Abbreviations:*   H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders.

between host-associated fishes (e.g. damselfishes) and coral refugia can enhance water circulation (Goldshmid et al. 2004), which can moderate bleaching susceptibility of the coral host itself (Chase et al. 2018).

In extreme cases, the abundance and richness of reef fishes may decline >60% following extensive collapse of reef habitat and structure (Pratchett et al. 2018). Resident predatory fishes that depend on reef structure, including the top fisheries targets on the GBR (coral trout), show a range of vulnerabilities to projected future conditions at both larval and adult life stages (Munday et al. 2013a, Johansen et al. 2014, 2015, Clark et al. 2017, Messmer et al. 2017, Pratchett et al. 2017b). In the context of direct effects, unable to meet the energetic costs of living in a warmer environment, larger-bodied coral trout may be more heavily impacted than smaller-sized individuals, with significant ramifications to fisheries and functioning (Messmer et al. 2017, Scott et al. 2017b). Indirectly, the dependency of resident predatory fishes on tabular corals in particular presents a concerning case where changes in habitat functioning through the loss of coral complexity could have cascading impacts on fisheries production functioning (Kerry & Bellwood 2012, 2015a,b). Conversely, cephalopod populations are proliferating globally (Doubleday et al. 2016), as recognised in the increasing trends in cephalopod fisheries catches (Caddy & Rodhouse 1998, Rodhouse et al. 2014). Cephalopods did not score as vulnerable here (Table 5), in line with global trends and suggestions that they may fare better in a future ocean compared to other marine taxa due to their 'live fast, die young' life cycles (Doubleday et al. 2016, Rosa et al. 2019).

Herbivorous fish groups were considered generally resilient, with densities of some grazing species (e.g. parrotfishes) even documented to increase postdisturbance, perhaps due to the increased algal production that typically follows coral mortality (Diaz-Pulido & McCook 2002, Cheal et al. 2008, 2010, Wilson et al. 2009, Graham et al. 2015, Russ et al. 2015, Hempson et al. 2018c, Roth et al. 2018). However, grazing intensity can decline in line with reduced coral cover as denser algal growth outweighs and minimises the impact of grazers, and simplified habitat complexity increases predation exposure (Cheal et al. 2010, Bozec et al. 2013, Pratchett et al. 2018, Rogers et al. 2018a). The functional roles of the diversity of nominally herbivorous species will vary depending on algal density and the state of the reef (Chong-Seng et al. 2014). Habitat degradation reduces postsettlement success of corals, and shifts towards algal-dominated systems may limit reef recovery (Roth et al. 2018). Coral-algal phase shifts have documented impacts on fisheries productivity (Ainsworth & Mumby 2015, Rogers et al. 2018a), and herbivores protected from fisheries activity in no-take areas may enhance reef recovery (Mumby et al. 2014, Chung et al. 2019). While changes in ecosystem states are a dynamic process (van de Leemput et al. 2016), in general, resilience and recovery of coral reefs will depend on the reversibility of seaweed blooms postdisturbance, with grazing herbivores deemed particularly critical (Arthur et al. 2006, Bellwood et al. 2006a, Hughes et al. 2007b, Diaz-Pulido et al. 2009, Adam et al. 2011, 2015b, Doropoulos et al. 2013, Bonaldo et al. 2014, Mumby et al. 2014, Bennett et al. 2015, Graham et al. 2015). Effective herbivore management through herbivore management areas (HMAs) is an emerging resilience-building tool in response to widespread and severe coral bleaching events (Chung et al. 2019).

Sponge-dominated reefs may increase in occurrence in a future ocean (Norstrom et al. 2009, Gonzalez-Rivero et al. 2011, Pawlik 2011, Bell et al. 2013, Easson et al. 2014, Farnham & Bell 2018), although for *Cliona*, the most abundant bioeroding sponges on the GBR, densities and benthic cover have not increased, and trends are likely to be site specific (Ramsby et al. 2017). Interestingly, phototrophic sponges appear to be more resilient to ocean warming and acidification than their heterotrophic counterparts, which may influence community structures towards phototrophic species (Bennett et al. 2017, 2018). Stark increases in the density of the colonial ascidian, *Didemnum molle*, have also been documented following warming and widespread coral bleaching on the GBR, perhaps linked to reduced competition for space and nutrients and/or reduced predation pressure (Tebbett et al. 2019). It will be increasingly important to determine the competitive relationships between non-coral phase shift drivers (e.g. algae, sponges, ascidians) and how they alter trophic pathways and energy flows on future coral reefs (Norstrom et al. 2009, Maldonado et al. 2015, Bell et al. 2018, Tebbett et al. 2019).

For other marine invertebrates, additive stress from corallivorous gastropods (e.g. *Drupella*) and sea stars (e.g. CoTS, *Culcita*) through coral predation may reduce the resilience and recovery of corals to climate change stressors (Bruckner et al. 2017, Shaver et al. 2018, Bruckner & Coward 2019, Keesing et al. 2019). Marine worms were not considered vulnerable to any stressor, except for *Spirobranchus* to ocean warming, owing to its dependence on live coral substrate and a range of coral-host associations (Strathmann et al. 1984, DeVantier et al. 1986, Dai & Yang 1995, Ben-Tzvi et al. 2006, Rowley 2008), though increased water circulation close to the coral surface as caused by *Spirobranchus* may decrease host susceptibility to bleaching (Strathmann et al. 1984), as posited for other coral-associated groups (Chase et al. 2018).

*Ocean warming*

Marine organisms are more vulnerable to warming than terrestrial taxa, making increasing ocean temperatures one of the most broadly confronting contemporary stressors (Richardson & Schoeman 2019). The effects of warming on coral reefs are most pronounced, as tropical species already exist within narrow thermal tolerance ranges at their upper limits (Hoegh-Guldberg 1999, Pörtner & Farrell 2008, Pandolfi et al. 2011, Hoey et al. 2016a). While there are high levels of variability in species responses and tolerances to climate change stressors, changing temperature regimes

are likely to have significant impacts on species ranges, reproduction, physiology, taxonomy and diversity, productivity and functioning.

Recent temperature-induced bleaching events have had catastrophic impacts on coral reefs globally. On the GBR, back-to-back warming anomalies over 2016 and 2017 resulted in mass bleaching and mortality of corals, particularly in the northern sections of the reef, where coral cover decreased by >80% (Hughes et al. 2017b, 2018b). This has contributed to significant alterations to whole-reef community structure and patterns of reproduction and recruitment (Hughes et al. 2018b, 2019a, Stuart-Smith et al. 2018).

Host-associated phototrophic microbes and most coral groups rated among the most vulnerable to ocean warming (Table 5). Thermal sensitivity of the coral holobiont is well established, with the expulsion of microbial symbionts from the coral host following extended exposure to warm conditions (Brown 1997, Fitt et al. 2001, Bourne et al. 2008, 2016, Baird et al. 2009). This results in a range of physiological and ecological impacts on corals – the coral bleaching phenomenon – with similar effects on other zooxanthellate-host organisms, including tridacnid clams (Buck et al. 2002, Leggat et al. 2003), sponges (Vicente 1990), sea anemones (Lesser et al. 1990) and algal species including CCA (Anthony et al. 2008). Bleaching impairs the transfer of nutrients from the zooxanthellae to the host, impacting tissue development, skeletal growth, biomass, fecundity and autotrophy while increasing susceptibility to disease and host mortality (Szmant & Gassman 1990, Glynn 1996, LeTissier & Brown 1996, Fitt et al. 2001). Yet the relative abundance and local adaptation of particular *Symbiodinium* cells (e.g. Clade D) can increase thermal tolerance in their coral hosts (Howells et al. 2012, 2013, Stat et al. 2013, Bay et al. 2016, Barfield et al. 2018).

Specific coral species and morphologies are documented to be more heavily impacted by ocean warming, with branching and tabular groups (acroporids, pocilloporids) typically most prone to bleaching (Gleason 1993, Baird & Marshall 1998, 2002, Marshall & Baird 2000, Obura 2001, McClanahan et al. 2004, Adjeroud et al. 2005, Thompson & Dolman 2010, Kennedy et al. 2018). Yet these faster-growing corals are critical to postbleaching recovery (Adjeroud et al. 2009, Linares et al. 2011, Ortiz et al. 2014, 2018), and there may be some resilience to the coral bleaching phenomenon through thermally tolerant zooxanthellae and microbiomes (Berkelmans & van Oppen 2006, Epstein et al. 2019b), switches to heterotrophic feeding (Grottoli et al. 2006, Ferrier-Pages et al. 2011), intraspecies resilience across life stages (Putnam et al. 2010, Alvarez-Noriega et al. 2018) and adaptive responses owing to genomic history (Howells et al. 2013, Bay & Palumbi 2015, Dixon et al. 2015, Quigley et al. 2018). High levels of connectivity, most notably in the south poleward direction, along the GBR may facilitate the genetic migration and spread of warmer heat-tolerant alleles to higher latitudes as the climate warms (Poloczanska et al. 2013, Matz et al. 2018).

### Ocean acidification

Changes in ocean chemistry (e.g. pH and carbonate ions) are attributable to increased anthropogenic $CO_2$ in the atmosphere and corresponding $CO_2$ dissolved by the world's oceans (Kleypas et al. 1999, Caldeira & Wickett 2005, Orr et al. 2005). Resultant decreases in seawater pH and the reduced availability of carbonate ions will directly impair the ability for calcifying organisms to develop their skeletons and shells, including for corals (Hoegh-Guldberg 2005, Przeslawski et al. 2008, De'ath et al. 2009, Anthony et al. 2011b, Fabricius et al. 2011, Wild et al. 2011, Connell et al. 2013, Dove et al. 2013). Coral reefs are among the most sensitive ecosystems to changes in ocean chemistry, as they are fundamentally dependent on calcification to support both habitat and production functioning (Hoegh-Guldberg 2005, Anthony et al. 2011b, Albright et al. 2016a).

CCA ranked as the most vulnerable algal group to climate change stressors, while other algae may benefit from waters higher in temperature (warming) and $CO_2$ (acidification), with a competitive advantage over corals (Diaz-Pulido & McCook 2002, Diaz-Pulido et al. 2007, 2009, 2011b), though this is not the case for all macroalgae (Bender et al. 2012, 2014a). CCA may even be more sensitive

than some corals, exhibiting greater skeletal dissolution due to its high magnesium-calcite carbonate form, and reduced productivity, diversity, growth and survival when exposed to ocean acidification and/or warming (Anthony et al. 2008, Nelson 2009, Diaz-Pulido et al. 2012, Ordonez et al. 2014, McCoy & Kamenos 2015, Cornwall et al. 2019). Variability in natural conditions as driven by diel cycles (particularly in the intertidal) may heighten the sensitivity of CCA to decreases in ocean pH, converse to that suggested for organisms exposed and adapted to naturally extreme conditions (Camp et al. 2018a, Johnson et al. 2019). For example, it is suggested that large benthic Foraminifera show varied responses to ocean change stressors due to their exposure to extreme conditions in shallow-water intertidal environments (Fujita et al. 2011, Doo et al. 2014, Schmidt et al. 2014, 2016, Prazeres et al. 2015). However, any impact on the ability for foraminiferans to calcify will have long-term impacts on reef carbonate dynamics and sediment processes (Dawson et al. 2014).

Records of skeletal growth of massive *Porites* corals indicate a measurable decrease in coral calcification on the GBR over the past few decades (De'ath et al. 2009, 2013) but with high spatial and temporal variability in trends (D'Olivo et al. 2013) and potentially just reflecting short-term responses to thermal stress events (Cantin & Lough 2014). Reduced calcification rates have also been reported for a range of branching corals on the GBR and elsewhere, including for acroporids and pocilloporids (Manzello 2010, Pratchett et al. 2015, Anderson et al. 2017, 2018) and in total carbonate budgets (Case Study 2). Structural branching coral forms are possibly more vulnerable to ocean acidification than robust massive forms (Fabricius et al. 2011, Madin et al. 2012). There are also notable changes in the diversity of the coral microbiome under acidified conditions, which may have concomitant implications for reef structure, recruitment and total functioning (Mouchka et al. 2010, Krause et al. 2012, Doropoulos & Diaz-Pulido 2013, Webster et al. 2013a,b, 2016, Grottoli et al. 2018, Wee et al. 2019). However, the coral microbiome can enhance the transgenerational adaptive plasticity of corals in support of reef adaptation and resilience (Torda et al. 2017, Webster & Reusch 2017).

Coral reefs may switch to a state of net dissolution in the coming decades due to changes in ocean temperature and chemistry, with significant impacts on net ecosystem calcification (Silverman et al. 2012, 2014, Albright et al. 2013, 2018, Kennedy et al. 2013, Cyronak et al. 2018, Eyre et al. 2018, McMahon et al. 2019), sediment dynamics (Eyre et al. 2014, Cyronak & Eyre 2016) and reef recovery (Osborne et al. 2017). On Lizard Island, GBR, net ecosystem calcification decreased by ∼46% between 2009 and 2016, measured immediately after extensive coral bleaching (McMahon et al. 2019). Parallel to decreases in calcification, bioerosion rates are accelerating in line with ocean change, which is itself emerging as a significant stressor in terms of reef health and future reef resilience (Reyes-Nivia et al. 2013, DeCarlo et al. 2015, Manzello et al. 2017, Schönberg et al. 2017). The total carbonate budget across the GBR may soon be in a state of net dissolution and erosion, as may already be the case for some reefs (Case Study 2). This trajectory indicates that the GBR may enter a critical negative state in which erosive processes surpass carbonate accretion in a changing ocean, with critical impacts on habitat and production functioning, as suggested for other reefs (Kennedy et al. 2013, Manzello et al. 2017). However, the ability for some bioeroding organisms, like clionid sponges, to persist in a future ocean may also be impacted (Achlatis et al. 2017, Fang et al. 2018, Ramsby et al. 2018a).

Most marine invertebrate groups rated as highly vulnerable to the impacts of ocean warming and acidification (Table 5), with an abundance of research and reviews documenting survival bottlenecks across life-history stages, particularly for calcifying marine larvae and adults (Przeslawski et al. 2008, Byrne 2011, Bhadury 2015, Przeslawski et al. 2015, Espinel-Velasco et al. 2018). Tropical sea urchin larvae are considered among the most vulnerable (Byrne et al. 2013). Unsurprisingly, calcifiers were considered the most vulnerable to ocean acidification here (Table 5). Yet the effects of ocean acidification and the energetic stress of hypercapnia extend well beyond the calcification process, being observed to cause a range of sensory, cognitive and behavioural abnormalities across reef invertebrate and fish life histories (Munday et al. 2009a, 2012, 2014, Briffa et al. 2012, Devine

et al. 2012, Domenici et al. 2012, Allan et al. 2013, Watson et al. 2014, 2017, Ferrari et al. 2017, Jarrold et al. 2017, Espinel-Velasco et al. 2018), as well as altered predatory-prey dynamics (Munday et al. 2010, Allan et al. 2013, Heinrich et al. 2016, Watson et al. 2017, Spady et al. 2018). Ocean acidification will also impact settlement success on coral reefs through changes in the nature and distribution of suitable settlement cues and substrates, including CCA and biofilm (Doropoulos et al. 2012a, Doropoulos & Diaz-Pulido 2013, Espinel-Velasco et al. 2018).

Ocean acidification may even enhance certain processes, including bioerosion rates (Reyes-Nivia et al. 2013, Enochs et al. 2015, Schönberg et al. 2017), with potential impacts on reef carbonate budgets (Wisshak et al. 2014, Manzello et al. 2017). Light intensity may work to ameliorate the negative effects of acidification on photosynthesising species like corals (Dufault et al. 2013, Wall et al. 2017) and giant clams (Watson 2015). Tropical deposit-feeding sea cucumbers may partially mediate or buffer the impacts of ocean acidification through their bioturbation activity and contributions to reef biogeochemistry (Schneider et al. 2011, 2013, Wolfe et al. 2018). This has been posited for the mega-consumer and excreter of coral carbonates *Bolbometopon muricatum* (Goldberg et al. 2019), but this remains poorly addressed for parrotfishes in general. Seagrasses, macroalgae and a range of other species may also contribute to the biogenic buffering of reef carbonate chemistry owing to their relative roles in the balance between photosynthesis (i.e. $O_2$ production) and respiration (i.e. $CO_2$ production) (Anthony et al. 2011a, McCulloch et al. 2012, Smith et al. 2013, Cornwall et al. 2014, Mongin et al. 2016a, Page et al. 2016, DeCarlo et al. 2017). This presents a potential management strategy through *in situ* cultivation of macroalgae (Mongin et al. 2016a).

## Cyclones

While tropical cyclones and storms are not expected to increase in occurrence in a changing climate, they are predicted to increase in severity (Lough 2007). The likelihood of more intense cyclones within timeframes of coral recovery by the mid-century presents significant global threat to coral reefs and those that depend on them (Cheal et al. 2017). Cyclones were suggested to have the strongest impact on sessile marine invertebrates: branching corals (tabular, staghorn, other species), sponges (heterotrophic, phototrophic) and giant clams (Tridacnidae) (Table 5). Zooplankton scored low, yet cyclone and storm events can drive homogenisation of zooplankton communities with potential knock-on effects to higher trophic levels (McKinnon et al. 2003). At the whole-reef scale, mean rates of coral loss on the GBR are projected to be $-0.67\%$ $y^{-1}$, largely attributed to cyclone damage (Mellin et al. 2019). At the colony level, morphology plays an important role in the biophysical impacts of cyclones, which are often most severe for fragile branching corals compared to robust massive forms (Woodley et al. 1981, Connell et al. 1997, Hughes & Connell 1999, Adjeroud et al. 2005, Madin 2005, Madin & Connolly 2006, Madin et al. 2014).

The long-term effects of cyclones (i.e. habitat degradation) may have the greatest impact on coral reef fishes and fisheries production (Cheal et al. 2002), but impacts will vary across communities depending on species, depth ranges and exposure gradients (windward, protected) (Ceccarelli et al. 2016). Site-attached reef fishes (e.g. cryptobenthics, damsels, planktivores, cleaner wrasse) scored as the most vulnerable fish groups to cyclones (Table 5). Small fish species that rely on corals for survival may be particularly vulnerable to the habitat loss and increased predation pressure attributed to cyclone damage (Lassig 1983, Harmelin-Vivien 1994, Coker et al. 2009, Ceccarelli et al. 2016). Conversely, resident predatory fishes, which also depend on coral habitat, may be largely resilient to a range of environmental disturbances on the GBR (Emslie et al. 2017). Damselfish assemblages have generally been well retained within their respective regional settings on the GBR, with assemblage degradation only associated with major coral losses (Emslie et al. 2019). Operating on site-specific cleaning stations, cleaner wrasse populations were documented to decline by 80% following a sequential cyclone and El Niño (warming) event on Lizard Island, GBR (Triki et al. 2018). Following extensive habitat loss due to tropical Cyclone Ita, some invertivorous fishes increased in biomass (the titan triggerfish [*Balistoides viridescens*], darkspot tuskfish [*Choerodon monostigma*]

and sidespot goatfish [*Parupeneus pleurostigma*]), suggesting they may benefit from novel resources made available for exploitation postdisturbance (Brandl et al. 2016). Grazing fishes (e.g. detritivores, parrotfishes) may help to maintain fish diversity postdisturbance on some reefs (Wilson et al. 2009, Ceccarelli et al. 2016).

*Fisheries*    Ultimately, management of climate change stressors depends on fast action towards a low-carbon economy, but this must be augmented with local action to prevent degradation of reef structures and associated losses of ecosystem functioning and services (Kennedy et al. 2013, Albright et al. 2016a, Cinner et al. 2016). Overfishing is considered one of the greatest local threats to coral reefs (Jackson et al. 2001, Garcia & Moreno 2003, Bellwood et al. 2004, Newton et al. 2007, Cinner et al. 2016, 2018). Our partitioning of species here to broader taxonomic and functional levels does not fully encapsulate species-specific vulnerabilities to overfishing but rather the groups most broadly at risk. Impacts from fishing were greatest for predatory reef fishes (resident and transient) and for deposit-feeding sea cucumbers (Table 5). While fishing intensity is relatively low at regional scales, commercial fisheries have increased in effort (~40%) and catch (~50%) since the 1990s (Mapstone et al. 2004). Regardless, fin-fish fisheries are generally well managed on the GBR (Williamson et al. 2004, DEE 2017), with reef resilience enhanced through marine park zoning (Mellin et al. 2016). Unlike on other reefs globally, the fishing of herbivores is marginal on the GBR.

The primary fin-fish species targeted on the GBR is the coral trout (*Plectropomus* spp.), considered here as a resident piscivore. An estimated 749 tonnes of coral trout are commercially harvested from the GBR each year, with >100,000 additional individuals harvested by recreational spear and line fishers annually (DEE 2017). Globally, many *Plectropomus* populations are in decline due to the combined effects of overfishing and habitat degradation (Frisch et al. 2016a). On the GBR, coral trout, and a range of other predatory fishes, benefit from no-take zones through increases in biomass, density and size compared to sites open to fishing (Williamson et al. 2004, Heupel et al. 2009, Miller et al. 2012, Emslie et al. 2015, Casey et al. 2017, Castro-Sanguino et al. 2017, Frisch & Rizzari 2019), including in the context of recreational spearfishing (Case Study 3). No-take reserves also preserve the natural behaviour of coral trout, with potential influences on genetic and social structures (Bergseth et al. 2016). In a global context, the status of *P. leopardus* was recently re-evaluated from a Near Threatened to a Least Concern species (Choat & Samoilys 2018), and its fishery on the GBR is well monitored and managed (DEE 2017). For some larger target species, such as sharks, illegal harvest in no-take zones may continue to have significant impacts on population structures (Stevens et al. 2000, Davis et al. 2004, Robbins et al. 2006, McCook et al. 2010, Bergseth et al. 2017, Weekers & Zahnow 2018, Frisch & Rizzari 2019). The Queensland shark control programme also contributes to the extraction of these predators, with around 500–700 sharks removed from Queensland waters each year (QGSO 2019). There has been a regional depletion of shark populations over the past half-century since the onset of this control programme, with concurrent declines in body size and probability of encountering mature individuals, suggesting sharks on the Queensland coastline are more vulnerable to exploitation than previously thought (Roff et al. 2018).

Deposit-feeding sea cucumbers are particularly prone to overfishing due to their ease of collection and general lack of scientific information on their biology and ecology to empower management (Uthicke et al. 2004, Purcell et al. 2013). The sea cucumber (bêche-de-mer) fishery currently operating on the GBR has a history of exploitation, with trends of sequential population declines across species with high market value (Eriksson & Byrne 2015), and continued occurrence of illegal harvest inside the Marine Park bounds (Conand 2018). In 2004, a rotational harvest scheme was implemented as a management tool, but concerns have been raised regarding its effectiveness, as recovery of depleted populations may still be marginal, and caches of high-valued species continue to decline (GBRMPA 2014b, Purcell et al. 2016b). At least ten sea cucumber species found on the GBR are listed as Vulnerable to Extinction on the IUCN Red List for Threatened Species (Conand et al. 2014, Purcell

**CASE STUDY 3: FUNCTIONAL IMPACTS OF RECREATIONAL SPEARFISHING ON THE GREAT BARRIER REEF**

*Thea Bradford, Kennedy Wolfe, Peter Mumby*

Of the recreational fishing methods, spearfishing is a small but contentious component (Godoy et al. 2010, Young et al. 2015). Given the well-documented impacts of line fishing from discarded pollution, lost gear, the requirement of bait and frequent levels of bycatch, spearfishing may be considered the more sustainable practise (Frisch et al. 2008). Yet in a comparison between line and spearfishers on the GBR, despite a similar catch composition and landing fewer fish overall, the mean size of fish caught by spearfishers was significantly greater (Frisch et al. 2008). Spearfishing is a highly selective method where participants can target specific individuals based on species and size, with limited impacts on non-target species (Dalzell et al. 1996, Bejarano et al. 2014). So, while spearfishing may have a seemingly smaller impact on the marine environment, selectivity towards large individuals (that are likely fecund) and particular trophy species may result in negative impacts to viable breeding stocks (Hughes et al. 2007a, Meyer 2007, Frisch et al. 2008, 2012, Godoy et al. 2010). For example, just three years after the introduction of spearfishing on an inshore reef near Townsville, vast decreases in the number (54%) and size (27%) of coral trout (*Plectropomus* spp.) – the primary fisheries target on the GBR – were recorded (Frisch et al. 2012). There is potential for recreational line and spearfishing to have broadly equivalent impacts on the marine environment (Frisch et al. 2008), but the lack of information on spearfishing often causes it to be overlooked in fisheries management (Johansson et al. 2013, Pavlowich & Kapuscinski 2017), as for recreational fishing in general.

A survey of over 140 spearfishers active on the GBR was conducted to determine which functional groups of coral reef fishes were preferred by spearfishers. From a list of 22 common GBR fishes (Table CS3.1), spanning nominal herbivores ($n = 8$), invertivores ($n = 3$) and piscivores ($n = 11$), coral trout (*Plectropomus* spp.) were outlined as the preferred targets (Figure CS3.1), as in recreational line-based and commercial fisheries on the GBR (Leigh et al. 2014, DEE 2017). The coral trout fishery on the GBR is considered well managed (DEE 2017), which is reflected in the recent re-evaluation of this group from Near Threatened to Least Concern (Choat & Samoilys 2018). Nominally piscivorous species (including Lutjanidae, Lethrinidae and *Plectropomus*) represented ∼75% of the preferred catch of spearfishers, while nominal herbivores were lesser preferred (Figure CS3.1). This may be associated with the campaign aimed at spearfishers to limit herbivore catches on the GBR to protect species that reduce algal growth and support reef health and functioning (GBRMPA 2016, 2018a). Tuskfishes (*Choerodon* spp.) were the preferred invertivores (Figure CS3.1), which are broadly distributed across the GBR (Platten et al. 2002, Fairclough et al. 2008). As a Near Threatened and monandric protogynous hermaphroditic species where males only occur in the largest size bracket (Fairclough & Nakazono 2004), the black-spot tuskfish (*C. schoenleinii*) may be particularly vulnerable to the selectivity of spearfishing. Interestingly, the venus tuskfish (*C. venustus*) can alter its sex ratio in response to overfishing (Platten et al. 2002). Regardless, the reproductive biology of tuskfishes has resulted in rapid population declines on other coral reefs owing to overfishing (Ebisawa et al. 1995, Cornish 2003, Fairclough & Nakazono 2004).

While spearfishing has the potential to impact viable fish stocks (Hughes et al. 2007a, Meyer 2007, Frisch et al. 2008, 2012, Godoy et al. 2010), the Queensland (and Australian) spearfishing community has been highly responsive to previous management campaigns and exhibits self-regulatory and monitoring approaches that are vital to fisheries conservation and advocacy

Table **CS3.1** List of species included in surveys of spearfishers operating on the GBR

| Family | Species | Common names | Guild | IUCN listing | Size at maturity (cm) | Max size (cm) | Legal catch size (cm) | Legal bag limit | References |
|---|---|---|---|---|---|---|---|---|---|
| Acanthuridae | *Acanthurus dussumieri* | Eyestripe surgeonfish | H | LC | N/A | 54 | 25 | 5 | DeMartini et al. (2014) |
| | *Naso unicornis* | Bluespine unicornfish | H | LC | 30–35 | 70 | 25 | 5 | |
| Scaridae | *Bolbometopon muricatum* | Green humphead parrotfish | H | V | 65 | 130 | 25 | 5 | Chan et al. (2012) |
| | *Cetoscarus bicolor* | Bicolour parrotfish | H | LC | 30 | 50 | 25 | 5 | |
| | *Chlorurus bleekeri* | Bleeker's parrotfish | H | LC | N/A | 49 | N/A | N/A | Barba (2010) |
| | *microrhinos* | Steephead parrotfish | H | LC | 37 | 70 | N/A | N/A | Mellin et al. (2007) |
| | *Scarus ghobban* | Blue-barred parrotfish | H | LC | 41 | 90 | 25 | 5 | Longenecker et al. (2014) |
| Siganidae | *Siganus lineatus* | Goldlined rabbitfish | H | LC | 19–24 | 43 | N/A | N/A | Fairclough & Nakazono (2004) |
| Labridae | *Choerodon schoenleinii* | Black-spot tuskfish | I | NT | 25 | 100 | 30 | 6 | |
| | *venustus* | Venus tuskfish | I | LC | 24 | 65 | 30 | 6 | Platten et al. (2002) |
| Lethrinidae | *Monotaxis grandoculis* | Bigeye seabream | I | LC | 27.5 | 60 | 25 | 5 | |
| | *Lethrinus miniatus* | Redthroat emperor | P | LC | 36.1 | 90 | 38 | 8 | |
| | *xanthochilus* | Yellowlip emperor | P | LC | 42.4 | 70 | 25 | 5 | Carpenter et al. (2016) |
| Lutjanidae | *Aprion virescens* | Green jobfish | P | LC | 44.9 | 112 | 38 | 5 | |
| | *Lutjanus argentimaculatus* | Mangrove jack | P | LC | 57 | 150 | 35 | 5 | |
| | *johnii* | Golden snapper | P | LC | 44 | 97 | 35 | 5 | Kamali et al. (2006) |
| | *rivulatus* | Maori seaperch | P | LC | 40 | 80 | 25 | 5 | Longenecker et al. (2014) |
| | *sebae* | Red emperor | P | LC | 54.2 | 116 | 55 | 5 | |
| | *Macolor niger* | Black and white snapper | P | LC | 38 | 75 | 25 | 5 | Longenecker et al. (2014) |
| Serranidae | *Epinephelus cyanopodus* | Purple cod (Blue Maori) | P | LC | 31–35 | 122 | 38 | 5 | Lau & Parry Jones (1999) |
| | *Plectropomus leopardus* | Coral trout | P | LC | 32–17 | 120 | 38 | 7 | Choat & Samoilys (2018) |
| Rachycentridae | *Rachycentron canadum* | Cobia | P | LC | 75 | 200 | 70 | 2 | Babatunde et al. (2018) |

*Notes:* Data obtained from the online FishBase resource, unless otherwise stated. Legal limit data are taken from the Department of Agriculture and Fisheries, Queensland Government.

*Abbreviations:* H, herbivore; I, invertivore; P, piscivore; LC, least concern; V, vulnerable; NT, near threatened; N/A, data not available.

Pie chart legend:
- Herbivores (8)
- *Choerodon* (2)
- Other invertivores (1)
- *Plectropomus* (1)
- Other piscivores (10)
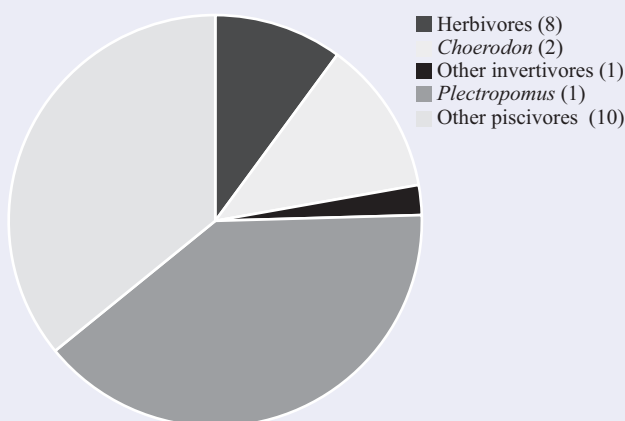
**Figure CS3.1**   Contribution of select coral reef fishes to the estimated catch of spearfishers active on the GBR. Number of species in each group in parentheses.

(Young et al. 2014, 2016, GBRMPA 2016). We highlight the importance of 1) educating groups on spearfishing-selectivity for species with vulnerable reproduction (e.g. coral trout, tuskfishes) and 2) monitoring catch trends for key species within the spearfishing community to inform self-regulation. Quantitative data on catch sizes, target species and catch per unit effort are needed, particularly for target species and those with vulnerable reproductive biology.

et al. 2014, Richards & Day 2018) and three species of teatfish are proposed to be listed in CITES Appendix II (Di Simone et al. 2019). There is particular concern for the black teatfish (*Holothuria whitmaei*), as its fishery, which was closed in 1999 due to widespread overharvest (Uthicke et al. 2004, Eriksson & Byrne 2015), may be reopening (DAF 2018) without fisheries-independent data to indicate whether populations have recovered. Quantitative information on bêche-de-mer populations along and across the GBR is imperative to inform management independent of fisheries.

Interestingly, no other group scored as vulnerable to fisheries. A range of fishing-related impacts are documented on the GBR, resulting from derelict fishing gear that can entangle corals and increase disease susceptibility (Williamson et al. 2014a), anchor and vessel damage (Beeden et al. 2014a, Kininmonth et al. 2014), frequent by-catch from commercial fisheries (Hill & Wassenberg 2000) and illegal practises in no-take zones (Davis et al. 2004, Arias & Sutton 2013, Williamson et al. 2014a, Bergseth et al. 2015, Weekers & Zahnow 2018). The impact of recreational spearfishing is assessed in detail in Case Study 3. We acknowledge that assessment beyond the broad taxonomic and functional groups examined here is necessary to determine specific impacts from fisheries on the GBR. It will also be important to assess fisheries operating outside of coral habitat, including soft-bottom, interreefal, coastal and intertidal habitats where many commercially important invertebrates on the GBR are targeted, including prawns and scallops (Gribble 2003, Courtney et al. 2008, 2015, GBRMPA 2014b). Future work should also consider social, cultural and economic values of fisheries targets on the reef.

*Population outbreaks*   There are a range of species, particularly non-coral marine invertebrates, that exhibit marked population fluxes on coral reefs (Norstrom et al. 2009). The boom-and-bust phenomenon of the Echinodermata is well documented (Uthicke et al. 2009). On the GBR, outbreaks of *Acanthaster* cf. *solaris* (CoTS) are the most extensive, destructive and researched outbreak candidate, gaining considerable traction in reef management (Westcott et al. 2016, Sweatman &

Cappo 2018). As scored here, population outbreaks (namely in consideration of CoTS) were outlined to have the greatest potential impact on tabular, staghorn and other branching corals (Table 5). *Acropora* and *Montipora* are the preferred coral genera of CoTS across the Pacific (Laxton 1974a, Pratchett et al. 2014, Westcott et al. 2016), though even the less-preferred coral species are consumed during extreme outbreaks or when food is scarce (Chesher 1969, Pearson & Endean 1969). At the whole-reef scale, corallivory by CoTS in outbreak densities has been attributed to ~42% of the declines in live coral cover on the GBR (De'ath et al. 2012). However, this statistic is likely to be much lower at present in light of extensive coral bleaching in 2016 and 2017 (Hughes et al. 2017b, 2018b,c).

Outbreaks of other marine invertebrates have received considerably less attention on the GBR and in general. High densities of *Drupella* sp. (Muricidae) can have significant impacts on reef condition, documented to reduce live coral cover by >75% on some reefs (Turner 1994, Scott et al. 2017a). Their effects can be even more significant following bleaching-induced coral mortality, which can impact coral resilience and recovery (Bruckner et al. 2017, Keesing et al. 2019), similar to other corallivorous gastropods, including *Coralliophila* (Muricidae) (Shaver et al. 2018) and *Dendropoma* (Vermetidae) (Smalley 1984, Shima et al. 2010). While these gastropods are present on the GBR, such extensive impacts have not been documented (Cumming 2009). Stark increases in the density of the colonial ascidian *Didemnum molle* were recently documented on Lizard Island following pervasive coral bleaching (Tebbett et al. 2019). While corallivorous species like CoTS and *Drupella* have direct impacts on the persistence of corals through predation, rapid expansions of opportunistic sessile organisms, like these ascidians, can impact reef recovery and resilience through competition for food and space and potential toxicity (Bak et al. 1996, Tebbett et al. 2019). Even at highly localised scales, population outbreaks of alternative opportunistic invertebrates, including sea cucumbers and sea stars, can have repercussions on coral recruitment, recovery and functioning (Zhang et al. 2018, Bruckner & Coward 2019). Ecosystem states are dynamic in terms of time and space (van de Leemput et al. 2016), and phase shifts beyond the typical coral-algal model are increasingly common as reefs degrade (Norstrom et al. 2009).

In general, there has been little documentation of extensive impacts from invasive or introduced species in the marine environment of the GBR, with a greater representation and impacts documented for mainland and island habitats (GBRMPA 2014b).

*Diseases*    Diseases are poorly understood for corals and other marine species on the GBR, despite documentation of widespread proliferation in some cases (Richardson 1998, Willis et al. 2004, Roff et al. 2011, Shore & Caldwell 2019). Disease proliferation in other marine environments is a portent of the devastating impacts and rapid rate of spread that can occur, including the *Diadema* die-off in the Caribbean (Hughes 1994, Mumby et al. 2006b, Feehan & Scheibling 2014) and sea star wasting disease on the US west coast (Bates et al. 2009, Hewson et al. 2014, Eisenlord et al. 2016, Montecino-Latorre et al. 2016). While expert scores were considerably lower for disease than for a number of other stressors, acroporids (tabular and staghorn) rated as the most vulnerable to disease (Table 5). White Syndrome primarily impacts tabular acroporids compared to other coral species and functional forms (Hobbs & Frisch 2010, Hobbs et al. 2015). Coral disease can reduce net growth rates of corals, particularly tabular acroporids, by ~20% (Roff et al. 2008, Maynard et al. 2011).

In the marine environment, disease proliferation is largely induced by temperature anomalies (Bruno et al. 2007, Harvell et al. 2007, Sato et al. 2009, 2011, 2016, Maynard et al. 2011, Ruiz-Morenol et al. 2012, van de Water et al. 2016, Chen et al. 2017) but can also be expedited by plastic pollution (Lamb et al. 2018), runoff and sedimentation (Haapkyla et al. 2011, Pollock et al. 2016), cyclone damage (Sato et al. 2018), tourism (Lamb & Willis 2011, Lamb et al. 2014, van de Water et al. 2015) and fisheries activity (Diaz-Pulido et al. 2009, Page et al. 2009, Graham et al. 2011a, Williamson et al. 2014a, Lamb et al. 2015, 2016). While the transmission of coral disease between individuals and among populations remains understudied (Shore & Caldwell 2019), it seems that

any considerable stressor can enhance disease susceptibility on coral reefs, particularly inshore on the GBR (MacNeil et al. 2019). Disease management on the GBR focuses on continued research and monitoring of disease outbreaks to inform local response plans (Maynard et al. 2011, Beeden et al. 2012). To date, it seems that Australia's biosecurity strategies regarding terrestrial, agricultural and human-based diseases typically receive greater attention in contingency planning (Craik et al. 2017).

*Water quality*    Water quality stressors (nutrients, sediments, pollutants) were not considered severe threats in the context of offshore reefs (Table 6), assumedly driven by low exposure at distance from the coastline. This is most likely because the three water quality stressors assessed here are closely related to aeolian processes. Water quality scores did not consider impacts from other sources of pollution, including shipping, noise pollution, plastics and oil and gas. Broader consideration of these pollution types should be considered in future work. When assessed in context of nearshore reefs, nutrients, sediments and pollutants were considered to have greater impacts across our functional groups (Table 6).

Declining water quality is considered one of the greatest threats to the long-term health of the GBR but most critically for inshore reefs (Brodie & Waterhouse 2012, Lam et al. 2018, MacNeil et al. 2019). While consistent exposure to poor water quality may render inshore reefs more resilient (Browne 2012, Perry et al. 2012b), they typically exhibit slower rates of growth and recovery (MacNeil et al. 2019, Mellin et al. 2019). Microbial groups scored among the most vulnerable to water quality stressors, particularly host-associated groups (Table 6). Microbes can be the first biological responders to environmental perturbation (Bourne et al. 2016, Glasl et al. 2017, 2018a), with populations that vary in response to external conditions (e.g. season, water quality) and habitat type (Kelly et al. 2014, Tout et al. 2014, Angly et al. 2016, Frade et al. 2016, Agusti et al. 2019). Such environmental parameters can drive the spatial distribution and temporal dynamics of pelagic microorganisms across different habitats of the GBR (Case Study 4).

Spatially, nutrient (e.g. chlorophyll *a*) levels on the GBR typically increase from north to south and from outer to inner coastal regions, supporting bottom-up processes from the plankton along these gradients (Skerratt et al. 2019). It appears that dissolved inorganic nitrogen, primary production, phytoplankton biomass and zooplankton grazing are elevated in La Niña years, driven by greater average winds, rainfall and river discharge (Skerratt et al. 2019). A range of species in the plankton (e.g. copepods, Appendicularia) are reported to increase in abundance on anthropogenically disturbed reefs, possibly due to increases in terrestrial runoff and nutrients (Carrillo-Baltodano & Morales-Ramirez 2016, Dupuy et al. 2016).

Sediment loads on inshore reefs were considered a significant stressor for many of the species examined here (Table 6), in line with the literature (Bainbridge et al. 2009, 2014, Brodie et al. 2013, Tsatsaros et al. 2013, Waterhouse et al. 2013). Only a small proportion of land-derived sediment reaches mid- to outer-reefs on the GBR (Bartley et al. 2014). Sediments can have a range of impacts on coral reef communities through elevated turbidity gradients, reduced light availability and the physical smothering of sessile organisms, and fine sediments typically have greater impacts on coral reefs than course sediments (Erftemeijer et al. 2012). On the GBR, macroalgal and bioeroding communities show a positive relationship with suspended sediment concentrations, contrasting the negative relationship observed for coral and CCA cover (Fabricius & De'ath 2001b, 2004, Fabricius et al. 2005, Hutchings et al. 2005, Bessell-Browne et al. 2017b). Sediments and high turbidity alter reef structure, reproduction, larval success, recruitment, bioerosion and species interactions on inshore reefs (Babcock & Davies 1991, Fabricius 2005, 2005, Hutchings et al. 2005), with extensive dredging activity posing considerable risk (Erftemeijer et al. 2012, Jones et al. 2016, Bessell-Browne et al. 2017a, Pineda et al. 2017b, Tebbett et al. 2017d).

Sessile and filter-feeding invertebrates are possibly most susceptible to sediment loads, including corals, sponges and giant clams (Elfwing et al. 2003, Przeslawski et al. 2008). However, some nearshore reefs appear resilient to turbidity, maintaining relatively rapid accretion rates and high

## CASE STUDY 4: MICROBIAL COMMUNITIES AS INDICATORS OF WATER QUALITY ON THE GREAT BARRIER REEF

*Pedro R. Frade, Nicole Webster, David Bourne*

Microorganisms are fundamental drivers of biogeochemical cycling in coral reef ecosystems (Gast et al. 1998, Bourne & Webster 2013b) and are critical to the health of keystone marine invertebrates, including corals (Bourne et al. 2016). The current lack of available microbial data collected at sufficient spatial and temporal resolution hinders our capacity to identify the contributions that microbes make to a functioning reef and reef resilience (Dinsdale et al. 2008). Faced with the growing impacts of rapid climate change (Hughes et al. 2017a, Osborne et al. 2017), identification of microbial taxa that contribute to a healthy reef is critical. This case study synthesises available information on pelagic microbial communities across GBR regions (Table CS4.1; Figure CS4.1). Relative microbial abundances were used to identify patterns in communities along inshore to offshore gradients in the context of riverine floodwaters and water quality plumes (Angly et al. 2016).

Pelagic microbial communities across the GBR respond in a deterministic way to environmental fluctuations and drivers. This means that microbial community dynamics can be modelled to better understand how ecosystem functioning can predict changes to reef health and redress knowledge gaps that may guide future interventions aimed at mitigating environmental stressors. For example, the cyanobacterial family Prochlorococcaceae is more common under oligotrophic conditions (offshore), while Synechococcaceae becomes increasingly dominant in nutrient-rich eutrophic waters (inshore) (Figure CS4.2) (Dinsdale et al. 2008). The relative abundance of these two groups varies between wet and dry seasons, as evidenced on the mid-shore Yongala reef, which switches from Prochlorococcaceae dominance to Synechococcaceae dominance in the wet season, likely owing to influence from terrestrial freshwater runoff (Figure CS4.2) (Dinsdale et al. 2008). These two photoautotrophic bacterial families have different capacities to use organic nitrogen (Scanlan & West 2002, Zubkov et al. 2003), and so the Prochlorococcaceae:Synechococcaceae relative abundance ratio can be used as an indicator for nutrient enrichment at a range of spatial and temporal scales (Figure CS4.2).

**Table CS4.1** Summary of published and unpublished microbial 16S rRNA data sets for the GBR; BPA = BioPlatforms Australia (https://data.bioplatforms.com/).

| Region | No. samples | No. locations | Rarefaction depth | Sequencing platform | Taxonomic assignment | Primer pair and refs | Reference |
|---|---|---|---|---|---|---|---|
| Tully | 78 | 7 | 250 | 454 | SILVA and Greengenes | pyroLSSU926F/ pyroLSSU1392R | Angly et al. (2016) |
| Burdekin | 48 | 3 | 25,000 | Illumina Miseq 2 × 300 | SILVA | 27F/519R | Glasl et al. (2019) |
| Coral Sea | 9 | 6 | 100,000 | Illumina Miseq 2 × 300 | SILVA | 27F/519R | BPA |
| Yongala (Burdekin) | 97 | 1 | 30,000 | Illumina Miseq 2 × 300 | SILVA | 27F/519R | BPA |
| Heron Island | 16 | 4 | 50,000 | Illumina Miseq 2 × 300 | SILVA | 515F/806Rb | Epstein et al. (2019a) |
| Mackay | 8 | 4 | 1,350 | 454 | GreenGenes | 63F/533R | Alongi et al. (2015) |

Another example of a microbial-based indicator exists in the ratio between Pelagibacteraceae and SAR86, which is negatively correlated with increasing nutrient levels. Levels of typical copiotrophs such as families OCS155, Flavobacteraceae, Cryomorphaceae and Rhodobacteraceae could be modelled against levels of oligotrophs such as Pelagibacteraceae and SAR86 to generate new indices indicative of eutrophication (e.g. Haas et al. 2016). Typical opportunistic bacteria, including those exhibiting virulence towards benthic organisms (e.g. in the families Rhodospirillaceae, Rhodobacteraceae and Vibrionaceae), could also be used as indicators of reef health and/or degradation. Microbial baselines could be used to assess impacts from coastal eutrophication, anthropogenic disturbance and climate change, as microorganisms represent the first responders to environmental change and may mitigate or exacerbate the impacts of disturbance for higher trophic levels. How microbial assemblages translate to changes in benthic composition (macroalgal versus coral cover) and reef health requires attention (Glasl et al. 2019). Establishment of microbial baselines through a network of microbial observatories spanning key habitats along inshore to offshore gradients in the northern, central and southern GBR would enable a robust assessment of the microbial contribution to reef functioning and health.
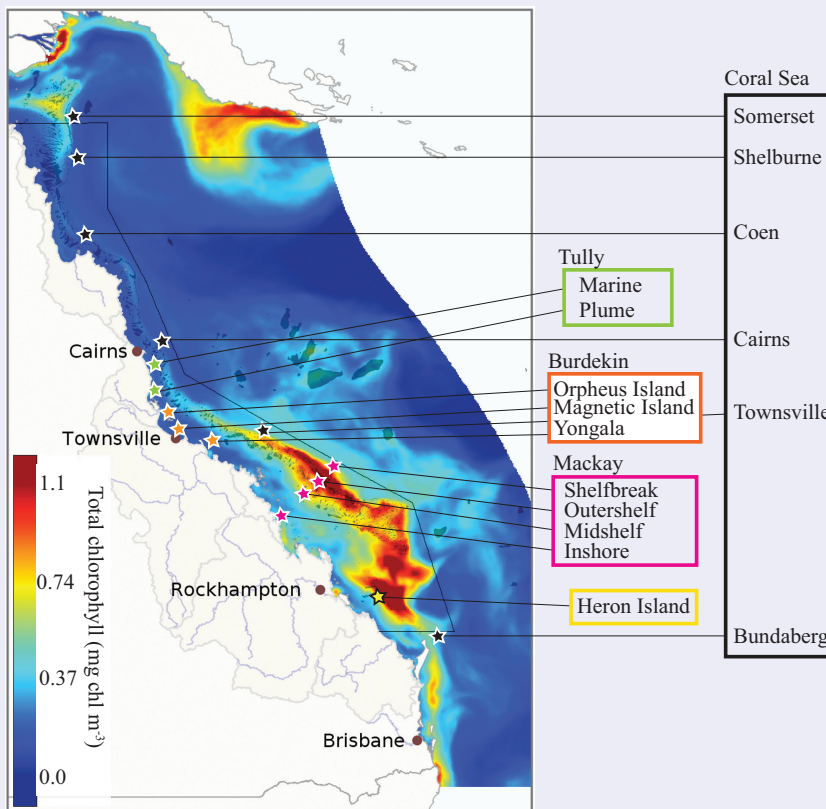


**Figure CS4.1**   Regions and locations on the GBR covered in the literature for pelagic microbial data sets (see Table CS4.1). Chlorophyll data obtained from eReefs (June 2016) (CSIRO GBR4 Hydrodynamic Model v2.0), with online map generation by AIMS.
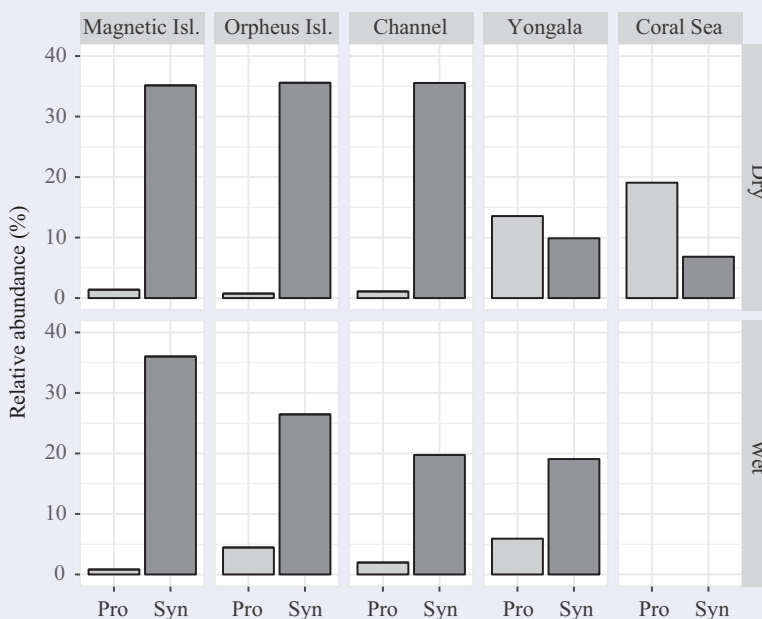
**Figure CS4.2** Relative abundance of the cyanobacteria Prochlorococcaceae (Pro) and Synechococcaceae (Syn) during wet and dry seasons in the Burdekin region (see Figure CS4.1). Data provide comparison between inshore (Magnetic Island, Orpheus Island and Channel), mid-shore (Yongala) and open ocean (Coral Sea) regions. Coral Sea only sampled in dry season.

coral cover (Browne et al. 2010 2013, Browne 2012, Perry et al. 2012b) but with trade-offs in feeding regimes (Anthony 2000, Anthony & Fabricius 2000, Anthony & Connolly 2004), morphology (Browne et al. 2010, Padilla-Gamino et al. 2012, Duckworth et al. 2017) and skeletal density (Rocker et al. 2017). Sponges rated among the most vulnerable to sediments and pollutants (Table 6), yet both sponges and their microbiomes seem relatively resilient to high sediment loads on the GBR (Pineda et al. 2017b,c, Strehlow et al. 2017), and some species may even thrive (Bell et al. 2015). While responses are variable (Pineda et al. 2017a), the diversity of sponges, even at small cryptic scales, may offer some resilience to sediment and pollutant loads (Schönberg 2001, 2016). Increases in the benthic cover of *Cliona*, the most abundant bioeroding sponge on the GBR, are greatest when algal cover and nutrient levels are low (Ramsby et al. 2017).

For reef fish communities, increased suspended sediments can impact foraging, growth, larval development, behaviour and predator-prey interactions (Wenger et al. 2011, 2012, 2013, 2014). Foraging success of visual predators like planktivorous damselfishes can be significantly impaired in turbid environments (Wenger et al. 2012, Johansen & Jones 2013). Herbivorous fishes rated among the most vulnerable to sediments (Table 6), with some species shown to decrease grazing activity when sediments loads are too high in the EAM (Bellwood & Fulton 2008, Goatley & Bellwood 2012, Goatley et al. 2016, Gordon et al. 2016b). This can be expedited by turf canopy height, whereby taller canopies trap sediments with negative impacts on herbivory and coral recruitment (Carpenter & Williams 1993, Birrell et al. 2005, Bellwood & Fulton 2008, Arnold et al. 2010, Goatley & Bellwood 2012, Clausing et al. 2014, Lam et al. 2018). Interestingly, some detritivores may be particularly important in removing sediment and detritus from the EAM, facilitating herbivory by other species (Goatley & Bellwood 2010, Marshell & Mumby 2012, 2015).

Habitat degradation associated with coral bleaching and freshwater flood plumes (Williamson et al. 2014b) has been shown to drive dietary shifts in both juvenile (Wen et al. 2016) and adult (Hempson et al. 2017) coral trout. This trophic plasticity involved consumption of non-preferred fishes in line with changes in foraging behaviour (Wen et al. 2016) and prey biomass (Hempson et al. 2017). Although dietary adaptive capacity may mitigate short-term impacts of sedimentation and habitat degradation, it may result in a shortened and simplified trophic structure with a longer-term toll on ecosystem functioning (Graham et al. 2007, Estes et al. 2011, Hempson et al. 2017, Feary et al. 2018). These stressors impact predator-prey dynamics are particularly important to characterise, particularly for key fisheries targets with ontogenetic shifts in diet, like coral trout (Case Study 1).

Pesticides, herbicides, trace metals and agricultural nutrients (e.g. nitrogen, phosphorus) that influence eutrophication are commonly measured on nearshore reefs of the GBR at concentrations above Australian water quality guidelines (Lewis et al. 2009, 2012, Brodie & Waterhouse 2012, Waterhouse et al. 2012, Brodie et al. 2013). However, few toxic pollutants on the GBR approach harmful concentrations and, if so, are typically only recorded during short-term runoff pulses (van Dam et al. 2011). Further, there is limited empirical evidence on how pesticides scale up to impact inshore ecosystem processes, functioning and services (Fichez et al. 2005, van Dam et al. 2011, de Valck & Rolfe 2018). In the context of nearshore systems on the GBR, there is a lack of evidence that mangrove and seagrass biomes are negatively impacted by water quality stressors, but elevated nutrient levels, substrate availability and low grazing pressure suggest that nearshore benthic communities are shifting towards macroalgal abundance, with negative impacts on reef functioning (Schaffelke et al. 2005).

On the GBR, the herbicide Diuron has received considerable attention, which can impact photosynthesis, fecundity, larval development and survival in a range of groups, including corals, CCA, foraminiferans and sea urchins (Negri et al. 2005, Cantin et al. 2007, Magnusson et al. 2008, 2012, Shaw et al. 2009,). Regarding bottom-up effects, biofilms (EAMs) may be resilient to herbicides, but their community structure can be altered depending on exposure thresholds (Magnusson et al. 2012). *In situ* nutrient dosages of nitrogen and phosphorus impacted coral growth, recruitment and skeletal density but only when loading was high and generally with sublethal effects (Koop et al. 2001, Bell et al. 2007). Elevated nutrient levels can also enhance microbioerosion, making it imperative to manage water quality as coral reefs degrade (Chazottes et al. 2017). Most significantly, elevated nutrients have been attributed to CoTS outbreaks on the GBR through the enhancement of success in pelagic larval life stages, which has received considerable attention in the literature (Brodie et al. 2005, Fabricius et al. 2010, Wooldridge & Brodie 2015, Babcock et al. 2016a, Wolfe et al. 2017, Uthicke et al. 2018, Wolff et al. 2018), although the links are tenuous and unresolved (Pratchett et al. 2014, 2017a, Wolfe et al. 2017).

Rainfall is highly variable in northeast Australia, and there is no real consensus on projections for precipitation events in the coming decades (Whetton et al. 2005). However, the intensity of drought and rainfall events is expected to increase, elevating risks associated with flood events and water quality (Lough 2007, Lovelock & Ellison 2007, Adame et al. 2019). Overall, water quality stressors are likely to combine with other environmental factors with significant additive impacts, particularly in the context of thermal stress (Wooldridge & Done 2009, Negri et al. 2011, van Dam et al. 2011, Lewis et al. 2012, van Dam et al. 2012, 2015, Banc-Prandi & Fine 2019). Early monitoring of runoff loads, particularly following heavy rainfall and flood events, has resulted in tighter regulations and catchment management in the GBR region (Brodie & Waterhouse 2012, Brodie et al. 2012). Even though water quality issues have been a strong management focus on the GBR, current initiatives to improve or reverse pollutant loads are not being met (de Valck & Rolfe 2018). A better understanding of the direct impacts of pollutants (e.g. pesticides, metals, nutrients) on coral reef organisms, and the functioning and services they provide, is essential to ensure management goals are biologically relevant and postdisturbance recovery is supported (Fichez et al. 2005, van Dam et al. 2011).

## *Total vulnerability and recoverability*

Using the IPCC Vulnerability Framework (IPCC 2007), corals were outlined as the most vulnerable across the nine stressors for both inner reef and offshore regions (Table 7). Vulnerability scores were generally higher for inner reefs compared to reefs offshore, owing to the additional impacts from water quality in close proximity to the coastline. Branching and tabular corals were rated the most vulnerable of our 70 groups but with tabular corals rated to have a higher level of recoverability (Table 7). Host-associated phototrophic microbes were the most vulnerable microbial group, considered especially vulnerable inshore, as for CCA (Table 7). The most vulnerable invertebrates were coral-associated decapods, several mollusc groups (particularly giant clams; Tridacnidae) and deposit-feeding sea cucumbers (Table 7). Piscivores (resident, transient) were considered the most vulnerable of the reef fishes with the lowest recovery potential (Table 7), strongly influenced by their potential to be impacted by fisheries (Table 5). Staghorn and massive corals were predicted to have the lowest recovery potential for corals, and the triton snail was rated lowest for recovery overall (Table 7). Once considered abundant, densities of triton snails on the GBR have remained extremely low since their extensive overharvest in the 1930s (Endean 1969, Endean & Stablum 1973, Hall et al. 2017). Deposit-feeding sea cucumbers were also suggested to have particularly low recovery potential (Table 7), as bêche-de-mer fisheries operating on the GBR follow global trends of overharvest with no fisheries-independent data available to suggest overfished populations have recovered (Eriksson & Byrne 2015, Purcell et al. 2016b).

## *Combined assessment of functionally important and vulnerable groups*

In order to identify key species for targeted management on the GBR, we compared scores for functional importance against scores for vulnerability (Figure 4). Using the median values for both axes, four quadrants were established to represent priority targets (Figure 4);

1. Intervention (high priority): Functionally important and vulnerable groups that should be considered top priorities for management.
2. Intervention (low priority): Important groups that are not as vulnerable but may still be considered for management to conserve a functioning reef.
3. Protection: Vulnerable groups that were not considered as critical to reef functioning but may require protection to ensure they are not lost.
4. Monitor: Low-rated importance and vulnerability suggests little action may be needed, but populations should still be monitored, especially when certainty is low.

Not surprisingly, most coral groups scored highly for both measures and are considered top priority (Figure 4). Specifically, tabular and branching groups (staghorn, other) ranked highest. Host-associated phototrophic microbes also ranked as a top priority, although they were scored to be less vulnerable than these coral groups (Figure 4). The remaining microbial groups were considered lower priority owing to their low scores for vulnerability (Figure 4), despite free-living microbes (i.e. those in seawater or sediment) and bacteria emerging as important bioindicator tools for monitoring reef health (Case Study 4) (Glasl et al. 2017, 2018a), as for phytoplankton (Revelante & Gilmartin 1982, Revelante et al. 1982, Furnas 1992). Coral-associated decapods ranked highly, along with a range of other invertebrates, including zooplankton, bivalves and giant clams, triton snails and other gastropods (herbivores, predators). Regular sea urchins (e.g. *Diadema*) also fell within this top priority space, perhaps due to lessons learned from the Caribbean (Hughes 1994, Mumby et al. 2006a,b). Top-priority algal groups were the calcifiers (CCA, calcareous) owing to their higher-rated vulnerabilities compared to the remaining algal groups. Despite their great contributions to a functioning reef, algal turfs and macroalgae were categorically considered low priority for management owing to lower-rated vulnerabilities (Figure 4). However, the opportunistic nature of

**Table 7** Total potential impact (PI) and vulnerability (V) of 70 functional groups on the GBR, including their predicted recoverability and certainty of scores

| Taxa | Functional group | Inner GBR | | Outer GBR | | Recoverability | Certainty |
|------|-----------------|-----------|-----|-----------|-----|----------------|-----------|
| | | PI | V | PI | V | | |
| Microbes | Phototrophic | 30.00 | 40.00 | 11.00 | 14.67 | 0.75 | 0.75 |
| | Host-associated | 62.00 | 99.20 | 27.25 | 43.60 | 0.63 | 0.50 |
| | Chemoautotrophic | 14.00 | 18.67 | 5.00 | 6.67 | 0.75 | 0.63 |
| | Heterotrophic | 19.00 | 25.33 | 10.00 | 13.33 | 0.75 | 0.63 |
| Algae | Phytoplankton | 10.00 | 13.33 | 0.25 | 0.33 | 0.75 | 0.75 |
| | Algal turfs | 11.00 | 14.67 | 1.25 | 1.67 | 0.75 | 0.75 |
| | Leathery | 8.25 | 16.50 | 3.50 | 7.00 | 0.50 | 0.50 |
| | Foliose | 13.25 | 17.67 | 2.50 | 3.33 | 0.75 | 0.63 |
| | Calcareous | 23.25 | 46.50 | 12.50 | 25.00 | 0.50 | 0.50 |
| | CCA | 47.00 | 62.67 | 23.00 | 30.67 | 0.75 | 0.50 |
| Sponges | Heterotrophic | 44.33 | 76.00 | 27.89 | 47.81 | 0.58 | 0.50 |
| | Phototrophic | 47.11 | 80.76 | 24.00 | 41.14 | 0.58 | 0.50 |
| | Boring | 17.81 | 26.71 | 3.47 | 5.21 | 0.67 | 0.58 |
| | Cryptic | 29.00 | 49.71 | 6.25 | 10.71 | 0.58 | 0.50 |
| Coral | Tabular | 82.70 | 110.27 | 65.20 | 86.94 | 0.75 | 0.75 |
| | Staghorn | 83.03 | 147.62 | 65.53 | 116.51 | 0.56 | 0.69 |
| | Branching (other) | 79.81 | 116.09 | 63.73 | 92.70 | 0.69 | 0.69 |
| | Massive | 41.76 | 83.51 | 30.82 | 61.64 | 0.50 | 0.75 |
| | Encrusting | 45.51 | 66.19 | 32.51 | 47.28 | 0.69 | 0.69 |
| | Free-living | 37.87 | 55.08 | 28.62 | 41.63 | 0.69 | 0.56 |
| | Soft corals | 43.03 | 68.86 | 31.72 | 50.76 | 0.63 | 0.63 |
| | Foraminifera | 26.31 | 38.26 | 19.37 | 28.17 | 0.69 | 0.44 |
| Worms | Nematodes | 0.00 | 0.00 | 0.00 | 0.00 | 0.75 | 0.63 |
| | Nemertea | 0.25 | 0.33 | 0.25 | 0.33 | 0.75 | 0.38 |
| | Polychaetes | 0.25 | 0.33 | 0.25 | 0.33 | 0.75 | 0.38 |
| | *Spirobranchus* | 28.00 | 37.33 | 16.00 | 21.33 | 0.75 | 0.38 |
| Crustaceans | Decapods (H) | 29.00 | 38.67 | 25.00 | 33.33 | 0.75 | 0.38 |
| | Decapods (P) | 36.25 | 58.00 | 32.25 | 51.60 | 0.63 | 0.38 |
| | Coral-associated | 54.25 | 108.50 | 42.25 | 84.50 | 0.50 | 0.50 |
| | Barnacles | 26.00 | 34.67 | 19.00 | 25.33 | 0.75 | 0.38 |
| | Stomatopods | 22.25 | 29.67 | 18.25 | 24.33 | 0.75 | 0.38 |
| | Cleaner shrimp | 30.00 | 48.00 | 26.00 | 41.60 | 0.63 | 0.50 |
| | Infauna | 11.25 | 18.00 | 10.25 | 16.40 | 0.63 | 0.50 |
| | Zooplankton | 30.25 | 40.33 | 25.50 | 34.00 | 0.75 | 0.50 |
| | Parasitic | 14.25 | 19.00 | 13.25 | 17.67 | 0.75 | 0.50 |
| Molluscs | Gastropods (H) | 37.00 | 59.20 | 32.25 | 51.60 | 0.63 | 0.50 |
| | Gastropods (P) | 21.11 | 33.78 | 17.11 | 27.38 | 0.63 | 0.50 |
| | Triton snails | 21.36 | 56.96 | 17.36 | 46.30 | 0.38 | 0.50 |
| | *Drupella* | 36.25 | 48.33 | 32.25 | 43.00 | 0.75 | 0.63 |
| | Tridacnidae | 62.00 | 106.29 | 51.25 | 87.86 | 0.58 | 0.67 |
| | Bivalves | 46.00 | 73.60 | 38.25 | 61.20 | 0.63 | 0.63 |
| | Chitons | 19.00 | 25.33 | 19.00 | 25.33 | 0.75 | 0.50 |
| | Cephalopods | 19.61 | 26.15 | 7.75 | 10.33 | 0.75 | 0.50 |
| Echinoderms | Seastars (H) | 18.00 | 24.00 | 13.25 | 17.67 | 0.75 | 0.50 |
| | Seastars (P) | 15.00 | 20.00 | 11.00 | 14.67 | 0.75 | 0.50 |
| | CoTS | 12.00 | 16.00 | 11.00 | 14.67 | 0.75 | 0.75 |

(*Continued*)

**Table 7 (*Continued*)** Total potential impact (PI) and vulnerability (V) of 70 functional groups on the GBR, including their predicted recoverability and certainty of scores

| Taxa | Functional group | Inner GBR | | Outer GBR | | Recoverability | Certainty |
|---|---|---|---|---|---|---|---|
| | | PI | V | PI | V | | |
| | Sea cucumbers (DF) | 35.25 | 70.50 | 31.25 | 62.50 | 0.50 | 0.50 |
| | Sea cucumbers (SF) | 17.00 | 22.67 | 12.25 | 16.33 | 0.75 | 0.50 |
| | Sea urchins (regular) | 30.00 | 40.00 | 25.25 | 33.67 | 0.75 | 0.50 |
| | Sea urchins (irregular) | 26.25 | 42.00 | 25.25 | 40.40 | 0.63 | 0.50 |
| | Brittle stars | 14.25 | 19.00 | 13.25 | 17.67 | 0.75 | 0.50 |
| | Feather stars | 18.00 | 24.00 | 14.00 | 18.67 | 0.75 | 0.50 |
| Fishes | Cryptobenthic | 39.56 | 52.74 | 29.11 | 38.81 | 0.75 | 0.67 |
| | Farmers | 27.11 | 36.15 | 11.67 | 15.56 | 0.75 | 0.67 |
| | Scrapers (scarids) | 22.00 | 29.33 | 6.00 | 8.00 | 0.75 | 0.67 |
| | Browsers (nasos) | 13.44 | 20.17 | 4.11 | 6.17 | 0.67 | 0.67 |
| | Browsers (siganids) | 13.78 | 20.67 | 4.44 | 6.67 | 0.67 | 0.75 |
| | Browsers (other) | 13.78 | 23.62 | 4.44 | 7.62 | 0.58 | 0.50 |
| | *Bolbometopon* | 23.56 | 40.38 | 10.89 | 18.67 | 0.58 | 0.75 |
| | Excavators (other) | 23.67 | 35.50 | 7.67 | 11.50 | 0.67 | 0.67 |
| | Detritivores | 22.22 | 29.63 | 11.56 | 15.41 | 0.75 | 0.58 |
| | Planktivores | 40.56 | 60.83 | 30.11 | 45.17 | 0.67 | 0.75 |
| | Corallivores | 56.11 | 96.19 | 38.44 | 65.90 | 0.58 | 0.58 |
| | Invertivores (labrids) | 24.11 | 32.15 | 11.67 | 15.56 | 0.75 | 0.67 |
| | Invertivores (other) | 25.78 | 44.19 | 13.33 | 22.86 | 0.58 | 0.67 |
| | Invertivores (lutjanids) | 17.44 | 34.89 | 10.44 | 20.89 | 0.50 | 0.58 |
| | Eels | 25.00 | 50.00 | 14.33 | 28.67 | 0.50 | 0.50 |
| | Piscivores (residents) | 52.11 | 104.22 | 36.67 | 73.33 | 0.50 | 0.58 |
| | Piscivores (transients) | 44.89 | 89.78 | 31.11 | 62.22 | 0.50 | 0.75 |
| | Cleaner wrasse | 26.22 | 34.96 | 20.56 | 27.41 | 0.75 | 0.63 |

*Note:* Values are shown for inner and outer reefs. Dark cells = top 10th percentile of scores (bottom 10th for recoverability); light cells = top 25th percentile.

*Abbreviations:* H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders

these algal groups can drive phase shifts away from coral dominance, and for this very reason, they should not be ignored in management, particularly on inshore reefs where nutrient enrichment from water quality can enhance algal growth (Vermeij et al. 2010, Gordon et al. 2016a), including on the GBR (Schaffelke et al. 2005, Lam et al. 2018). Phototrophic and heterotrophic sponges were top-priority sponge groups, while the more functionally important cryptic and boring sponges were considered more resilient (Figure 4).

For the reef fishes, although scoring lower for their total functional importance compared to other fish groups, cleaner wrasse and cryptobenthic fishes were the only two fish groups to fall within the top priority space (Figure 4). For cleaner wrasse, which may not be the most directly important or vulnerable of the reef fishes, this score was largely attributed to their low ecological redundancy. Interestingly, those that were considered among the most functionally important groups (e.g. *Bolbometopon*, scarids, damselfishes, detritivores) were not considered highly vulnerable (low priority), while those that were the most vulnerable (e.g. piscivores, corallivores, planktivores) were not ranked among the key groups for maintaining a functioning reef (Figure 4). This highlights the importance of using a multi-level approach in assessing species' functionality.

For each group of species, we combined their functional importance per process and vulnerability per stressor in every combination to calculate the relative impact of each stressor at various levels
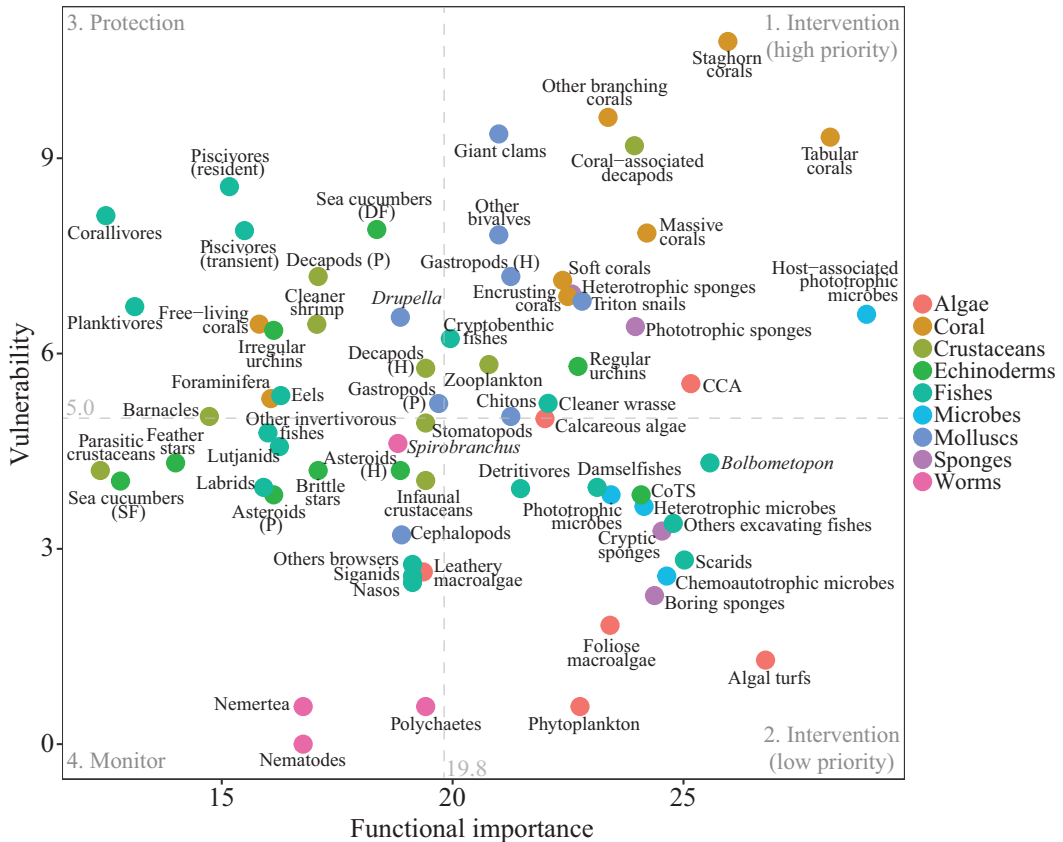
**Figure 4** Assessment of the functional importance and vulnerability of 70 species groups. Dotted grey lines represent the median values for each axis creating four management quadrats; 1) Intervention (high priority), 2) Intervention (low priority), 3) Protection, and 4) Monitor. Colours represent taxonomic groups. H = herbivores, P = predators, DF = deposit feeders, SF = suspension feeders.

of taxonomy and ecosystem processes (see methods). This analysis presents weighted impacts of stressors for species at their highest levels of functioning and vulnerability. These data may be particularly useful in guiding where attention could be focussed to maintain highly weighted species-stressor-process combinations.

The proportional impact of each stressor varied across our taxonomic groups and between inner reef and offshore regions (Figure 5A,B). As previously, global change stressors (ocean warming, ocean acidification, cyclones) were considered to have the greatest potential impact overall, especially offshore (Figure 5B). On inshore reefs, the proportional impact of global change stressors on biological functioning was dampened by a greater influence from water quality stressors (nutrients, sediments, pollutants) (Figure 5B), as would be expected (Brodie & Waterhouse 2012, Lam et al. 2018, MacNeil et al. 2019). This will likely be exacerbated as the intensity of rainfall events increases over the coming decades (Lough 2007). Interestingly, the proportional impact of water quality stressors superseded ocean change stressors on inshore reefs for some taxa (e.g. microbes, algae, sponges, fishes) (Figure 5A), attributing to the importance of addressing local management in conjunction with global stressors and a low-carbon economy (Kennedy et al. 2013, Albright et al. 2016a, Cinner et al. 2016). Corals were the primary taxonomic group considered to be impacted by outbreaks, likely almost entirely in the context of CoTS on the GBR. Echinoderms and fishes
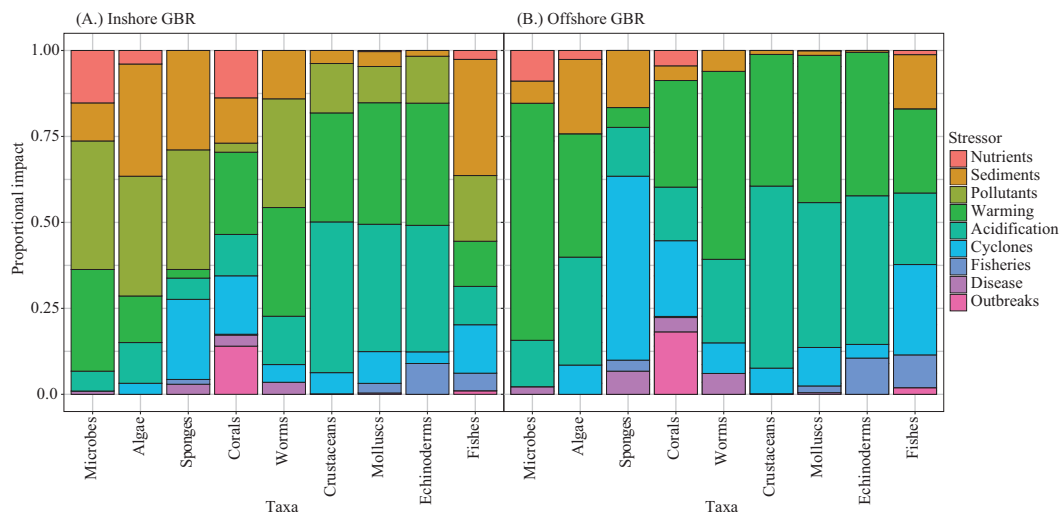
**Figure 5** The proportional impact of each stressor on taxonomic groupings (A) inshore and (B) offshore. Each column represents the relative proportion of the functional importance and vulnerability of all species groups within the taxa-stressor combination.

were the major groups impacted by fisheries (Figure 5A,B). The functional contributions of sponges seemed disproportionately impacted by cyclones compared to other taxonomic groups, particularly offshore where there was less exposure to impacts from sediments and pollutants (Figure 5B).

This analysis was deconstructed at the level of our 70 functional groups, providing important information on the most critical stressors to consider when looking to maintain each species group at their highest level of functioning. For many of the mobile invertebrate groups (i.e. crustaceans, molluscs and echinoderms), the impact of ocean change stressors was greatest, even in context of inshore reefs (Figure 6), as reviewed for adult and larval life stages across this great diversity of species (Przeslawski et al. 2008, 2015, Byrne 2011). For most herbivorous fish groups (e.g. browsers, excavators and scrapers), water quality stressors, particularly sediments, were considered to have the greatest proportional impact on their functioning (Figure 6), including offshore (Figure 7). This is in line with the literature that suggests grazing activity can be significantly impaired when sediment loads are too high in their algal food source (Bellwood & Fulton 2008, Goatley & Bellwood 2012, Goatley et al. 2016, Gordon et al. 2016b). As such, functioning of several algal groups, including turfs, was considered to be greatly impacted by sediment loads (Figures 6 and 7). Of the marine worms, only *Spirobranchus* was considered vulnerable to a number of stressors. Nemerteans and polychaetes were suggested to be almost entirely impacted by cyclones (Figures 6 and 7) – an artefact of their low-rated vulnerabilities as a whole. Scores for nematodes, nemerteans and polychaetes reflect the data gaps and uncertainty in the biology and ecology of these groups in a broader context of reef functioning and threat sensitivity. Fisheries were suggested to have a disproportionate impact on deposit-feeding sea cucumbers and were the major stressor impacting functioning of piscivorous fishes (resident and transient) (Figures 6 and 7). It would be important to partition these broad categories for piscivores at greater resolution in future work. Tabular, staghorn and other branching corals were the groups most impacted by outbreaks, with the functioning of some fish groups that depend on corals for shelter (i.e. corallivores, cryptobenthic, planktivores) also partially impacted. This reflects the ability for our scoring system to capture indirect impacts of stressors on reef functioning. Interestingly, water quality stressors seemed to have a broader and proportionately greater impact on functioning for many species than outbreaks, including offshore (Figure 7).
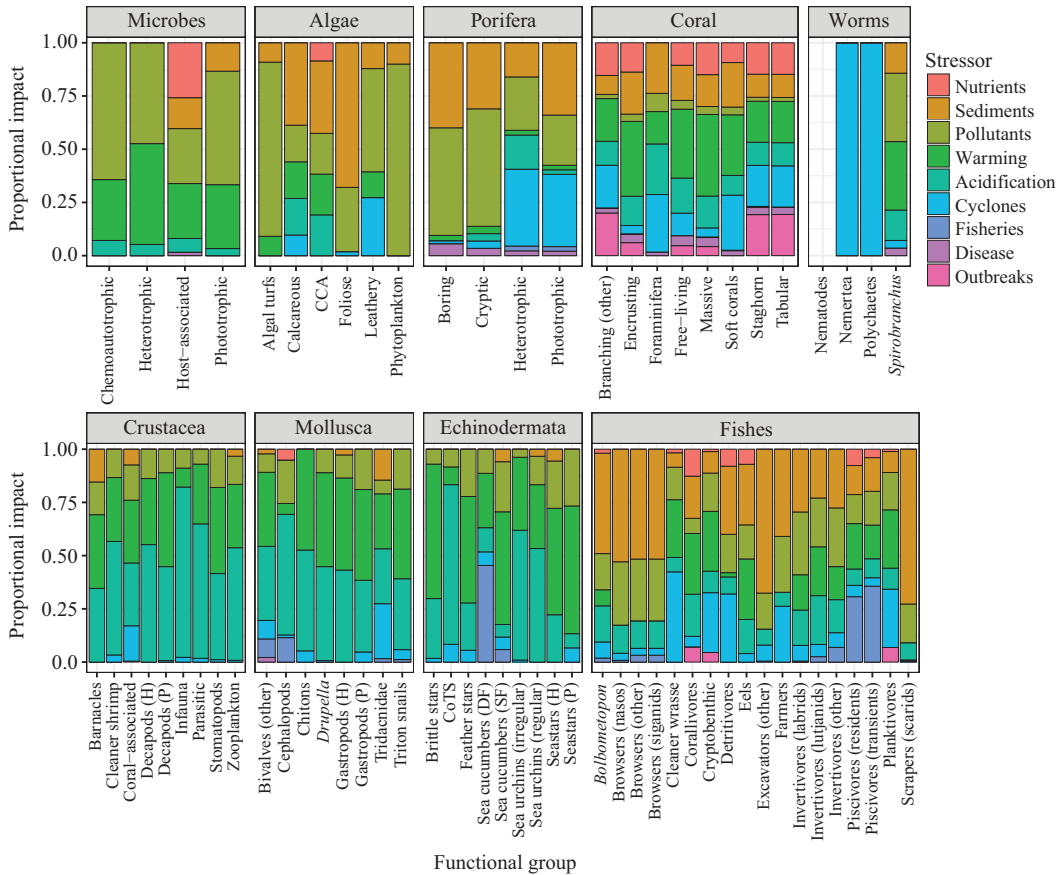
**Figure 6** The proportional impact of each stressor on our 70 groups of species as a factor of their functional importance inshore.

*Process-level vulnerability*

To examine the impact of our nine stressors on ecosystem processes, the additive functional importance and vulnerability of each taxa were calculated across each process-stressor combination. This allowed the determination of the relative impact of each stressor at the level of our nine ecosystem processes, which was weighted by species at their highest level of functioning. Despite the observed differences in the proportional impact of stressors on taxa separately (as previously), analyses at the level of ecosystem processes showed little variation in potential impact (Figure 8A, B). Global change stressors were calculated to have the greatest proportional impact on ecosystem processes, especially offshore (Figure 8B). As previously, impact from water quality stressors on ecosystem processes were proportionately greater inshore (Figure 8A). Though generally, there was little difference in the proportional impact of stressors between inshore and offshore habitats other than the added stress from pollutants (Figures 8–10). Few toxic pollutants on the GBR approach harmful concentrations and, if so, are typically only recorded during short-term runoff pulses near shore (van Dam et al. 2011).

This analysis became more informative when examined as a proportion of each stressor separately. The impact of fisheries was evidently greatest for the predation process (Figures 9 and 10), likely driven by combined importance and vulnerability of the two large predatory fish groups (residents and transients) at this level of functioning. This could be assumed to be driven by
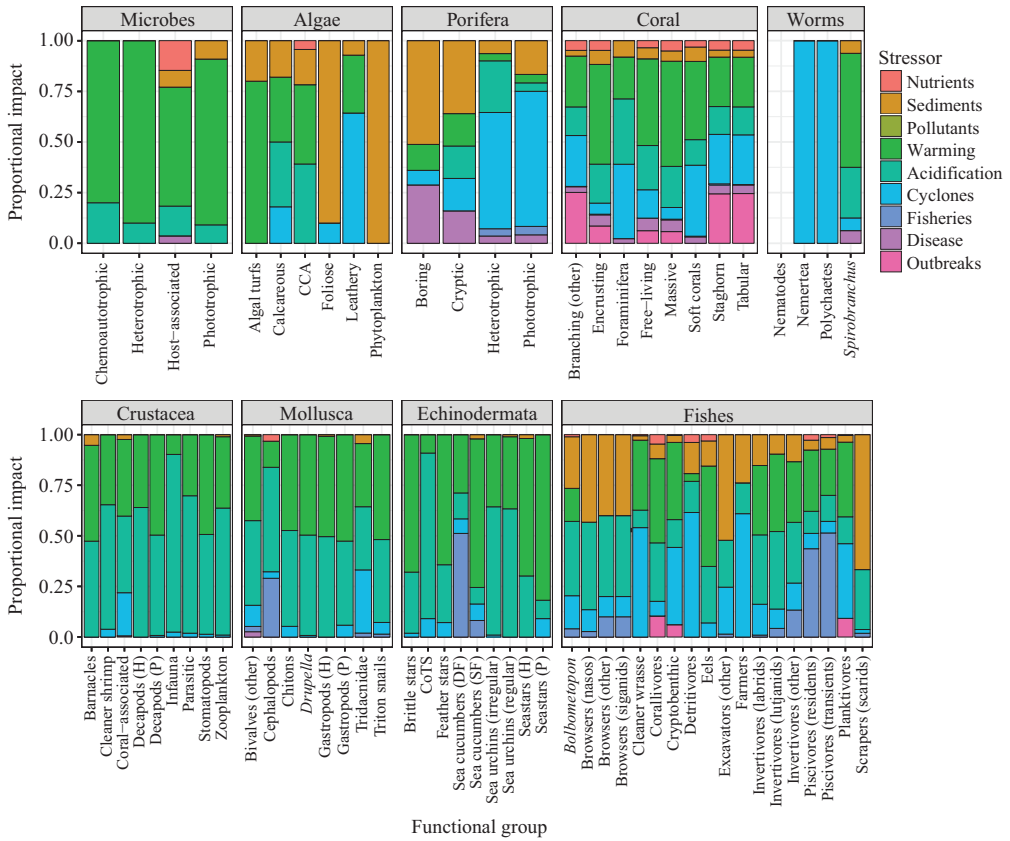
**Figure 7** The proportional impact of each stressor on our 70 groups of species as a factor of their functional importance offshore.
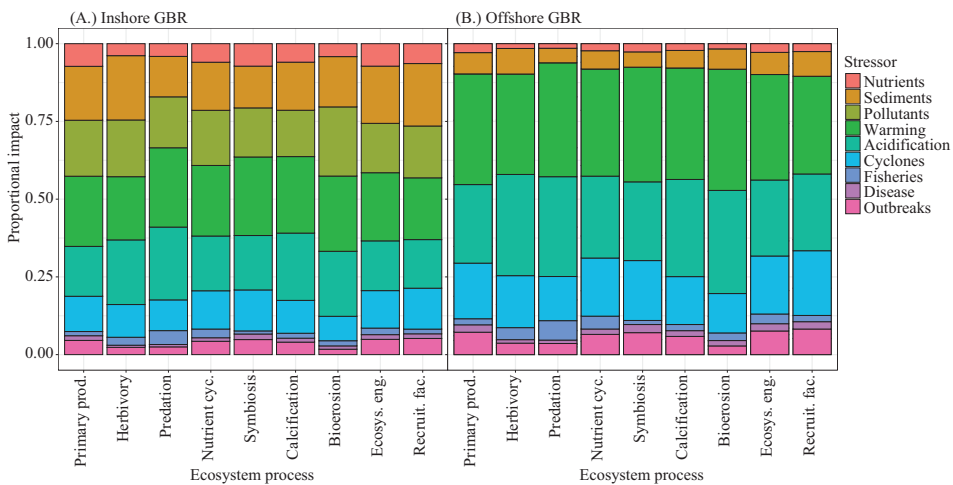


**Figure 8** The proportional impact of each stressor on ecosystem processes (A) inshore and (B) offshore. Each column is a relative proportion of the functional importance and vulnerability of all species groups within each process-stressor combination.
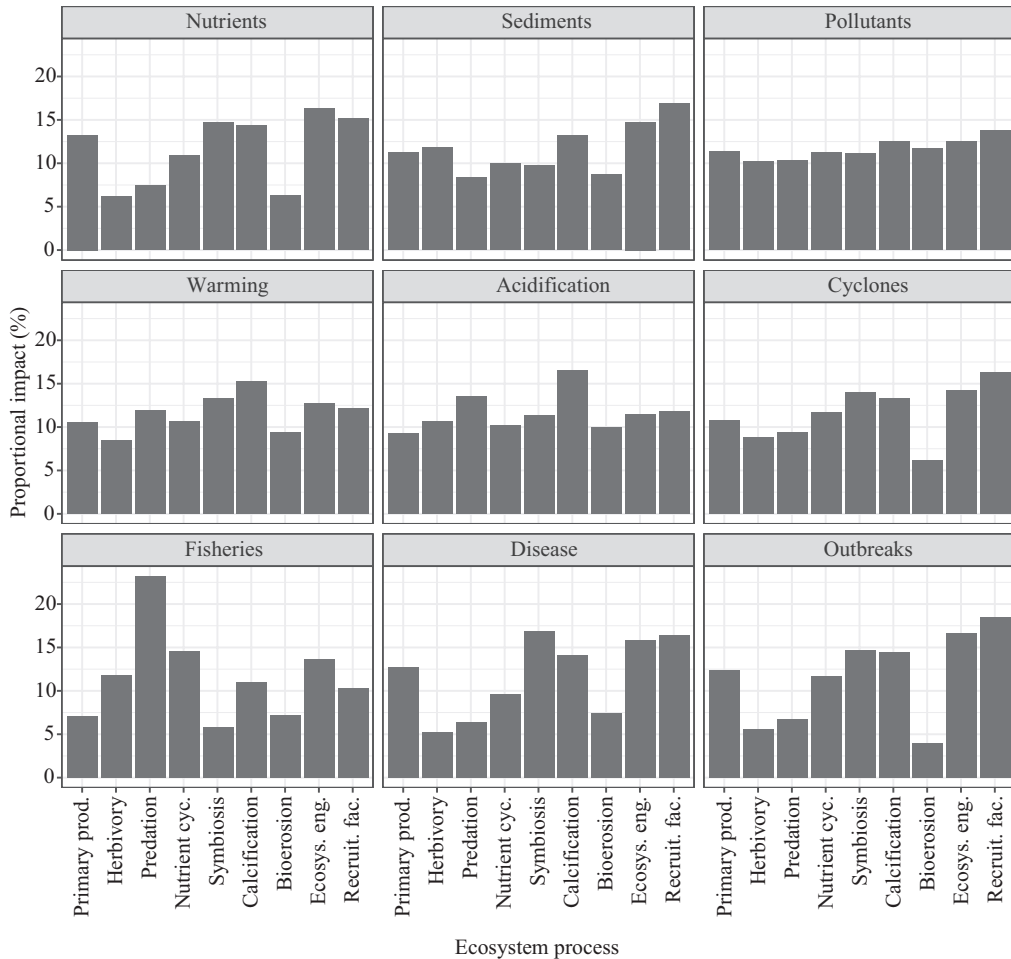
**Figure 9**  The proportional impact of each stressor on ecosystem processes in context of inshore regions of the GBR. Each column represents the relative proportion of the functional importance and vulnerability within each stressor.

triton snails, which rated highest for predation in context of CoTS, but these gastropods were not considered vulnerable to fisheries here, as records of exploitation are only anecdotal (Endean 1969), and collection of *Charonia tritonis* on the GBR has been prohibited for several decades (Hall et al. 2017). Generally, stressors had the lowest proportional impact on the bioerosion process (Figures 9 and 10), in line with the literature suggesting bioerosion is likely to increase in a future ocean and is itself an emergent stressor on coral reefs (DeCarlo et al. 2015, Manzello et al. 2017, Schönberg et al. 2017). Ocean acidification had the greatest proportional impact of species considered important for the calcification process (Figures 9 and 10), as would be expected. For a number of stressors (nutrients, warming, cyclones, outbreaks and disease), potential impacts were tightly coupled for symbiosis, calcification, ecosystem engineering and recruitment facilitation processes (Figures 9 and 10). This likely reflects the fundamental role of corals and their symbionts in the ecosystem process that support habitat functioning. Yet overall, the proportional impacts on many ecosystem processes within each stressor were relatively homogenous (Figures 9 and 10) attributed to the broad sweeping effects stressors can have in complex systems like coral reefs.
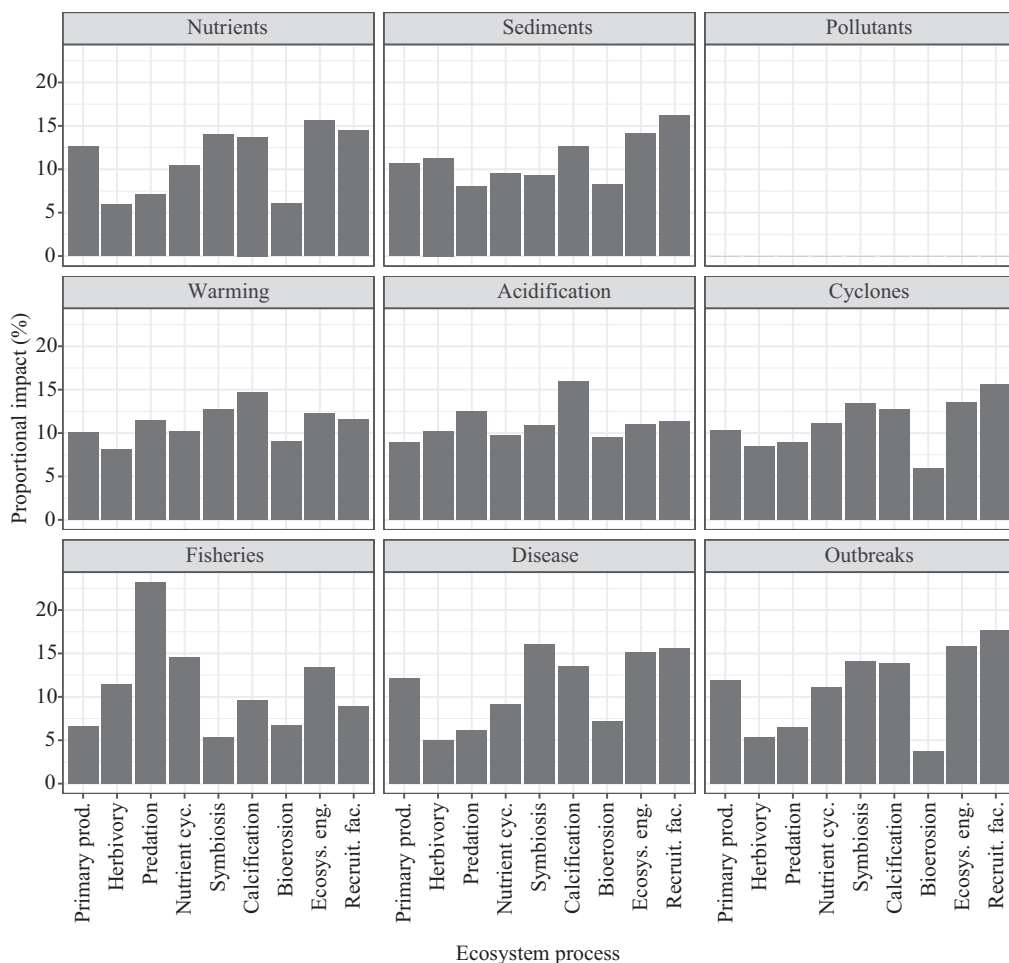
**Figure 10** The proportional impact of each stressor on ecosystem processes in context of offshore regions of the GBR. Each column represents the relative proportion of the functional importance and vulnerability within each stressor. Data absent for pollutants offshore due to null score for exposure (see methods).

## *Addressing manageability*

Experts were elicited to rate species based on their potential responsiveness to management action and the feasibility of implementing management strategies (i.e. spatial scale, time, energy, cost) (see methods). Groups that scored in the top 66th percentile were categorised as a higher priority for management that would likely benefit from direct measures of protection or even represent cases where management has already proved effective. Those in the bottom 33th percentile were deemed lower management priorities that may indirectly benefit from broader-scale management schemes (e.g. marine zoning) and/or require innovative approaches. In any case, maintaining current systems of zoning and compliance provides a baseline to management to preserve species, functioning and biodiversity on coral reefs (GBRMPA 2014c, 2018b). Note that this assessment was in context of the biological functioning of each taxa and was not an assessment of other important elements in strategic assessments, including social, cultural and economic reef values (GBRMPA 2014c).

Interestingly, species that scored lowest for their functional importance and vulnerability on the GBR were also regarded as the least manageable (Figure 11). This may reflect expert bias and the
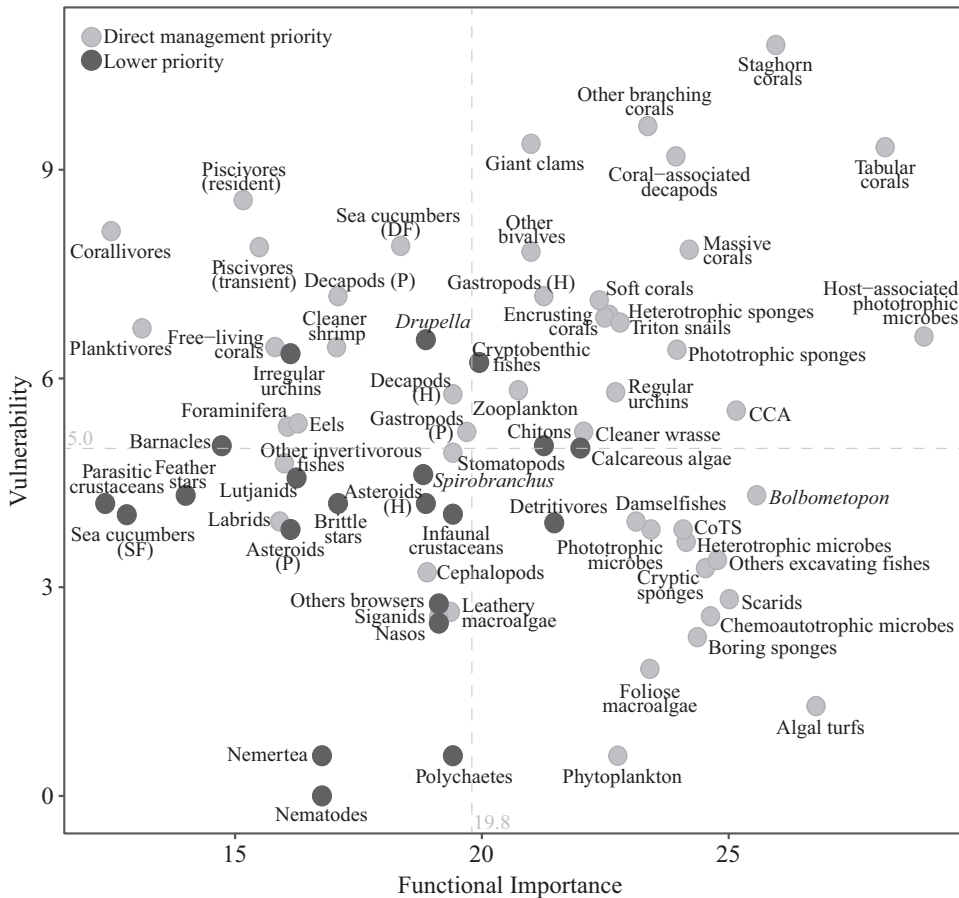
**Figure 11** Perceived manageability of each species group relative to their rated functional importance and vulnerabilities on the GBR. Dotted grey lines represent the median values for each axis. H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders.

assumption that important and vulnerable groups should be managed but also demonstrates strong support for the protection of highly rated groups. Invertebrates were most frequently considered unmanageable (Figure 11), reflecting the difficulties inherent in monitoring and managing small, often cryptic species. This was reflected in the Crustacea, where barnacles, infaunal species and parasites scored low, along with all four groups of marine worms (Figure 11). Five groups of reef fishes (cryptobenthics, *Naso* sp., other browsers, detritivores, lutjanids) rated as low priority (Figure 11), most likely stemming from the direct comparison of these groups to other reef fishes rather than their actual inability to be managed. In context of the biology of these groups, cryptobenthic fishes are incredibly diverse and abundant, with rapid population turnovers that ensure persistence against extreme predation pressure (Depczynski & Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018, 2019), suggesting an inherent resilience. This is also true for the broad distributions and/or high densities of many detritivorous fishes, including blennies (Wilson 2000, 2001, 2004), and surgeonfishes, particularly *Ctenochaetus striatus* (Tebbett et al. 2018). Interestingly, microbes, which are ubiquitous and relatively poorly understood, were considered manageable candidates. This may reflect recent research suggesting that some groups (e.g. bacteria and free-living microbes in seawater or sediment) can be used as bioindicators to monitoring reef health, particularly regarding water quality (Case Study 4) (Glasl et al. 2017, 2018a) and potential Symbiodiniaceae community

regulation in support of reef restoration (Quigley et al. 2018). All corals were considered manageable, including the non-coral group Foraminifera, as were phytoplankton and zooplankton (Figure 11).

## *Addressing scientific certainty*

Scientific certainty, as expressed by our expert panel, varied among the 70 functional groups (Figure 12). Uncertainty was most evident for mobile marine invertebrate groups, reflecting the comparatively poor knowledgebase we have regarding non-coral invertebrates on the GBR and generally (Ponder et al. 2002, Przeslawski et al. 2008). While certainty was high for some key species, such as CoTS and bivalves, for most non-coral marine invertebrates, including marine worms, crustaceans and echinoderms, certainty was poor (Figure 12). Along with CoTS, scientific certainty was greatest for *Bolbometopon*, tabular corals and algal turfs, which have received great attention both in the literature and in this review. The lowest certainty for a reef fish group was for eels (muraenids) (Figure 12). Interestingly, certainty was relatively high for cephalopods despite surprising data deficiencies regarding the biology and ecology of this group on the GBR and elsewhere. Conversely, certainty was low for triton snails despite the body of literature devoted to this gastropod owing to



**Figure 12** Scientific (expert) certainty in scores for functional importance and vulnerability of the 70 functional groups. Shading reflects scores of high (light) to low (dark) certainty. Dotted grey lines represent the median values for each axis. H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders.

its role in CoTS predation (Endean 1969, Pratchett et al. 2014, Westcott et al. 2016, Cowan et al. 2017, Hall et al. 2017). The perceived depletion of *Charonia tritonis* on the GBR, and elsewhere, was the basis for the 'predator removal hypothesis' regarding CoTS outbreaks (Endean 1969). However, records of their exploitation are mainly anecdotal, and the lack of scientific data and official harvest records suggest these gastropods may have always been rare on many coral reefs (Hall et al. 2017). Regardless, triton snails were scored to have low potential recoverability (Table 7), as while limited data exists, exploitation has occurred for *Charonia* species on many coral reefs globally, where their numbers remain low (Salm 1978, Nijman et al. 2016, Hall et al. 2017).

These high or low relative values for certainty are highlighted here to inform and support our findings and recommendations – an important elicitation process (Knol et al. 2010, Polasky et al. 2011). For groups that scored highly overall with a high level of certainty, management seems most appropriate; that is, we are sure that they are functionally important, vulnerable and manageable on the GBR. Groups with comparatively low levels of certainty are briefly reviewed subsequently under precautionary principles so that no groups were overlooked due to data deficiencies, particularly for those where uncertainty was disproportionate to their relative importance and/or vulnerability. In most cases of uncertainty, we conclude that more empirical data are required to explicitly characterise their functional significance and vulnerabilities and to predict ecological consequences in their absence. The desired outcome for these data-deficient groups is to reduce uncertainty through increased research and monitoring.

## Cryptic predators: Eels and octopuses

Due to the difficulties surveying the cryptic habitats they typically occupy, little data exist for muraenids (eels) on the GBR and reefs in general. They likely span many trophic levels, with adults ranging from just a few centimetres to >3 m, and from sandy-bottom to complex reef rubble and intertidal habitats (Böhlke & Randall 2000). Many muraenids actively hunt within the intricacies of the reef framework often inaccessible to other large predators, sometimes occupying nocturnal niches with diets that include fishes, crustaceans, worms and cephalopods (Hiatt & Strasburg 1960, Hixon & Beets 1993, Fishelson 1997, Young & Winn 2003, Gilbert et al. 2005). Unlike a diversity of other reef fishes, including large resident piscivores, muraenids optimise habitat use within the reef and rubble matrix (i.e. dead coral) rather than exhibiting dependence on live coral, suggesting they may fare better as coral reefs degrade. Yet how trophic pathways within the reef matrix scale up to fisheries productivity are poorly understood. As for muraenids, a broad knowledge gap is evident for cephalopods, particularly octopuses that exist in a similar trophic space. Benthic predators like octopuses and muraenids are likely key predators within the reef matrix where large predatory fishes cannot access, but this remains to be quantified. Data gaps for cephalopods are surprising given their broad cross-shelf distributions occupying cryptobenthic to pelagic habitats (Moltschaniwskyj & Doherty 1995) and their contributions to fisheries productivity as both predators and prey (Connell 1998, Beukers-Stewart & Jones 2004, Taylor & Bennett 2008). Surprisingly little information exists regarding their functional ecology on the GBR and in general (Ponder et al. 2002). Interestingly, cephalopod populations are proliferating globally, and they may fare better in a future ocean compared to other marine taxa due to their 'live fast, die young' life cycles (Doubleday et al. 2016, Rosa et al. 2019).

## Deposit-feeding sea cucumbers

Although they have important roles in bioturbation, carbonate chemistry, nutrient cycling, benthic productivity and infaunal community structure (Uthicke & Klumpp 1998, Uthicke 1999, 2001, Wolkenhauer et al. 2010, Schneider et al. 2011, 2013, Lee et al. 2017, Wolfe & Byrne 2017a, Wolfe et al. 2018), sea cucumbers may be more influential in lagoon systems – outside of the focal habitat here. Large deposit-feeding holothuroids are likely to have a greater influence on ecosystem-scale

carbonate chemistry in closer association to reef structure (Schneider et al. 2013, Wolfe et al. 2018). As recognised by our expert panel, they are among the most vulnerable species to overfishing on the GBR (Uthicke et al. 2004, Purcell et al. 2013, 2016b, Eriksson & Byrne 2015), as globally recognised (IUCN Red List for Threatened Species) (Conand et al. 2014, Purcell et al. 2014, Richards & Day 2018). Empirical data on their recruitment and reproduction (e.g. Wolfe & Byrne 2017b, Balogh et al. 2019), and natural population densities, are essential to characterise before fisheries impacts on wild populations can no longer be differentiated. This is particularly true for the black teatfish (*Holothuria whitmaei*), in light of the recent discussions to reopen its fishery (DAF 2018) without any fisheries-independent data since its closure (owing to overfishing) in 1999.

## Marine worms

This broad group boasts an incredible diversity across a range of functioning and taxa, from microscopic infaunal nematodes, to parasitic platyhelminths, to large predatory polychaetes, to sessile filter-feeders (Hutchings et al. 2019). For polychaetes alone, there are currently over 130,000 species recognised worldwide, but there has not yet been a comprehensive survey of the polychaetes, or marine worms, of the GBR. Marine worms are often highly cryptic, and new species are frequently identified when taking the time to look, as demonstrated from a two-week polychaete workshop on Lizard Island that described 91 new species (Aguado et al. 2015, Capa et al. 2015, Hutchings & Kupriyanova 2015). Bioerosion is perhaps the most well-documented functional role of marine worms on the GBR (Hutchings & Kiene 1986, Hutchings 2008), but the lack of spatially explicit information on their population densities across the GBR hinders the ability to upscale their contributions into carbonate budget calculations (see Case Study 2). The Christmas tree worm (*Spirobranchus*) has received specific attention in the literature, owing to the benefits it provides for its coral host (Strathmann et al. 1984, DeVantier et al. 1986, Dai & Yang 1995, Ben-Tzvi et al. 2006, Rowley 2008). Marine worms are an important food source for many reef organisms, including invertivorous reef fishes (Case Study 1), but explicit trophic contributions are notoriously difficult to quantify for soft-bodied cryptic fauna, and attention to these gaps in knowledge is required.

## Cryptic sponges

In general, the functional ecology of sponges is better documented on Caribbean reefs than for the Indo-Pacific, including the GBR (Wilkinson 1983, 1987, Maldonado et al. 2015, Mumby & Steneck 2018). Although conspicuous sponges ranked in the top-priority space, largely owing to their higher-ranked vulnerability (Figure 4), cryptic (and boring) sponges scored higher in their functional importance and are highlighted here under precautionary principles, owing to the uncertainty in their scores (Figure 12). Cryptic sponges can be the most significant invertebrate bioeroders on coral reefs (Neumann 1966, Glynn & Manzello 2015), a process likely to be accelerated in a future ocean (Wisshak et al. 2014). The contribution of cryptic sponges to reef and rubble consolidation is well appreciated (Wulff & Buss 1979, Wilkinson 1983, Hutchings 2011), facilitating recruitment processes and reef recovery (Fox et al. 2003, Fox & Caldwell 2006, Biggs 2013). Sponge aggregations can enhance local biodiversity through habitat provisioning, making it important to determine the competitive relationships between sponges and other phase-shift drivers (e.g. algae) and how changes in the dominance of these organisms may alter trophic pathways and energy flows on coral reefs (Maldonado et al. 2015, Bell et al. 2018). There may be interesting outcomes in a future ocean as sponge-dominated reefs become increasingly common (Norstrom et al. 2009, Gonzalez-Rivero et al. 2011, Pawlik 2011, Bell et al. 2013, Easson et al. 2014, Farnham & Bell 2018), but possibly shifting from heterotrophic towards phototrophic communities (Bennett et al. 2017, 2018, Bell et al. 2018). For *Cliona*, the most abundant bioeroding sponge genus on the GBR, tolerance to ocean warming may be low (Ramsby et al. 2018a). Yet while clionid benthic cover does not appear to be increasing at the regional scale, it seems greatest when algal cover and nutrient levels are low (Ramsby et al. 2017).

## Crustaceans

As for the marine worms, the functional and taxonomic diversity of crustaceans on the GBR is poorly characterised. Crustaceans are the most diverse marine arthropods and are often termed 'insects of the sea', spanning microscopic copepods, to parasitic isopods, to predatory decapods, to filter-feeding barnacles (Hutchings et al. 2019). Crustaceans are abundant in all habitats of the GBR, with ~1300 recorded species, but the cryptic nature of many of these groups makes them inherently difficult to examine and quantify (Ponder et al. 2002). This includes those that exist in the plankton, such as copepods, which are the most well-studied and important group numerically in the zooplankton in waters of the GBR, constituting ~80% of the mesozooplankton abundance (McKinnon & Thorrold 1993, McKinnon et al. 2005, 2007). Among the most broadly recognisable crustaceans are the decapods (crabs, shrimps and lobsters), owing to their larger size and commercial value. The dendrobranchiates (prawns) are not generally common on coral reef structures but are common in coastal and interreefal sediment habitats where they support an important trawl fishery on the GBR (Gribble 2003, GBRMPA 2014b). Stomatopods (e.g. mantis shrimp) are possibly the most flamboyant crustaceans on coral reefs, with vivid colouration, remarkable vision (Marshall et al. 1994, Porter et al. 2010) and active and aggressive 'spearing' and 'smashing' hunting techniques, sometimes targeting larger fish prey (deVries et al. 2016, Goatley et al. 2017, Hutchings et al. 2019). Owing to their association with corals, coral-associated decapods (e.g. *Trapezia*, *Tetralia*) have received considerable attention in the literature (see: Stella et al. 2011b), as reflected by a higher relative certainty in expert scores here (Figure 12). The contribution of crustaceans to marine food webs is fundamental and has gained slightly more traction than for the worms, as the hard exoskeletons of crustaceans are more easily identified in gut content analyses (see Case Study 1). However, explicit quantification of population productivity, bioavailability and trophic transfers of crustaceans to higher order predators is essential to our understanding of reef trophodynamics and production functioning.

# Conclusions

## Management of the Great Barrier Reef

Composed of ~3000 individual reefs, the GBR is possibly the most complex natural system in the world (Knowlton 2012, Day 2016). This coral reef ecosystem supports many high-value sectors, including trade, fisheries and tourism, estimated to provide ~AU$6 billion to the Australian economy annually (McCook et al. 2010, Stoeckl et al. 2011, Brodie & Waterhouse 2012, Knowlton 2012, O'Mahoney et al. 2017). Due to its global and ecological significance, the GBR has been managed as a national Marine Park since 1975 (GBRMP Act 1975) and in 1981 became the first coral reef to be granted World Heritage status by the United Nations Educational, Scientific and Cultural Organisation (UNESCO). Management has since focussed on resource use, with a particular devotion to the preservation of biodiversity (McCook et al. 2010) to maintain its OUV. The GBR Rezoning Plan (2004), implemented in July 2004, increased the area of the Marine National Park (Green) Zone from <5% to 33% of the total GBRMP area, enhancing protection of reefs from activities including shipping, fisheries and recreation (Fernandes et al. 2005, Day 2016). This scheme continues to demonstrate significant contributions to the management of biodiversity, ecosystem resilience and socioeconomic values, and so the GBR is often hailed for its gold standard for reef management (McCook et al. 2010, Day 2016).

Given the size of the GBR, spatial confines in jurisdiction have created complexity for ecosystem-based management on the reef, particularly involving land-based riparian and coastal activities (e.g. water quality, riverine discharge, port development) (Brodie & Waterhouse 2012, Day 2016). In addition, parts of the World Heritage Area of the GBR fall outside the Marine Park, further

complicating jurisdictional boundaries and management (GBRMPA 2014c). While biodiversity conservation has historically been considered pivotal to ecosystem-based management of the GBR through successes in marine park zoning (Fernandes et al. 2010, McCook et al. 2010, Day 2016), it is increasingly necessary to target management provisions towards key taxa to support ecosystem functioning and stability in a future ocean (Richards & Day 2018).

In this comprehensive review guided by expert elicitation, we document a diversity of species that are critical to ecosystem functioning on the GBR. This presents the first attempt to rate and compare the functional importance, vulnerability and manageability of the incredible diversity of organisms on a coral reef spanning microbes to predatory fishes. As a result, functional groups remained relatively broad, but greater detail can be found in the following sections where priority groups and species are highlighted. It is noted that this assessment was through the lens of classical reef crest and reef slope habitats on the GBR and that whole-ecosystem management is necessary to maintain the integrity of the reef. Regardless, many of the attributes examined here, at the level of species, ecological processes and ecosystem functioning, are of OUV and contribute greatly to the integrity and cultural values of the GBR and its World Heritage property (GBRMPA 2014c) and for coral reefs in general. So here we provide a first step to inform holistic management approaches aiming to preserve important reef species, values and processes.

In the following sections, we reiterate findings in case-specific compilations of the literature for priority groups that met expectations (Who were the winners?) and provided novel cases (Who were the surprises?). Future work aiming to protect the biodiversity values of coral reefs may use the information compiled here to inform dynamic research and management to safeguard ecosystem functioning (Richards & Day 2018). We highlight suggested areas where management and/or science could increase monitoring and integrate novel approaches while commending current management success in spatial planning (Day 2002) and conservation initiatives (e.g. GBRMPA 2017, 2018a) on the GBR, which seem to effectively capture priority groups and functional entities. It appears that functional groups that met expectations may already benefit from specific incorporation in management initiatives and broad-scale habitat protection as offered by the GBRMP zoning system, as discussed in the following sections. Novel cases are outlined as those that may benefit most from this process-based assessment, as they are not specifically considered in current management strategies. In any case, a default management strategy should exist in education, which can enhance pro-environmentalism, self-efficacy, stewardship, compliance and the transfer of information regarding reef conservation (Zeppel 2008, Myers et al. 2012, Beeden et al. 2014b, Elmer et al. 2017, Vercelloni et al. 2018, Curnock et al. 2019).

### Who were the winners?

*Branching and tabular corals*   Of the coral groups addressed here, tabular, staghorn and other branching corals scored highest in combination for their functional importance and vulnerability on the GBR. The roles of branching and tabular corals in reef ecosystem functioning are fundamental and have been extensively documented. Throughout the Indo-Pacific, fast-growing branching species like *Acropora* and *Pocillopora* contribute most to rapid increases in coral cover (Connell et al. 1997, Pratchett et al. 2015), most notably during years without major disturbance events (Thompson & Dolman 2010). As addressed in Case Study 2, the relative contribution of corals of the *Acropora* genus to net ecosystem calcification outweighs that of other coral groups and calcareous algae, with the greatest contribution to the carbonate budget of the GBR. Reproduction, recruitment and growth rates of structural branching and tabular species are highly variable across time and space (Browne 2012, Browne et al. 2013, Pratchett et al. 2015, Anderson et al. 2017, Anderson et al. 2018), as they can be the most susceptible groups to a range of stressors, including coral bleaching (Baird & Marshall 1998, Marshall & Baird 2000, Loya et al. 2001) and ocean acidification (Fabricius et al. 2011, Madin et al. 2012). Yet they appear to be persistently key to rapid reef growth and

postdisturbance recovery (Pearson 1981, Connolly & Muko 2003, Ortiz et al. 2014, 2018). Ensuring that species key to carbonate production, a positive carbonate budget and reef recovery are protected is a key focus of resilience-based management on the GBR (GBRMPA 2017, 2018a). Thus, current management strategies on the GBR are aligned with maintaining a key species identified in this process-based assessment.

Rates of recovery for coral assemblages are dependent on the relative contributions of new recruits and adult persistence (Connell et al. 1997, Linares et al. 2011, Gilmour et al. 2013, Pratchett et al. 2015). Following localised bleaching in the central GBR in 2001–2002, increases in coral cover up to 10% y$^{-1}$ were primarily driven by tabular *Acropora hyacinthus*, almost entirely attributed to growth of existing corals (Linares et al. 2011). Recent mass-bleaching on the GBR resulted in significant declines in coral recruitment by $\sim$89%, with brooding *Pocillopora* species replacing spawning *Acropora* in the recruitment panel for the first time documented (Hughes et al. 2019a). This supports the suggestion that *Pocillopora* species may be more thermally resilient (Epstein et al. 2019b), owing to the local adaptation required in brooding reproductive modes where gene flow is retained (Ayre & Miller 2004, Miller & Ayre 2004, Baums 2008, Torda et al. 2013a,b). It is increasingly important to determine how coral larval density and supply may scale up to support reef recovery (Doropoulos et al. 2017a, 2018). If the recovery trajectory of *Acropora* and other branching corals are increasingly compromised, then shifts in dominance towards more robust and resilient taxa (e.g. *Porites*) can be expected (Fabricius et al. 2011, Pratchett et al. 2015).

Branching and tabular corals are the preferred target of CoTS (Colgan 1987, Pratchett 2007), and so current CoTS control initiatives should be maintained in support of reef resilience (Westcott et al. 2016). Tabular corals are also more susceptible to coral diseases, including the epizootic White Syndrome (Roff et al. 2006, 2008, 2011, Hobbs & Frisch 2010, Maynard et al. 2011, Hobbs et al. 2015). The five diseases found to affect *A. hyacinthus* also increase in prevalence as water temperature warms (Willis et al. 2004). Due to their morphology, physical impacts from storms and cyclones, vessel groundings and anchor damage are often more significant for branching and tabular corals compared to other coral morphologies (Riegl & Velimirov 1991, Riegl & Riegl 1996, Connell et al. 1997, Hughes & Connell 1999, Dinsdale & Harriott 2004, Madin 2005). But while frequent, anchor damage is considered to have a relatively low impact across the GBR (GBRMPA 2014b, Kininmonth et al. 2014), and current management efforts are proving effective in reducing coral damage in high-use areas through increased awareness and stewardship (Beeden et al. 2014a).

As recognised here, and previously (Ortiz et al. 2014, 2018, GBRMPA 2017), tabular corals are paramount to the resilience of the GBR. However, there may be low ecological redundancy of key tabular corals on the GBR, with just three species considered common; *A. hyacinthus*, *A. cytherea* and *A. clathrata*. There should be continued momentum in the protection of tabular corals on the GBR (GBRMPA 2017, 2018a), in conjunction with research, long-term monitoring programmes and plans to operationalise resilience-based management (GBRMPA 2018b). Tabular corals are easily recognisable and render themselves important features for monitoring by citizen science groups and in education in support of increased awareness, compliance and protection at their greatest level of functioning.

*Acropora hyacinthus* often dominates the reef crest and shallow reef slope on the GBR and coral reefs throughout the Indo-Pacific (Veron 1986), where it exhibits both asexual and sexual reproduction (Wallace 1985, Smith & Hughes 1999). This species is listed as Near Threatened on the IUCN Red List of Threatened Species (Aeby et al. 2008), along with a range of other scleractinian corals on the GBR (Richards & Day 2018). Internationally, all corals are listed on CITES Appendix II, which restricts and controls trade of 'at risk' species, and are important attributes of OUV that contribute to the World Heritage status of the GBR (GBRMPA 2014c). Acroporids have historically been the main targets of coral fisheries on the GBR but with minimal impact on their populations (McCormack et al. 2005).

*In situ* enhancement of coral larval supply and recruitment is an emerging tool to replenish degraded reefs (Heyward et al. 2002, Cooper et al. 2014, dela Cruz & Harrison 2017, Doropoulos

et al. 2019). Similarly, the culture of 'super corals' is an emerging management strategy aiming to enhance reef resilience and recovery via transplanting and outplanting of adapted corals (Auberson 1982, van Oppen et al. 2015, 2017, Barton et al. 2017, Beyer et al. 2018, Camp et al. 2018b, Forsman et al. 2018). There has been success transplanting fragments of *A. hyacinthus* and a range of other coral species onto reefs including in Japan (Okubo et al. 2005), the Maldives (Clark & Edwards 1995) and the Caribbean (Bruckner & Bruckner 2001, 2010, Ladd et al. 2018, 2019). However, there are potential limitations in larval seeding and transplant methods through altered coral-microbe communities and increased disease proliferation (Casey et al. 2015b), reduced species diversity and ecological functioning (Ladd et al. 2018, 2019), as well as spatial limitations at whole-reef scales. Regarding larval seeding techniques, enhancement of a diverse assemblage of coral species is imperative to reef recovery and functioning, and seeding from natural spawning slicks may offer promising opportunities for large-scale coral reef restoration (Heyward et al. 2002, Doropoulos et al. 2019). If targeted research on transplanting and outplanting corals for restoration were to develop further, then functionally important species like *A. hyacinthus* are suggested.

*Microorganisms*  Microbial communities, spanning both host-associated (e.g. corals, sponges, algae) and free-living (e.g. seawater, sediments) taxa, drive biogeochemical cycles in the ocean and undertake numerous functions that underpin the health of coral reef ecosystems (Falkowski et al. 2008, Krediet et al. 2013). They are key to the remineralisation of organic matter and efficient recycling of nutrients, especially in oligotrophic tropical waters (Capone et al. 1992, Tribble et al. 1994, Rasheed et al. 2002, Wild et al. 2005, Ferrier-Pages et al. 2016). The role of microbes in marine invertebrate recruitment and settlement dynamics is also well recognised (Webster et al. 2004, 2011, Siboni et al. 2012a). Their sweeping ratings to ecosystem functioning here are not surprising, though most groups had lower-rated vulnerabilities on the GBR compared to other functional groups.

We outline host-associated phototrophic microbes (e.g. Symbiodiniaceae) as the most critical microbe group to consider in management to maintain a healthy reef, as they are inextricably linked to the survival of their coral hosts (Bourne et al. 2016). Importantly, the relative abundance of particular *Symbiodinium* cells (e.g. Clade D) can increase thermal tolerance in their coral hosts (Howells et al. 2012, 2013, Stat et al. 2013, Bay et al. 2016), an important feature in a warming climate. As we become more aware of the functional roles of microbial communities on coral reefs, it is increasingly apparent that broad-scale community sequencing of the coral holobiont (coral host and microbial symbionts) is required in order to characterise metabolic pathways, coevolution and the acclimation/adaptation of coral reefs to environmental change (Bourne et al. 2016).

Microbes can be the first biological responders to environmental perturbation (Bourne et al. 2016, Glasl et al. 2017, 2018a), with populations that vary in response to external conditions (e.g. season, water quality) and habitat type (Kelly et al. 2014, Tout et al. 2014, Angly et al. 2016, Frade et al. 2016, Agusti et al. 2019). Such environmental parameters can drive the spatial distribution and temporal dynamics of pelagic microorganisms across different habitats of the GBR (Case Study 4). Free-living microbes and bacteria in reef seawater and sediments may be more sensitive indicators of environmental change than coral-microbes (Glasl et al. 2019). Specifically, the Prochlorococcaceae:Synechococcaceae relative abundance ratio provides an indicator of the contribution of nutrient enrichment in GBR waters, which seems to be sensitive both at spatial and temporal scales (Case Study 4). Yet, despite this potential, we have a poor understanding of how microbes provide resilience and buffering across the greater reef system or how they could be used as early warning signals for tipping points as habitats degrade.

Given that microbes have great potential to be used as early warning signals, it would be highly beneficial to establish baseline conditions of the coral reef microbiome, from host-associates to free-living communities, as the current lack of data hinders our potential to use microbes in reef-monitoring programmes. Incorporating the coral reef microbiome into long-term monitoring schemes could

provide useful information to assess and predict broader reef impacts from coastal eutrophication and climate change. This functional group is not part of a specific management initiative on the GBR at present, but programmes such as the Australian Marine Microbial Biodiversity Initiative (AMMBI) conducted by IMOS and Bioplatforms Australia (IMOS 2018) provide an opportunity to expand the sampling and biobanking of marine microbes. Currently, AMMBI includes just one site on the GBR, the Yongala, an iconic mid-shelf shipwreck (Brown et al. 2018). Establishment of microbial baselines through a network of microbial observatories spanning key habitats along inshore to offshore gradients of the GBR would enable a robust assessment of the microbial contribution to reef functioning and health. This would require a combination of analytical techniques (omic approaches: genomic and transcriptomic sequencing, metabolomics, epigenetics) to characterise communities, including *in situ* visualisation to link localisation with broader reef functioning.

*Crustose coralline algae*    CCA was outlined as the most important and vulnerable of the algal groups, in light of the low-rated vulnerability of algal turfs and other macroalgal groups to ecosystem stressors. It is broadly understood that some CCA are important components of the EAM, aiding in reef consolidation (e.g. *Porolithon*) (Matsuda 1989, Diaz-Pulido & McCook 2008), shaping cryptobenthic communities within the reef matrix (e.g. *Mesophyllum*, *Lithothamnion*) (Enochs & Manzello 2012), and in coral recruitment facilitation (e.g. *Titanoderma*) (Heyward & Negri 1999, Harrington et al. 2004, Arnold et al. 2010, Diaz-Pulido et al. 2010, Doropoulos et al. 2012a, 2018). CCA are calculated to be the primary non-coral contributors to net carbonate production on the GBR (Case Study 2) and elsewhere (Bak 1976, Perry et al. 2012a). The functional roles of CCA may be particularly important on reef crests, where they can dominate benthic cover >90% (Atkinson & Grigg 1984, Glynn et al. 1996), including for vertical surfaces with lower rates of sediment accumulation (Kennedy et al. 2017, Duran et al. 2018). Surveys of CCA on the GBR indicate that communities vary considerably in abundance, diversity and composition across the continental shelf and suggest that shelf positioning, habitat, grazing and water quality (e.g. sediment deposition and nutrient loads) are key factors affecting their distribution (Fabricius & De'ath 2001b, Dean et al. 2015). To ensure CCA is preserved at its highest level of functioning, it seems important to maintain the key processes necessary for CCA growth, which primarily involves facilitating high rates of herbivory and reducing sediment loads.

At present, CCA may benefit from the GBRMPA zoning scheme through the protection of particular sections of reef from direct impacts, including anchor damage and fisheries activity, but this is regionally specific. Species-specific information on the distribution and relative abundance of key CCA taxa (e.g. *Titanoderma*, *Porolithon*) is limited, and these groups would benefit from consideration in long-term monitoring programmes. On the GBR, CCA taxa abundant on offshore reefs include *Neogoniolithon*, *Lithophyllum* and *Porolithon* species (Diaz-Pulido & McCook 2008), but generally, they are data deficient, and information is restricted to a few locations on the GBR (Dean et al. 2015). Taxonomic information is very scarce, and the cryptic diversity evident in even the most well-known genera (e.g. *Porolithon*) is quite high (Gabrielson et al. 2018). Attention to these knowledge gaps requires urgent action to ensure CCA can be directly incorporated in management schemes for consideration by local (e.g. GBRMPA) and global (e.g. IUCN Red List) protection agencies, especially for priority species with key roles, such as *Titanoderma* and *Porolithon*, which work to uphold the OUV of the GBR and coral reefs in general.

Some common GBR species (*T. pustulatum*, *P. onkodes*, *Neogoniolithon* sp.) have the remarkable capacity to deter settlement of seaweed spores, which may be an increasingly important feature on future coral reefs to minimise coral-algal phase shifts (Arnold et al. 2010, Vermeij et al. 2011, Gomez-Lemos & Diaz-Pulido 2017), especially considering the active removal of macroalgae is an emergent management strategy (Ceccarelli et al. 2018). *Titanoderma* spp. is one of the preferred substrates for coral settlement, with one experiment showing settlement rates to be 15 time higher on this species compared to other CCA (Harrington et al. 2004). How this translates at the ecosystem

level *in situ* remains unclear. Ocean acidification may have direct impacts on coral reef settlement success through impacts on CCA (Doropoulos et al. 2012a, Doropoulos & Diaz-Pulido 2013, Espinel-Velasco et al. 2018), and so it seems critical to assess the potential ecosystem-level consequences that a loss of key coral settlement inducers could have on the recruitment success on coral reef species. Interestingly, coral larvae seem to show settlement preference towards red-coloured objects (e.g. plastic cable ties, buttons), compared to blue, green and white substrates, which reflects their propensity to settle to pink CCA and – at least in part – decouples the paradigm that settlement cues are solely biochemically driven (Mason et al. 2011, Gómez-Lemos et al. 2018). This may become an important consideration for reef restoration (Mason et al. 2011), particularly since CCA appear to be highly vulnerable to changes in ocean condition (i.e. warming and acidification), even more so than some coral species (Diaz-Pulido et al. 2007, 2012, Anthony et al. 2008).

*Algal turfs and the epilithic algal matrix*     Algal turfs were rated the most functionally important group regarding production functioning, and third overall, but were considered largely resilient to the range of stressors examined here. For this very reason, this group is highlighted here under precautionary principles in context of algal phase shifts in a changing ocean (Roth et al. 2018). Algal turfs are an assemblage of minute, often filamentous, algae that exhibit fast growth, high productivity and rapid colonisation rates. Within the epilithic algal matrix, turfing species dominate surprisingly large proportions of coral reefs (Diaz-Pulido et al. 2016), where they are critical to primary production in oligotrophic waters (Adey & Goertemiller 1987, Klumpp & McKinnon 1989), harbour detritus and microorganisms (Wilson et al. 2003) and host a diversity of cryptic invertebrates (Kramer et al. 2012). While the taxonomy of turfs and EAMs is complex, offshore reefs are often dominated by the red alga *Ceramium punctatum* and the blue-green algal family *Nostococaceae* (Scott & Russ 1987), while inshore reefs are typically dominated by the green algae *Acetabularia calyclus* and *Cladophora fascicularis*, the filamentous brown algae *Sphacelaria* spp. and the *Falkenbergia* stage of the red alga *Asparagopsis taxiformis* (Diaz-Pulido & McCook 2008).

EAMs cover high proportions of reef flats (50%–80%) and reef slopes (30%–70%) on the GBR, with particularly high productivity in summer (Klumpp & McKinnon 1992). They lay the foundations for benthic production functioning, with particularly important roles in the fixation of nitrogen and its rapid distribution across trophic pathways (Borowitzka et al. 1977, Borowitzka 1981, Wilkinson et al. 1984, Hatcher 1988, Larkum et al. 1988). Rates of turf algal productivity strongly predict herbivore biomass (Carpenter 1986, Russ 2003, Tootell & Steele 2016), and, conversely, herbivores directly regulate turf canopy height (Carpenter & Williams 1993, Mumby et al. 2013a). Herbivorous grazers are suggested to consume around half of the total annual net production of the EAM, making it directly available to the food web (Hatcher & Larkum 1983, Klumpp & Polunin 1990), particularly on reef flats (Bellwood et al. 2018).

There can be interesting top-down and bottom-up drivers of turfing seascapes on coral reefs, including from wave exposure, nutrification, sedimentation and herbivory (Carpenter & Williams 1993, Vermeij et al. 2010, Clausing et al. 2014, Bejarano et al. 2017, Tebbett et al. 2017a, Roff et al. 2019). Variability in turf assemblages occurs at small spatial scales (Harris et al. 2015), with thresholds in canopy heights and sediment depths (>3 mm) found to reduce herbivory, alter turf metabolism and impair coral recruitment (Carpenter & Williams 1993, Birrell et al. 2005, Bellwood & Fulton 2008, Arnold et al. 2010, Goatley & Bellwood 2012, Clausing et al. 2014, Doropoulos et al. 2017a,b, Lam et al. 2018). There is compelling evidence that the canopy height of turf algae can predict productivity, sedimentation, herbivory, wave exposure and recruitment success, which could be an important attribute to monitor so as to establish spatial data for this priority group on the GBR and on coral reefs in general. Further, turfs are a more pertinent stress when combined with sedimentation and/or nitrification. How dynamic states in turf algal productivity (e.g. turf height), nutrification, sedimentation and wave exposure (hydrodynamics) interact to impact ecological

functioning needs to be explicitly characterised. Precautionary measures should continue focus on water quality (e.g. eutrophication, sedimentation) in catchment and riparian management to facilitate natural moderation of turf growth through herbivory. Keeping turf canopy height low (<3 mm) is important for the successful recruitment of corals and other reef species (Roth et al. 2018).

Despite the lack of information on long-term trends in algal condition, major changes are expected to occur regarding their distribution, abundance and composition in a changing ocean, driving significant alterations to ecological functioning (Diaz-Pulido et al. 2007, 2011a). On turf- and macroalgal-rich reefs, the relative abundance and diversity of microbial communities also increase with the potential to influence nutrient pathways and reef health (Haas et al. 2016, Brown et al. 2019). Ocean acidification is likely to enhance algal turf productivity and biomass (Ober et al. 2016), cause shifts in epilithic communities to turfing and cyanobacteria assemblages (Diaz-Pulido & McCook 2002, Bender et al. 2014b) and increase rates of bioerosion and reef carbonate dissolution (Carreiro-Silva et al. 2005, Tribollet et al. 2006, Schönberg et al. 2017). Even marginal differences in turf canopy height impact micro-scale circulation and can alter turf metabolism and chemistry across diffusive boundary layers (Carpenter & Williams 1993). This will directly influence the balance between reef growth (calcification) and destruction (dissolution) in a future ocean, with predictions that coral reefs will switch to a state of net dissolution by the end of this century (Albright et al. 2018, Eyre et al. 2018). However, the raw contribution of microfloral borers to net reef erosion is difficult to quantify, and knowledge gaps remain (Case Study 2) (Hutchings 1986, Glynn & Manzello 2015). Concerns over shifting carbonate budgets should address all forms of bioerosion, including rates within the EAM and endolithic algae, especially given the propensity for turf algae to rapidly colonise dead coral substrate following perturbation (Diaz-Pulido & McCook 2002) and that bioerosion rates are likely to increase due to environmental change, with significant impacts on reef health and resilience. Rates of carbonate dissolution within the reef matrix also need to be quantified, as these cements may be more responsive to changes in the saturation state of calcium carbonate under ocean acidification scenarios (Reyes-Nivia et al. 2013).

At present, the primary management objective regarding algal turfs on the GBR exists in the maintenance of herbivore assemblages, particularly those that regulate the EAM, to reduce algal growth and facilitate the competitive dominance of reef-building corals. While herbivores are not a common fisheries target on the GBR (e.g. Case Study 3), herbivore-centric management campaigns are already underway to minimise herbivore landings in support of reef resilience in a changing ocean (GBRMPA 2016, 2017). Additionally, *in situ* cultivation of some macroalgal species has been suggested as a potential management strategy to, at least in part, mitigate or buffer ocean acidification and its effects on coral reefs through biogeochemical functioning (Mongin et al. 2016a).

*Crown-of-thorns starfish outbreaks (and triton snails)*     The pervasive impacts of coral predation by CoTS have been extensively documented (e.g. Pratchett et al. 2014, 2017a, Babcock et al. 2016a, Cowan et al. 2017, Wilmes et al. 2018). While high-density populations of CoTS can adversely affect whole reefs, their impacts at low densities are minor (Branham et al. 1971), as observed on the GBR for decades at One Tree Island (Maria Byrne, pers. comm.) and other largely unaffected reefs of the Capricorn Bunker Group (Sweatman et al. 2015). The driving forces behind CoTS population outbreaks are widely debated, but their extreme fecundity and reproductive potential (Uthicke et al. 2009, Babcock et al. 2016b, Rogers et al. 2017) and high levels of connectivity across the GBR (Matz et al. 2018) are likely strong determinants (Hock et al. 2014, 2017). Historically, research on the CoTS outbreak phenomenon has been significantly weighted towards the larvae (e.g. the nutrient runoff hypothesis; Lucas 1982) and adults (e.g. the predator removal hypothesis; Endean 1969), and management strategies and their implementation have developed in line with this research focus (Westcott et al. 2016).

For larvae, management has been centred on improving water quality in catchment areas to limit the potential success of early developmental stages in the plankton (Fabricius et al. 2010, Wolfe

et al. 2015b, Wooldridge & Brodie 2015), although CoTS larvae appear to have high resilience to oligotrophy (Olson 1987, Wolfe et al. 2015a, 2017, Carrier et al. 2018) and the remarkable ability to clone in the plankton (Allen et al. 2019). Outbreaks are also documented on reefs not influenced by anthropogenically driven eutrophication, including on the GBR and elsewhere (Lane 2012, Miller et al. 2015, Roche et al. 2015). Yet in the absence of strong evidence to the contrary, precautionary measures should continue to focus on improving water quality across catchment areas to mitigate the potential for runoff-induced eutrophication to enhance larval success.

For CoTS adults, management on the GBR has included the protection of the once-overfished triton snail (*Charonia tritonis*) (Endean 1969, Cowan et al. 2017) and the active and labour-intensive removal or culling of adults (Pratchett et al. 2014), including innovative injection and detection methods (Dayoub et al. 2015, Moutardier et al. 2015, Bostrom-Einarsson & Rivera-Posada 2016, Bostrom-Einarsson et al. 2018). Current measures of control (e.g. the NESP Integrated Pest Management project; Westcott et al. 2016) are commended, and continued development of this and other such programmes is encouraged, including involvement with citizen science groups and in education. The high rankings for triton snails within this report, particularly for the predation process, reflect their perceived niche role as key predators of CoTS and their historical vulnerability to overharvest, as reviewed previously (see Hall et al. 2017). Biocontrol of CoTS populations through triton snail predation would be most effective when aiming to keep non-outbreak populations at low densities so as to lessen the potential for outbreaks to initiate (Hall et al. 2017). There is evidence that CoTS are less abundant in no-take fishing zones on the GBR and elsewhere (Dulvy et al. 2004, Sweatman 2008, McCook et al. 2010), suggesting that heavy fishing may encourage outbreaks through suppression of a multi-level trophic cascade (i.e. reduced predation pressure across various life stages) (Cowan et al. 2017). Yet the lack of information on the basic biology of CoTS of any age-class *in situ* means that the relationship between fishing and outbreaks remains elusive (Sweatman & Cappo 2018). Information is particularly limited for CoTS juveniles (Case Study 5), although recent work demonstrates high densities of juvenile CoTS can be detected (Wilmes et al. 2016, 2018, 2020), and that juveniles can survive for years before the ontogenetic shift to coral (Deaker et al. 2020a,b). Characterising this life stage may provide an important opportunity to improve the early detection of outbreaks and their management (Sweatman & Cappo 2018).

## CASE STUDY 5:  JUVENILE CROWN-OF-THORNS STARFISH 'IN WAITING': THE MISSING LINK IN POPULATION AND CONNECTIVITY MODELS

*Dione Deaker and Maria Byrne*

Settlement of CoTS larvae is typically triggered by CCA or biofilm (Johnson et al. 1991, Wolfe et al. 2015b), where they begin their benthic life stage as small herbivorous juveniles, with an ontogenetic shift in diet to become coral predators as they grow (Yamaguchi 1974, Johansson et al. 2016, Kamya et al. 2018). As for the great diversity of marine invertebrates, the early life history stages of CoTS experience high mortality rates (Keesing et al. 2018, Wilmes et al. 2018). In order to seed a population outbreak of deleterious corallivorous adults, high survival rates of the herbivorous juvenile are required. However, the biology and ecology of juvenile CoTS are poorly characterised due to their highly cryptic nature.

In an experiment over 4.5 months (139 days), juvenile CoTS were raised on one of three diets: crustose coralline algae (CCA), *Amphiroa* sp. (calcifying algae) or biofilm (Figure CS5.1) and their growth rates quantified. As for adult CoTS, juveniles leave feeding scars on their algal food source (Figure CS5.1). Juveniles fed CCA and *Amphiroa* grew the same number of arms (Figure CS5.2A) and at the same rate until day 43, when those fed CCA began to grow faster
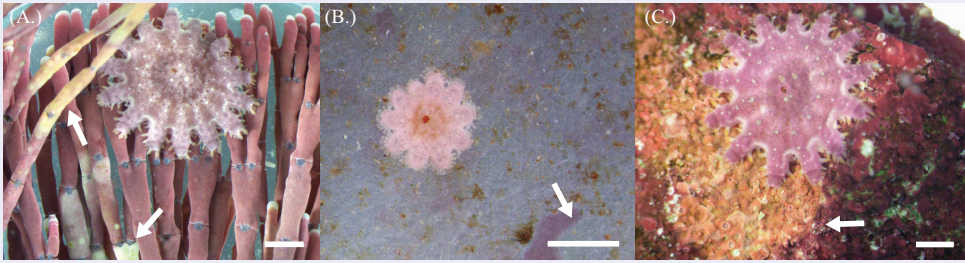
**Figure CS5.1**   Juvenile CoTS leave feeding scars (white arrows) on algal food sources; (A) *Amphiroa* sp., (B) biofilm and (C) CCA (scale bars = 2 mm).
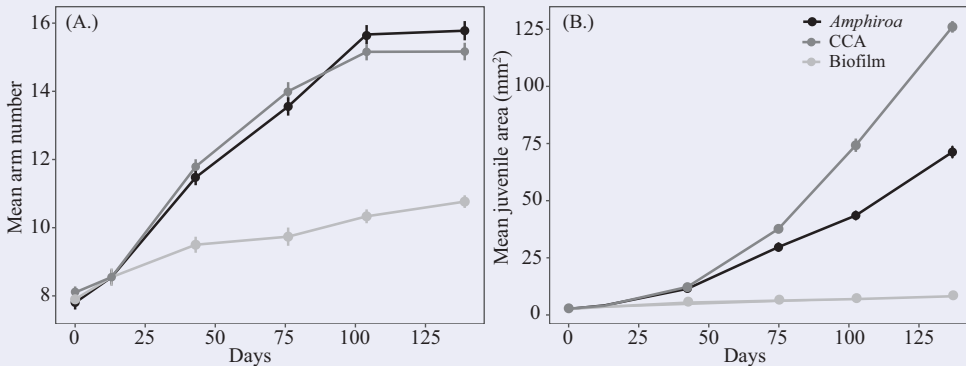


**Figure CS5.2**   Mean (±SE) (A) number of arms and (B) area of CoTS juveniles raised on one of three algal diets.

(Figure CS5.2B). Juveniles were able to consume and survive on biofilm, although growth was marginal (Figure CS5.2A,B). When offered a choice between the three diets, they selected either CCA or *Amphiroa* over biofilm, indicating that they can identify preferred food at this early life stage.

In general, CoTS have a broader diet range than previously recognised. Their ability to subsist on biofilm alone suggests that juvenile CoTS may be able to survive for extended periods of time in the coral rubble matrix (or other EAM habitat) following settlement and prior to their ontogenetic switch to corallivory. This may create a time lag across the larval–settlement–juvenile–outbreak continuum of the CoTS life history, which is currently uncaptured in population models. As juvenile growth rates are strongly linked to resource availability, current growth estimates that are largely based on laboratory cultures (e.g. Wilmes et al. 2016) may not reflect size-age relationships in nature. These 'juveniles in waiting' complicate our ability to understand the processes that drive CoTS outbreaks and require extra attention. Early warning signals for outbreaks may exist in the benthos through juvenile reserves, but where these exist remains largely unknown (Johnson et al. 1991, Wilmes et al. 2016, 2018). The characterisation of habitat preferences of CoTS juveniles has the potential to reshape how we survey, detect and manage CoTS on the GBR and on coral reefs in general.

*Herbivorous parrotfishes*   There is a diverse but critical range of roles in the regulation and removal of algae by nominally herbivorous fishes in coral reef ecosystems (Bellwood et al. 2006a, Burkepile & Hay 2008, 2011, Steneck et al. 2017). In our process-based assessment, scraping and excavating parrotfishes were among the most ecologically significant, driven by their roles shaping habitat functioning (bioerosion, ecosystem engineering, recruitment facilitation). Parrotfishes are the primary contributors to bioerosion on the GBR, as on other reefs (Perry et al. 2012a), with the capacity to exacerbate the total carbonate budget through their bioerosive processes (Case Study 2). The potential for this activity to influence or buffer reef biogeochemistry would be interesting to quantify in context of ocean acidification, particularly for mass excavators such as *Bolbometopon* (Goldberg et al. 2019), as posited for deposit-feeding sea cucumbers (Schneider et al. 2011, Purcell et al. 2016a, Vidal-Ramirez & Dove 2016, Wolfe et al. 2018).

There may be limited functional redundancy among parrotfishes, which demonstrate spatial variability in their contributions to herbivory, bioerosion, ecosystem engineering and recruitment facilitation across GBR (Hoey & Bellwood 2008). *Bolbometopon muricatum*, one of the largest parrotfishes on coral reefs, appears to be most significant on outer-shelf reefs, while *Scarus rivulatus* (scraper) and *Chlorurus* spp. (excavators) are more important on inner- and mid-shelf reefs (Hoey & Bellwood 2008). *Bolbometopon muricatum* is listed as Vulnerable on the IUCN Red List owing to its susceptibility to overfishing globally (Dalzell et al. 1996, Aswani & Hamilton 2004, Donaldson & Dulvy 2004, Chan et al. 2012, Bejarano et al. 2013, 2014); though it is generally not fished on the GBR (Case Study 3). Recruitment of this species may also be vulnerable to habitat loss attributed to water quality issues (Hamilton et al. 2017). Other parrotfishes common on the GBR are listed as Data Deficient or Least Concern by the IUCN and are currently seldom targeted by commercial and recreational fishers on the GBR. While the impact from fisheries seems low for herbivores at present, there has not yet been an assessment on the total extractive use of herbivores for the GBR.

Changes in herbivory can result in undesirable shifts in coral reef ecosystems (Carpenter 1990, Newman et al. 2006, Bozec et al. 2013, Mumby et al. 2013b, 2016, Ainsworth & Mumby 2015, Graham et al. 2015, Roff et al. 2015), with natural reversals from algal dominance back to coral-dominated states rarely observed (Diaz-Pulido et al. 2009, Rasher et al. 2013). It appears that high-diversity reefs across the Indo-Pacific have a better capacity to recover from disturbance without entering an algal-dominated phase, as observed on Caribbean reefs (Roff & Mumby 2012), though alternate ecosystem states are dynamic in terms of time and space on coral reefs (van de Leemput et al. 2016). Most herbivorous fish groups were considered resilient to environmental stressors here, with densities of some grazers (e.g. parrotfishes) even documented to increase post disturbance, perhaps due to the increased algal production that typically follows coral mortality (Cheal et al. 2008, 2010, Wilson et al. 2009, Graham et al. 2015, Russ et al. 2015, Hempson et al. 2018c). Removal of particular larger herbivores can even reduce coral recovery at least three-fold by allowing modest increases in some macroalgal genera that deter coral settlement (Doropoulos et al. 2016, Mumby et al. 2016). Long-term maintenance of reef habitat and production functioning requires sufficient parrotfish stocks (Mumby 2016). Protection through Herbivore Management Areas is an emerging resilience-building tool in response to severe coral bleaching on reefs where herbivores are key targets (Chung et al. 2019).

While herbivorous fishes were generally considered less vulnerable on the GBR than other functional groups, lessons learned from other coral reefs where they have been intensively overfished suggest that early protection should be considered to avoid shifting baselines (Bozec et al. 2016). In support of this, GBRMPA released a conservation initiative in 2016 aimed to deter fishers from targeting herbivorous groups, which act as 'natural lawnmowers and keep seaweed levels under control by grazing' (GBRMPA 2016, 2017). Maintaining herbivore assemblages, particularly those that regulate the EAM, would facilitate the competitive dominance of reef-building corals. In extreme cases of algal growth where intervention is necessary, protection of herbivores may be best coupled with active removal of macroalgae (Ceccarelli et al. 2018), though likely labour intensive. Outplanting of the native herbivorous grazing sea urchin, *Tripneustes gratilla*, to reduce the overgrowth of invasive

algal species has been a successful management focus on Hawaiian reefs for over a decade (Conklin & Smith 2005, Stimson et al. 2007, Westbrook et al. 2015, Neilson et al. 2018).

Wave exposure, nutrification and sedimentation can determine relationships between turf algal productivity and herbivory (Carpenter & Williams 1993, Vermeij et al. 2010, Clausing et al. 2014, Bejarano et al. 2017, Tebbett et al. 2017a, Roff et al. 2019), but tipping points need to be explicitly quantified to inform holistic management aiming to enhance the recruitment and the competitive dominance of reef-building corals. It is critical to note that the functional importance of key herbivores is dynamic with changing ecosystem states (Hempson et al. 2018c). For example, the removal of carbonates by mass-excavators (*Bolbometopon*) may be critical in systems where some corals dominate, but as fast-growing corals are lost and states shift to turf-dominance, species that regulate turfs would emerge as the key functional groups (Bellwood et al. 2019). Both research and management must be flexible to the dynamics of changing ecosystems to remain ecologically relevant.

## Who were the surprises?

*Chemoautotrophic microbes*    There is a growing awareness of the importance of chemoautotrophic microbes (e.g. Archaea) in many marine habitats. More information is known for this group in the water column, where they are highly prevalent and may have significant roles in carbon and energy cycling, particularly for the Thaumarchaeota of the Marine Group II Archaea (Jiao et al. 2010, Zhang et al. 2015, Angly et al. 2016, Liu et al. 2017). In benthic systems, they were probably first recognised as important components of the sponge microbiome, with specific roles in nitrogen and ammonia cycling (e.g. Thaumarchaeota, *Nitrospira*) (Taylor et al. 2007, Bayer et al. 2008, Webster & Taylor 2012, Bourne & Webster 2013a) and altered community dynamics following bleaching stress (e.g. *Crenarchaeota*) (Lopez-Legentil et al. 2008, 2010). In corals, a diverse endolithic community has also been identified, which is likely to be important for sustaining coral health through the exchange of nutrients, especially during periods of bleaching-related stress (Fine & Loya 2002). Motile archaeal communities are prevalent within the coral mucus and are likely involved in complex nutrient cycling (Kellogg 2004, Frade et al. 2016), while anaerobic methanotrophic Archaea (ANME) can be tightly coupled with nitrogen cycling and sulphate reduction in complex communities within coral polyps (Figure 13) (Wegley et al. 2007, Kimes et al. 2010, Bourne & Webster 2013a). There has also been an increased interest in microaerophilic and anaerobic processes within benthic substrates. Microbial communities vary between oxic (e.g. *Planctomycetaceae*, *Proteobacteria*) and anoxic (e.g. ANME) sediments, where they play functionally important roles in organic matter degradation and nutrient cycling (Figure 13) (Rusch et al. 2009, Rusch & Gaidos 2013).

To date, chemoautotrophic microbes have been poorly represented in the literature, owing to difficulties in culturing and detecting these groups. As such, their final ranking above phototrophic and heterotrophic microbes here is somewhat surprising. Archaeal communities are more strongly shaped by geography rather than host-specificity as displayed by other microbes and bacteria (Siboni et al. 2012b, Frade et al. 2016), although this may simply be an artefact of insufficient investigations that include archaeal-specific primers. On the GBR, prevalence of some chemoautotrophic microorganisms in the inshore lagoon system suggests seasonal variation in assemblages driven by floodwaters and consequent differences in water quality and suspended sediments (Case Study 4) (Angly et al. 2016), but improved detection and monitoring of microbial groups is required, including for spatially explicit Archaea.

Microbial communities can likely be used to provide early warning signals for ecosystem change (Bourne et al. 2016, Glasl et al. 2017, 2018a), but this emerging bioindicator tool requires further development. As in the microbes section above, chemoautotrophic microbes are not specifically included in a management strategy on the GBR, but AMMBI (Brown et al. 2018, IMOS 2018), and similar monitoring platforms provide the opportunity to expand sampling and biobanking of important marine microbe groups. If such monitoring requires a refined or targeted methodology, we recommend that this functionally important chemoautotrophic group be a prime candidate. In
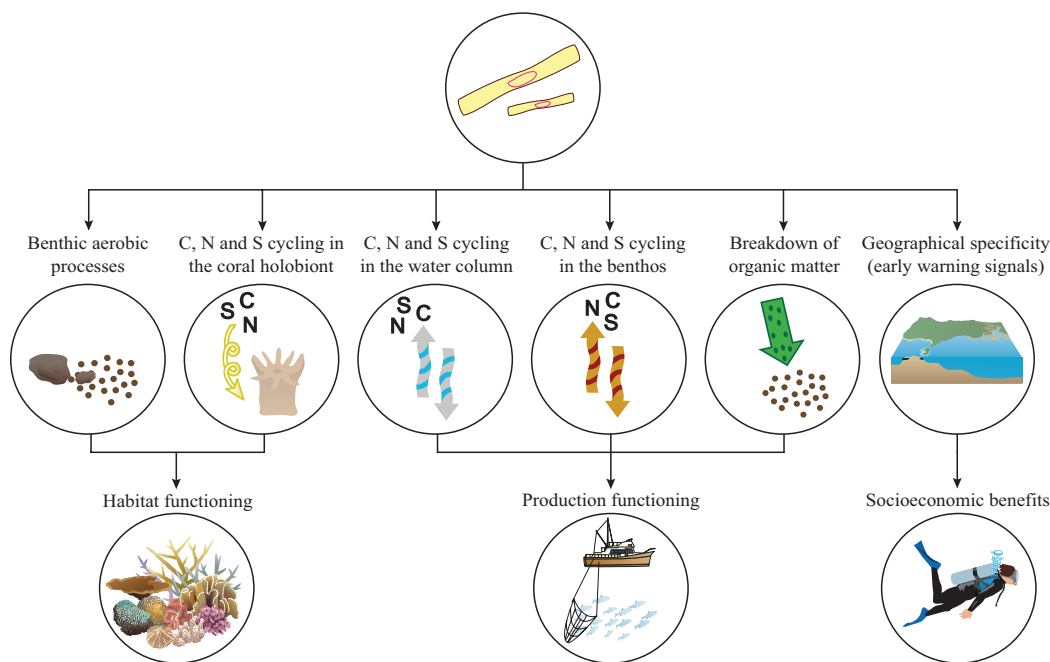
**Figure 13** Schematic of the influences of chemoautotrophic microbes (e.g. Archaea) on ecosystem processes, functioning and services. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

the meantime, precautionary measures should maintain focus on water quality while links between runoff (nutrients, sediments, etc.) and microbial assemblages are characterised.

*Cleaner wrasse*    Cleaner wrasses were the only fish group that scored in the top priority quadrant for important and vulnerable species (Figure 4) that were also considered a higher-priority candidate for management (Figure 11). This ranking was likely upweighted by their low functional redundancy, as cleaner wrasse scored lower for most processes compared to other fish groups. Cryptobenthic fishes scored alongside cleaner wrasse in their combination of functional importance and potential vulnerability (Figure 4) but were deemed a lower priority for management compared to the other fishes examined (Figure 11), likely owing to their incredible display of population productivity for a vertebrate (Depczynski & Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018, 2019).

The ecological importance of cleaning organisms and their cleaning stations in marine community dynamics has long been recognised, but is largely overlooked (Cote 2000, Vaughan et al. 2017). There are over 200 species of cleaner fishes from 106 genera, and over 50 species of cleaner shrimp from 11 genera, recorded to exhibit cleaning behaviour (Cote 2000, Vaughan et al. 2017). In context of the GBR, here we draw focus on the bluestreak cleaner wrasse (*Labroides dimidiatus*), as it has received considerable attention in the literature as a dedicated specialist cleaner. Though typically existing at very low densities, cleaner wrasse can shape reef fish assemblages through the active removal of deleterious ectoparasites, dead skin and mucus from client fishes (Figure 14). Parasitic gnathiid isopods rapidly reoccupy their fish hosts within 24 hrs on the GBR – where they are in high abundance – a process that requires clients to frequently return to cleaning stations (Grutter 1996, 2003). The effects of gnathiids on hosts vary, ranging from partial blemishes and lesions to death, with early life history stages of fishes most susceptible
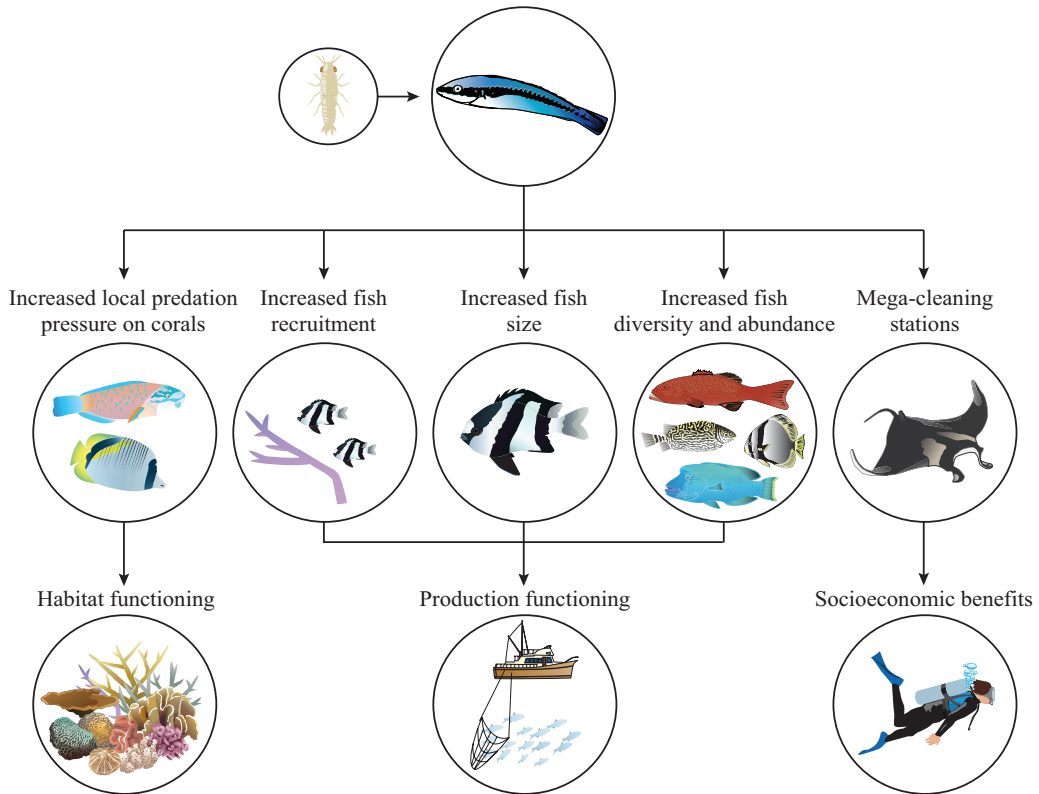
**Figure 14** Schematic of the influences of cleaner wrasse (*Labroides dimidiatus*) on ecosystem processes, functioning and services. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/) and (Hutson et al. 2018).

to parasitic micropredation (Grutter et al. 2008, 2011, Penfold et al. 2008, Sun et al. 2012, Jenkins et al. 2018, Duong et al. 2019).

Through the cleaning process, *L. dimidiatus* have been documented to reduce stress hormones in the client (Soares et al. 2011); increase fish size, density, diversity and survival (Grutter et al. 2003, Clague et al. 2011, Waldie et al. 2011); encourage juvenile recruitment (Sun et al. 2015) and enhance fish cognitive performance (Binning et al. 2018) (Figure 14). In a series of long-term (>8 year) removal experiments on the GBR, some reefs were up to 66% lower in fish abundance and 33% less species rich in the absence of *L. dimidiatus* (Waldie et al. 2011), with a 27% increase in the size of a model damselfish (Clague et al. 2011). In the context of ecosystem functioning, the symbiotic relationship established between cleaners and a diversity of marine fauna is likely to improve production functioning on coral reefs (Figure 14) – although direct links to fisheries productivity are yet to be quantified. Cleaners also have the potential to influence habitat functioning indirectly by attracting excavating (e.g. parrotfishes) and corallivorous (e.g. butterflyfishes) species to cleaning stations, increasing the exposure of coral communities to bioerosion and predation processes (Adam 2012). How cleaners influence reef resilience and health beyond fish-fish interactions (i.e. coral growth, reef recovery) requires attention.

In the context of ecosystem services, cleaners attract a diversity of marine megafauna, including manta rays, turtles, mola mola, sharks and large predatory fishes, to specific reef locations (Oliver et al. 2011, Jaine et al. 2012, Couturier et al. 2014, 2018, Murie & Marshall 2016). Established 'mega stations' (cleaning stations that attract megafauna) are primary targets for recreational divers and

tourist operators on reefs from Mozambique, through the Indo-Pacific and Caribbean, with direct socioeconomic benefits (Figure 14). Manta rays can spend ~8 hr per day engaging in cleaning activity, which inspire tourist hotspots (Marshall & Bennett 2010a,b, Rohner et al. 2013, Germanov et al. 2019). Additionally, their presence on cleaning stations can be used as indicators of environmental conditions of water quality, hydrodynamics and food availability (Armstrong et al. 2016, Barr & Abelson 2019). On the GBR, ecotourism in the southern-most coral cay, Lady Elliot Island, largely benefits from manta ray associations with cleaning stations (Couturier et al. 2014). Mega cleaning stations are also found on Osprey Reef in the Coral Sea (O'Shea et al. 2010), supporting high-revenue tourist operations (Stoeckl et al. 2010a,b). The influence of cleaners on regional- and global-scale socioeconomics seems so poorly appreciated, and their broader integration into ecosystem monitoring, citizen science and tourism initiatives seems important.

Little information exists regarding the vulnerabilities of cleaner wrasses. Globally, they are primary targets for the aquarium industry but are among the lowest survivors in amateur tank setups owing to their highly specialised diets and symbioses (Rhyne et al. 2017), though they are rarely harvested from the GBR (Roelofs 2008). *Labroides dimidiatus* is considered Least Concern by the IUCN (Shea & Liu 2010), but naturally existing at low densities with strong site fidelity, cleaner wrasse (and other cleaning organisms) may be particularly vulnerable to environmental perturbation (Rosa et al. 2014, Vaughan et al. 2017, 2018, Triki et al. 2018). Following the extreme weather events that affected the GBR during 2016, *L. dimidiatus* densities decreased by ~80% from long-term monitoring sites on Lizard Island (Triki et al. 2018). However, surveys beyond these long-term sites suggest *L. dimidiatus* may have increased in abundance around Lizard Island between 2011 and 15 (Ceccarelli et al. 2016). Though poorly characterised, it is probable that fast recovery of cleaner populations post disturbance would help re-establish cleaning interactions and the benefits they provide (Triki et al. 2018), particularly since gnathiid isopod densities show fast recovery post bleaching (Sikkel et al. 2019). It is important to understand how environmental stressors (e.g. bleaching) impact cleaners and their interactions on cleaning stations and to what extent a loss of cleaners would affect reef functioning.

The biological, functional and socioeconomic benefits of cleaning stations provide a strong case for the need to protect these localised habitats to maintain ecosystem functioning and the services cleaners support (Figure 14). At present, cleaner wrasse are not specifically protected on the GBR or elsewhere. We suggest that protecting cleaning stations as hubs of ecosystem functioning may be a more appropriate and successful management initiative than protecting the cleaners themselves. Owing to their site fidelity, local-scale assessments in support of reef resilience might assign some high priority to cleaners and cleaning stations as key features, as outlined in the GBRMPA Blueprint for Resilience regarding herbivores and tabular corals (GBRMPA 2017, 2018a).

*Bivalves*    Giant clams (Tridacnidae) and other bivalves (e.g. oysters) scored surprisingly high for habitat functioning, driven by processes of calcification and recruitment facilitation. Shell and 'bed' construction by bivalves can contribute significant structural complexity to the reef, with both alive and dead structures encouraging recruitment and providing refugia for a diversity of symbiotic and commensal organisms, a particularly important feature when coral cover is low (Beukers & Jones 1998, Lecchini et al. 2007, Cabaitan et al. 2008, Neo et al. 2015). This may be an increasingly important attribute to document and protect in a changing ocean. Shallow-water benthic bivalves are natural controllers of eutrophication and water quality through their filter-feeding processes (Figure 15), perhaps most importantly on nearshore reefs (Klumpp et al. 1992, Klumpp & Lucas 1994, Neo et al. 2015), enhancing an important aesthetic reef value (GBRMPA 2014c, Marshall et al. 2018, Vercelloni et al. 2018). Some bivalves are also important bioeroders, such as the boring clam, *Tridacna crocea*, which can dominate reef and intertidal areas on nearshore (e.g. Orpheus Island) and offshore (e.g. One Tree Island) reefs (Hutchings 1986). As bioerosive processes become more pervasive on coral reefs, knowledge gaps for non-parrotfish bioeroders on the GBR (including
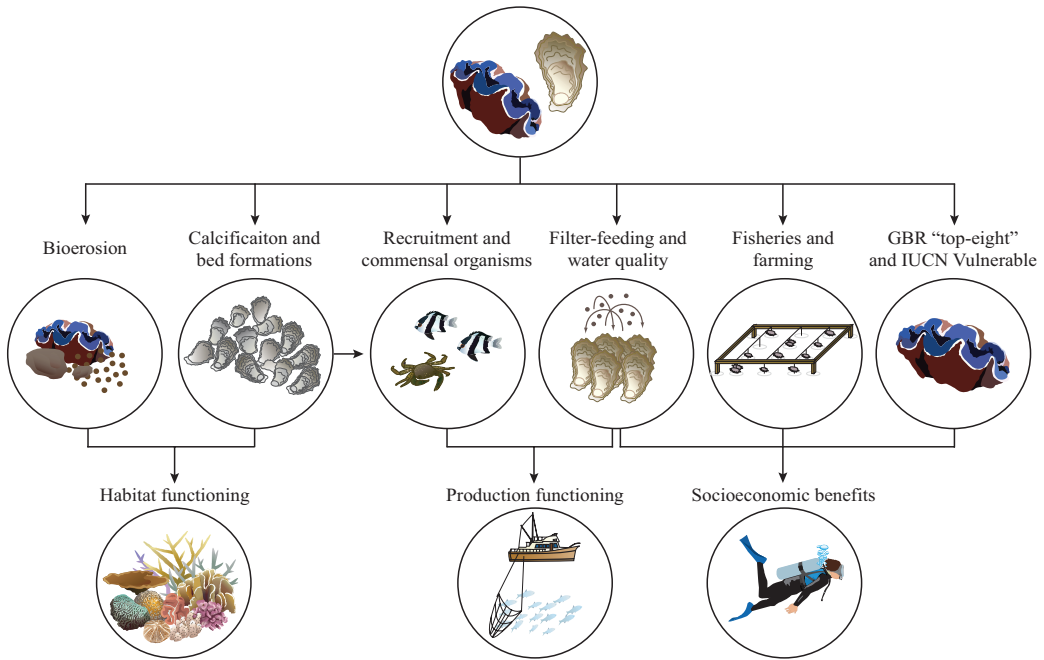
**Figure 15** Schematic of the influences of bivalves (e.g. Tridacnidae, oysters) on ecosystem processes, functioning and services. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

bivalves, sponges, microborers) should be filled to empower calculations on the total carbonate budget for the reef and predictions on future reef accretion and recovery processes.

As for corals, giant clams host zooxanthellae that aid in respiration and growth (Klumpp et al. 1992), but this makes them prone to bleaching under warm-water exposure (Buck et al. 2002, Leggat et al. 2003). As calcifying organisms, molluscs and their thinly calcified veliger larvae are among the most vulnerable to changing ocean temperature (warming) and chemistry (acidification) (Przeslawski et al. 2008, Byrne 2011, Przeslawski et al. 2015), including impacts on juvenile survival of some tridacnids (Watson et al. 2012). Ocean acidification may also accelerate bioerosion processes within bivalve bed formations (Wisshak et al. 2014), but suitably high levels of light may work to ameliorate the negative effects of ocean acidification on some tridacnids (Watson 2015). Improving water quality would enhance the potential for light levels to ameliorate the negative impacts of ocean change on photosynthetic tridacnids, particularly for nearshore populations.

Many commercially important bivalves have been decimated by local stressors such as fisheries and habitat and water quality degradation (Kirby 2004, Bersoza Hernández et al. 2018), including on the GBR (Gillies et al. 2015). The most important bivalve to fisheries on the GBR may be the saucer scallop, *Amusium japonicum ballotti*, which operates as a trawl-fishery with a range of management implications (Courtney et al. 2008, 2015), but this occurs beyond the focal reef-centric habitat investigated here. Oysters (*Saccostrea cucullate*, *Saccostrea echinate*, *Isognomon ephippium*, *Pinctada* spp.) and mussels (*Trichomya hirsuta*) may have once been significant reef formers on the GBR, particularly in the sheltered and intertidal habitats of estuaries, nearshore reefs and mangroves, but were also primary shellfish fisheries targets (Gillies et al. 2015, Lewis et al. 2015). Subtidal oyster reefs appear to be functionally extinct over their former range along the east coast of Australia (Beck et al. 2011), but the extent of this on the GBR is historically poorly characterised.

Giant clams, namely the larger species *T. gigas* and *T. derasa*, experienced heavy exploitation through poaching on the GBR (Pearson 1977, Dawson 1985), with all tridacnids consequently listed on Appendix II of CITES by 1985. Both *T. gigas* and *T. derasa* are also listed as Vulnerable on the IUCN Red List of Threatened Species (Wells 1996a,b, Richards & Day 2018). Giant clams are the only invertebrates listed in the 'top-eight' species to see on the GBR (https://www.barrierreefaustralia.com/info/great8/), a significant tourism drawcard. Experimental aquaculture and cultivation of *T. gigas* has occurred on the GBR previously (Orpheus Island) (Crawford et al. 1988, Lucas et al. 1989), with bed formations that still exist integrated in the reef framework today. Population transplants and aquaculture of functionally important bivalves deserves consideration to optimise benefits from the natural infrastructures of reef-forming molluscs, including fisheries production, shoreline protection, water filtration and tourism (Figure 15). Precautionary measures should maintain focus on water quality to enhance the resilience and survival of bivalves on the GBR and elsewhere.

*Coral-associated decapods*   Coral-associated decapods are strongly bound to their coral host, where they take refuge from a range of reef and cryptic predators, including squirrel fishes, wrasses and eels (Hiatt & Strasburg 1960). From a bottom-up perspective, coral-associated crabs can form up to 70% of a reef fish's diet, particularly for species with specialised morphologies that can access prey items from the intricacies of the coral framework (Hobson 1974, Rinkevich et al. 1991). The most common and well-recognised coral-associated crabs on the GBR include the *Trapezia*, *Tetralia* and *Cymo*, which primarily occupy acroporids and pocilloporids (Stella et al. 2011b). Interestingly, *Trapezia* typically occupy pocilloporid corals, while *Tetralia* are found in acroporids (Patton 1983, 1994), where they are both often observed grazing on their host's live tissue, mucus or fat bodies (Stimson 1990, Rinkevich et al. 1991, Castro 2000, Castro et al. 2004). This grazing activity is not considered to have negative effects on their host, given these coral crabs generally exist at low densities (~2 individuals per colony) (Rotjan & Lewis 2008, Stella et al. 2010, 2011b). Obligate-dwellers are considered highly beneficial to their coral hosts, as they actively defend the host from predators, including CoTS, *Drupella* and *Dendropoma*, and contribute to the removal of excess sediment that would otherwise smother the corals (Figure 16) (Glynn 1980, 1983, Pratchett 2001, Stewart et al. 2006, Stier et al. 2010, Stella et al. 2011b). Further, some obligates (e.g. *Cymo*) have been shown to slow the progression of disease in their coral host (Figure 16) (Pollock et al. 2013).

Coral-associated crabs can have pronounced effects on their hosts by reducing fouling algal epibionts by >65% (Coen 1988). In an experiment that removed trapezid crabs from their coral host, whole-colony mortality occurred in up to 80% of crab-less hosts within a month (Stewart et al. 2006), but how the localised benefits of coral crabs scale up to ecosystem and socioeconomic levels is ambiguous. The benefits and feedbacks between coral-associates and their hosts through removal experiments requires greater attention, including how shifts in baseline habitat quality (i.e. coral health) may impact invertebrate communities and trophic links to fisheries productivity. In light of intensifying degradation of coral reefs, any direct benefits to corals through management, as offered through the GBRMPA zoning scheme, would surely support broader resilience of coral-associated organisms to environmental change. There is no specific protection or management initiative outlined for coral-associated decapods at present, which would prove difficult to implement and monitor given their small and cryptic nature. Broader protection of their coral habitat and education on the importance of coral-associated organisms to reef functioning are likely to be the most reasonable and effective management strategies for this group.

The survival of coral-associates is inextricably linked to that of their host, and so obligate associates are considered particularly vulnerable to changes in live coral cover (Caley et al. 2001, Stella et al. 2011a,b). Among the most sensitive corals to thermal stress are *Acropora* and *Pocillopora* (Loya et al. 2001, McClanahan et al. 2004, van Woesik et al. 2011), the typical host genera of coral crabs. For trapeziids, coral bleaching has been shown to impact their densities
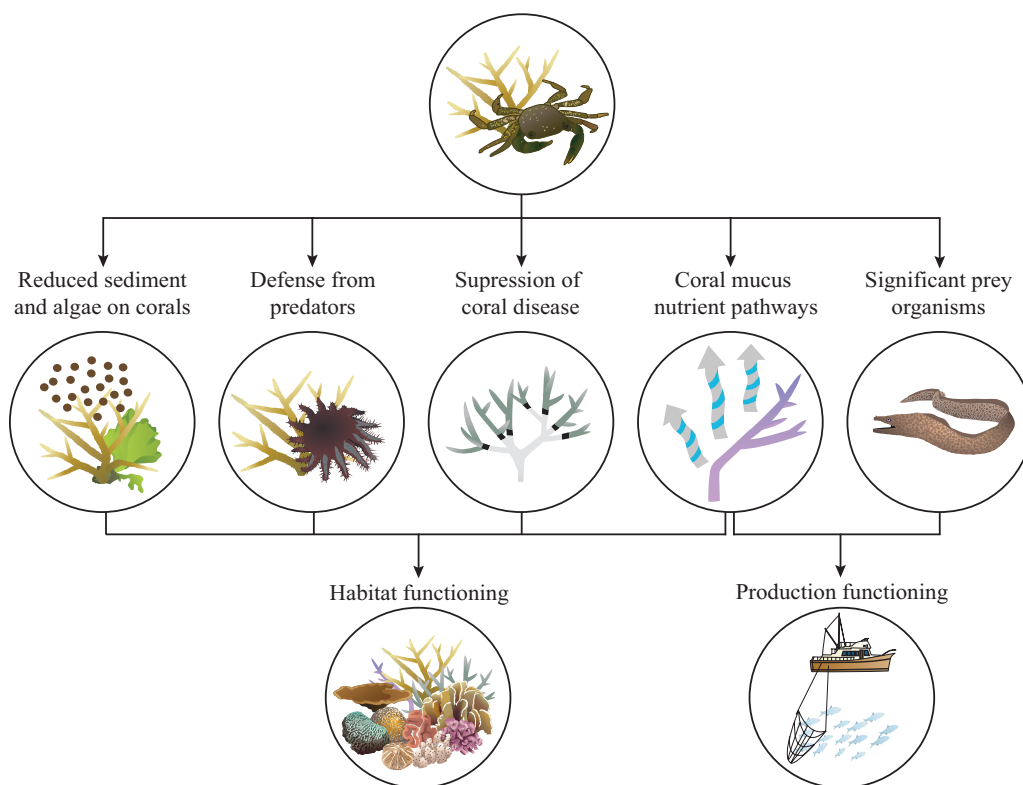
**Figure 16** Schematic of the influences of coral-associated decapods on ecosystem processes and functioning. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

and reproduction, which intensifies inter- and intraspecies competition (Glynn et al. 1985, Stella et al. 2011a, 2014). There are records of some trapeziids occupying dead coral habitat, which could suggest unanticipated resilience in the ability for these coral-obligates to occupy degraded and dead coral habitats (Head et al. 2015). However, this is usually a result of saturated population densities and increased territoriality, which forces losing individuals to traverse dead coral and rubble habitats in search of suitable (and available) live coral habitat, a behavioural trait that renders them vulnerable to predation and hinders their ability to fulfil their novel roles in coral reef functioning (Stella et al. 2011b). The ability for coral-associated decapods to sustain their populations in alternative habitats during periods of coral recovery requires attention, including their potential to enhance reef resilience as corals recover, particularly when coral mortality occurs at large spatial scales.

*Detritivorous fishes*    Although being rated as a critical functional group, especially regarding particular ecosystem processes (e.g. nutrient cycling), detritivorous fishes were not considered vulnerable nor a high-priority candidate for management. This is likely due to the broad distributions and/or high densities of predominant groups, including blennies (Wilson 2000, 2001, 2004) and surgeonfishes, particularly *Ctenochaetus striatus* (Tebbett et al. 2018). Regardless, detritivores are considered a key trophic group, representing ~40% of the biomass of EAM-grazing assemblages on the GBR (Wilson et al. 2003). They are fundamental components of nutrient pathways through the transfer of energy from the EAM to secondary consumers (Figure 17) (Crossman et al. 2001, 2005, Wilson et al. 2003, Bellwood et al. 2014). The rapid population turnover of blennies in particular
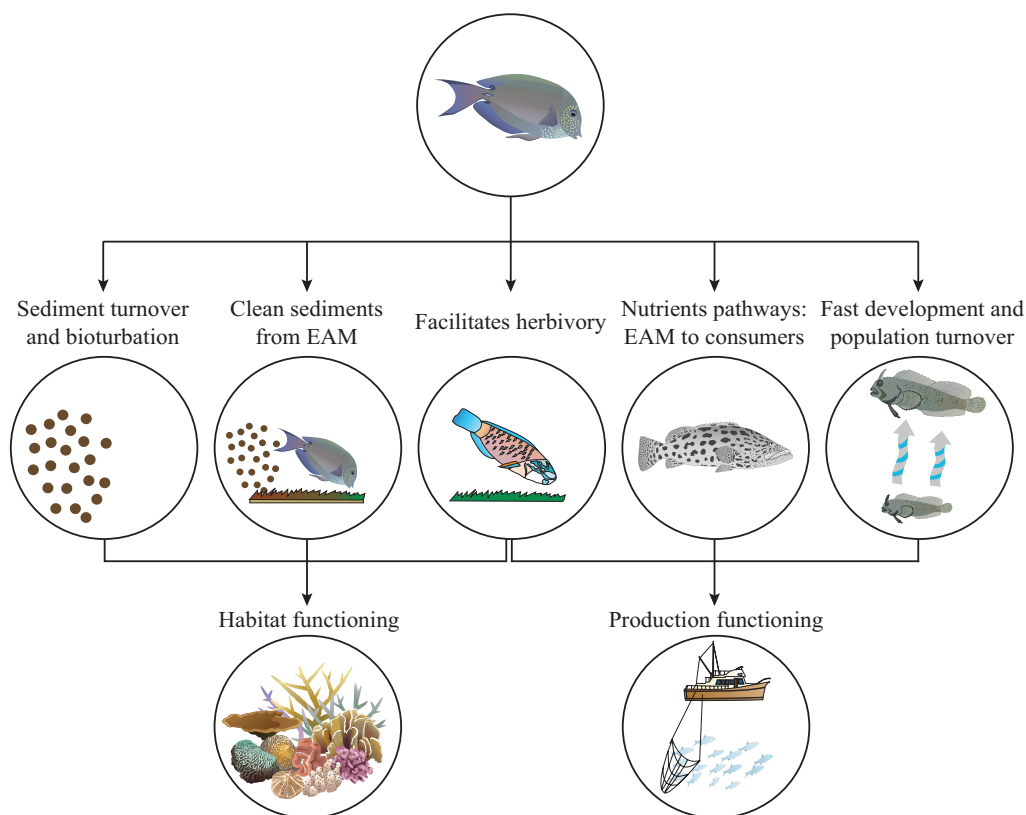
**Figure 17** Schematic of the influences of detritivorous fishes (e.g. blennies, *Ctenochaetus striatus*) on ecosystem processes and functioning. Symbols courtesy of the Integration and Application Network (ian. umces.edu/symbols/).

(Wilson 2004), which can account for ~60% of detritivore biomass in some habitats (Wilson 2001), attributes to their key role in reef trophodynamics with links to fisheries productivity (Figure 17). Further, post disturbance and associated losses in coral cover and fish diversity may be maintained by detrital- and EAM-grazers (Wilson et al. 2009, Ceccarelli et al. 2016). Given the importance of detritivores to particular ecosystem processes, it could be important to characterise additional key contributors to detritivory and sediment processing, including for other fishes and invertebrates like deposit-feeding sea cucumbers.

One expert noted that their scores for detritivores were primarily in context of *C. striatus*. This species is one of the most abundant and important surgeonfishes on Indo-Pacific reefs, including on the GBR (Trip et al. 2008), through its contributions to detritivory and sediment dynamics (Purcell & Bellwood 1993, Goatley & Bellwood 2010, Krone et al. 2011, Cheal et al. 2013, Tebbett et al. 2017b,d, 2018). While feeding on components of the EAM (e.g. detritus, bacteria), *C. striatus* selectively brushes associated particles from algal turfs. They may have low functional redundancy in this role removing sediments (Tebbett et al. 2017b, 2018), which has been shown to facilitate herbivory by other species (Goatley & Bellwood 2010, Marshell & Mumby 2012, 2015), with potential roles regulating coral-algal phase shifts (Cheal et al. 2010). *Ctenochaetus striatus* are selective feeders with a preference for coarser sediments. Fine sediments appear to impact their feeding behaviour and associations with the EAM, with implications regarding their vulnerability to sedimentation, as produced by dredging activities or heavy storm events (Tebbett et al. 2017c,d, Bellwood et al. 2018);

other EAM-feeders may not be as fussy (Tebbett et al. 2017c). As some detritivores can be highly sensitive to sediment loads, improving water quality across catchment areas, including reducing impacts from dredging activity, are management strategies that would likely benefit this group.

Although considered Least Concern by the IUCN, *C. striatus* has been extensively fished from some reefs like American Samoa (Trip et al. 2008, Choat et al. 2012). The aggregative spawning behaviour exhibited by this species, including on the GBR (Robertson 1983), could have specific implications for their management regarding seasonal spawning closures. There is a recreational catch limit of five individuals and a minimum size limit of 25 cm on the GBR, but they are not heavily targeted and exhibit particularly fast growth rates to a distinct size (Trip et al. 2008, Choat et al. 2012). The biology of *C. striatus* may render them particularly resilient across their expansive range, given fishing intensity remains low (Trip et al. 2008). Specific consideration of key detritivores, such as *C. striatus*, in reef monitoring programmes is recommended to ensure that groups with important contributions to ecosystem functioning are well documented and safeguarded in a future ocean. Management and education initiatives may also be implemented for detritivores, as already exist for herbivores and tabular corals (GBRMPA 2017, 2018a).

## Overview and synthesis

Ultimately, global protection of coral reefs depends on fast action towards a low-carbon economy, but this must be augmented with local action to prevent degradation of reef structures and associated losses of ecosystem functioning and services (Kennedy et al. 2013, Albright et al. 2016a, Cinner et al. 2016). Explicit identification and protection of key species that support positive ecological interactions is imperative to conservation and in providing targeted information to safeguard species, biodiversity and functioning into the future (Halpern et al. 2007, McClanahan et al. 2014, Rogers et al. 2015, Shaver & Silliman 2017, Richards & Day 2018). We present a broad review of the literature for priority coral reef species on the GBR and for typical reef crest and reef slope habitats more generally. While whole-ecosystem management is necessary to maintain the integrity of coral reefs, many of the attributes examined here, at the level of species, ecological processes and ecosystem functioning, are of OUV and contribute greatly to the integrity and cultural values of the GBR and its World Heritage property (GBRMPA 2014c). The information here provides a first step to inform holistic management aiming to preserve important reef species, values and processes and the opportunity to build out from the current framework in context of biological functioning to other important coral reef biomes (e.g. mangroves, seagrass meadows, interreefal areas) and values (e.g. social, cultural, economic).

The preservation of biodiversity is critical to maintain coral reef functioning (Clements & Hay 2019), but we must augment the precautionary principle of conserving biodiversity with predictive science that informs practical and specific solutions (Naeem et al. 2012). Conservation success depends on the recognition and inclusion of specific taxa that support positive interactions, with disproportionate benefits to ecosystem functioning (Halpern et al. 2007, Shaver & Silliman 2017, Renzi et al. 2019). We present a range of desired outcomes for priority groups (tabular corals, branching corals, microorganisms, crustose coralline algae, algal turfs, crown-of-thorns starfish and herbivorous parrotfishes) to empower research and holistic management. In the context of the GBR, past and present management schemes (e.g. GBRMPA zoning [Day 2002, Fernandes et al. 2005, 2009], Blueprint for Resilience [GBRMPA 2017, 2018a]) are commended for their efforts, and momentum should be maintained. Novel taxa (chemoautotrophic microbes, cleaner wrasse, bivalves, coral-associated crabs and detritivorous fishes) may benefit from consideration in these (or similar) initiatives, including expanding current research and monitoring programmes to effectively capture these groups to inform whole-system models. Many of these priority and novel taxa are distinct and identifiable, rendering themselves particularly attractive to future endeavours in education and citizen science, if not already captured. For novel candidates and groups where scientific certainty

was particularly low (cryptic predators, deposit-feeding sea cucumbers, marine worms, cryptic sponges and crustaceans), empirical data on their roles in ecosystem functioning and vulnerability to the growing number of stressors on coral reefs are imperative to ensure that functioning is adequately safeguarded at its highest degree.

## Acknowledgements

## References

Achlatis, M., van der Zande, R.M., Schönberg, C.H., Fang, J.K., Hoegh-Guldberg, O. & Dove, S. 2017. Sponge bioerosion on changing reefs: Ocean warming poses physiological constraints to the success of a photosymbiotic excavating sponge. *Scientific Reports* **7**, 10705.

Adam, T.C. 2012. Mutualistic cleaner fish initiate trait-mediated indirect interactions by influencing the behaviour of coral predators. *Journal of Animal Ecology* **81**, 692–700.

Adam, T.C., Burkepile, D.E., Ruttenberg, B.I. & Paddack, M.J. 2015a. Herbivory and the resilience of Caribbean coral reefs: Knowledge gaps and implications for management. *Marine Ecology Progress Series* **520**, 1–20.

Adam, T.C., Kelley, M., Ruttenberg, B.I. & Burkepile, D.E. 2015b. Resource partitioning along multiple niche axes drives functional diversity in parrotfishes on Caribbean coral reefs. *Oecologia* **179**, 1173–1185.

Adam, T.C., Schmitt, R.J., Holbrook, S.J., Brooks, A.J., Edmunds, P.J., Carpenter, R.C. & Bernardi, G. 2011. Herbivory, connectivity, and ecosystem resilience: Response of a coral reef to a large-scale perturbation. *PLOS ONE* **6**, e23717. doi:23710.21371/journal.pone.0023717.

Adame, M.F., Arthington, A.H., Waltham, N., Hasan, S., Selles, A. & Ronan, M. 2019. Managing threats and restoring wetlands within catchments of the Great Barrier Reef, Australia. *Aquatic Conservation: Marine and Freshwater Ecosystems* **29**, 829–839.

Adey, W.H. & Goertemiller, T. 1987. Coral-reef algal turfs – Master producers in nutrient poor seas. *Phycologia* **26**, 374–386.

Adjeroud, M., Chancerelle, Y., Schrimm, M., Perez, T., Lecchini, D., Galzin, R. & Salvat, B. 2005. Detecting the effects of natural disturbances on coral assemblages in French Polynesia: A decade survey at multiple scales. *Aquatic Living Resources* **18**, 111–123.

Adjeroud, M., Michonneau, F., Edmunds, P.J., Chancerelle, Y., de Loma, T.L., Penin, L., Thibaut, L., Vidal-Dupiol, J., Salvat, B. & Galzin, R. 2009. Recurrent disturbances, recovery trajectories, and resilience of coral assemblages on a South Central Pacific reef. *Coral Reefs* **28**, 775–780.

Aeby, G., Lovell, E., Richards, Z., Delbeek, J.C., Reboton, C. & Bass, D. 2008. *Acropora hyacinthus*. The IUCN Red List of Threatened Species 2008: e.T133479A3765052.

Aguado, M.T., Murray, A. & Hutchings, P. 2015. Syllidae (Annelida: Phyllodocida) from Lizard Island, Great Barrier Reef, Australia. *Zootaxa* 4**019**, 35–60.

Agusti, S., Lubián, L.M., Moreno-Ostos, E., Estrada, M. & Duarte, C.M. 2019. Projected changes in photosynthetic picoplankton in a warmer subtropical ocean. *Frontiers in Marine Science* **5**, 506. doi:510.3389/fmars.2018.00506.

Ainsworth, C.H. & Mumby, P.J. 2015. Coral-algal phase shifts alter fish communities and reduce fisheries production. *Global Change Biology* **21**, 165–172.

Albright, R., Anthony, K.R.N., Baird, M. et al. 2016a. Ocean acidification: Linking science to management solutions using the Great Barrier Reef as a case study. *Journal of Environmental Management* **182**, 641–650.

Albright, R., Caldeira, L., Hosfelt, J. et al. 2016b. Reversal of ocean acidification enhances net coral reef calcification. *Nature* **531**, 362–365.

Albright, R., Langdon, C. & Anthony, K.R.N. 2013. Dynamics of seawater carbonate chemistry, production, and calcification of a coral reef flat, central Great Barrier Reef. *Biogeosciences* **10**, 6747–6758.

Albright, R., Takeshita, Y., Koweek, D.A., Ninokawa, A., Wolfe, K., Rivlin, T., Nebuchina, Y., Young, J. & Caldeira, K. 2018. Carbon dioxide addition to coral reef waters suppresses net community calcification. *Nature* **555**, 516–519.

Allan, B.J.M., Domenici, P., McCormick, M.I., Watson, S.-A. & Munday, P.L. 2013. Elevated CO2 affects predator-prey interactions through altered performance. *PLOS ONE* **8**, e58520. doi:58510.51371/journal.pone.0058520.

Allemand, D., Tambutte, E., Zoccola, D. & Tambutte, S. 2011. Coral calcification, cells to reefs. In *Coral Reefs: An Ecosystem in Transition*. Z. Dubinsky & N. Stambler (eds). Dordrecht: Springer, 119–150.

Allen, J.D., Richardson, E.L., Deaker, D., Agüera, A. & Byrne, M. 2019. Larval cloning in the crown-of-thorns sea star, a keystone coral predator. *Marine Ecology Progress Series* **609**, 271–276.

Almany, G.R. 2004a. Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. *Oecologia* **141**, 105–113.

Almany, G.R. 2004b. Priority effects in coral reef fish communities of the Great Barrier Reef. *Ecology* **85**, 2872–2880.

Almany, G.R. & Webster, M.S. 2004. Odd species out as predators reduce diversity of coral-reef fishes. *Ecology* **85**, 2933–2937.

Alongi, D.M., Patten, N.L., McKinnon, D., Kostner, N., Bourne, D.G. & Brinkman, R. 2015. Phytoplankton, bacterioplankton and virioplankton structure and function across the southern Great Barrier Reef shelf. *Journal of Marine Systems* **142**, 25–39.

Altman-Kurosaki, N.T., Priest, M.A., Golbuu, Y., Mumby, P.J. & Marshell, A. 2018. Microherbivores are significant grazers on Palau's forereefs. *Marine Biology* **165**, 1–11.

Alvarado, J.J., Cortes, J., Guzman, H. & Reyes-Bonilla, H. 2016. Bioerosion by the sea urchin Diadema mexicanum along Eastern Tropical Pacific coral reefs. *Marine Ecology-an Evolutionary Perspective* **37**, 1088–1102.

Alvarez-Noriega, M., Baird, A.H., Bridge, T.C.L. et al. 2018. Contrasting patterns of changes in abundance following a bleaching event between juvenile and adult scleractinian corals. *Coral Reefs* **37**, 527–532.

Anderson, K.D., Cantin, N.E., Heron, S.F., Lough, J.M. & Pratchett, M.S. 2018. Temporal and taxonomic contrasts in coral growth at Davies Reef, central Great Barrier Reef, Australia. *Coral Reefs* **37**, 409–421.

Anderson, K.D., Cantin, N.E., Heron, S.F., Pisapia, C. & Pratchett, M.S. 2017. Variation in growth rates of branching corals along Australia's Great Barrier Reef. *Scientific Reports* **7**, 2920. doi:2910.1038/s41598-41017-03085-41591.

Andersson, A.J. & Gledhill, D. 2013. Ocean acidification and coral reefs: Effects on breakdown, dissolution, and net ecosystem calcification. *Annual Review of Marine Science* **5**, 321–348.

Angly, F.E., Heath, C., Morgan, T.C., Tonin, H., Rich, V., Schaffelke, B., Bourne, D.G. & Tyson, G.W. 2016. Marine microbial communities of the Great Barrier Reef lagoon are influenced by riverine floodwaters and seasonal weather events. *PeerJ* **4**, e1511. doi:1510.7717/peerj.1511.

Anthony, K.R.N. 2000. Enhanced particle-feeding capacity of corals on turbid reefs (Great Barrier Reef, Australia). *Coral Reefs* **19**, 59–67.

Anthony, K.R.N. 2006. Enhanced energy status of corals on coastal, high-turbidity reefs. *Marine Ecology Progress Series* **319**, 111–116.

Anthony, K.R.N. 2016. Coral reefs under climate change and ocean acidification: Challenges and opportunities for management and policy. *Annual Review of Environment and Resources* **41**, 59–81.

Anthony, K.R.N. & Connolly, S.R. 2004. Environmental limits to growth: Physiological niche boundaries of corals along turbidity-light gradients. *Oecologia* **141**, 373–384.

Anthony, K.R.N. & Fabricius, K.E. 2000. Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. *Journal of Experimental Marine Biology and Ecology* **252**, 221–253.

Anthony, K.R.N., Kleypas, J.A. & Gattuso, J.P. 2011a. Coral reefs modify their seawater carbon chemistry – Implications for impacts of ocean acidification. *Global Change Biology* **17**, 3655–3666.

Anthony, K.R.N., Kline, D.I., Diaz-Pulido, G., Dove, S. & Hoegh-Guldberg, O. 2008. Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 17442–17446.

Anthony, K.R.N., Maynard, J.A., Diaz-Pulido, G., Mumby, P.J., Marshall, P.A., Cao, L. & Hoegh-Guldberg, O. 2011b. Ocean acidification and warming will lower coral reef resilience. *Global Change Biology* **17**, 1798–1808.

Arias, A. & Sutton, S.G. 2013. Understanding recreational fishers' compliance with no-take zones in the Great Barrier Reef Marine Park. *Ecology and Society* **18**, 18.

Arias-Gonzalez, J.E., Delesalle, B., Salvat, B. & Galzin, R. 1997. Trophic functioning of the Tiahura reef sector, Moorea Island, French Polynesia. *Coral Reefs* **16**, 231–246.

Armstrong, A.O., Armstrong, A.J., Jaine, F.R.A., Couturier, L.I.E., Fiora, K., Uribe-Palomino, J., Weeks, S.J., Townsend, K.A., Bennett, M.B. & Richardson, A.J. 2016. Prey density threshold and tidal influence on reef manta ray foraging at an aggregation site on the Great Barrier Reef. *PLOS ONE* **11**.

Arnold, S.N., Steneck, R.S. & Mumby, P.J. 2010. Running the gauntlet: Inhibitory effects of algal turfs on the processes of coral recruitment. *Marine Ecology Progress Series* **414**, 91–105.

Arthur, R., Done, T.J., Marsh, H. & Harriott, V. 2006. Local processes strongly influence post-bleaching benthic recovery in the Lakshadweep Islands. *Coral Reefs* **25**, 427–440.

Aswani, S. & Hamilton, R.J. 2004. Integrating indigenous ecological knowledge and customary sea tenure with marine and social science for conservation of bumphead parrotfish (*Bolbometopon muricatum*) in the Roviana Lagoon, Solomon Islands. *Environmental Conservation* **31**, 69–83.

Ates, R. 1988. Medusivorous fishes, a review. *Zoologische Mededelingen* **62**, 29–42.

Ates, R. 1991. Predation on Cnidaria by vertebrates other than fishes. *Hydrobiologia* **216/217**, 305–307.

Atkinson, M.J. & Cuet, P. 2008. Possible effects of ocean acidification on coral reef biogeochemistry: Topics for research. *Marine Ecology Progress Series* **373**, 249–256.

Atkinson, M.J. & Grigg, R.W. 1984. Model of a coral reef ecosystem. 2. Gross and net benthic primary production at French Frigate Shoals, Hawaii. *Coral Reefs* **3**, 13–22.

Auberson, B. 1982. Coral transplantation – an approach to the reestablishment of damaged reefs. *Kalikasan – the Philippine Journal of Biology* **11**, 158–172.

Ayre, D.J. & Miller, K.J. 2004. Where do clonal coral larvae go? Adult genotypic diversity conflicts with reproductive effort in the brooding coral *Pocillopora damicornis*. *Marine Ecology Progress Series* **277**, 95–105.

Babatunde, T., Amin, S., Romano, N., Yusoff, F., Arshad, A., Esa, Y. & Ebrahimi, M. 2018. Gonad maturation and spawning of cobia, *Rachycentron canadum* (Linnaeus, 1766) off the Dungun coast, Malaysia. *Journal of Applied Ichthyology* **34**, 638–645.

Babcock, R. & Davies, P. 1991. Effects of sedimentation on settlement of *Acropora millepora*. *Coral Reefs* **9**, 205–208.

Babcock, R.C., Dambacher, J.M., Morello, E.B., Plaganyi, E.E., Hayes, K.R., Sweatman, H.P.A. & Pratchett, M.S. 2016a. Assessing different causes of crown-of-thorns starfish outbreaks and appropriate responses for management on the Great Barrier Reef. *PLOS ONE* **11**, e0169048. doi:0169010.0161371/journal. pone.0169048.

Babcock, R.C., Milton, D.A. & Pratchett, M.S. 2016b. Relationships between size and reproductive output in the crown-of-thorns starfish. *Marine Biology* **163**.

Bainbridge, Z.T., Brodie, J.E., Faithful, J.W., Sydes, D.A. & Lewis, S.E. 2009. Identifying the land-based sources of suspended sediments, nutrients and pesticides discharged to the Great Barrier Reef from the Tully-Murray Basin, Queensland, Australia. *Marine and Freshwater Research* **60**, 1081–1090.

Bainbridge, Z.T., Lewis, S.E., Smithers, S.G., Kuhnert, P.M., Henderson, B.L. & Brodie, J.E. 2014. Fine-suspended sediment and water budgets for a large, seasonally dry tropical catchment: Burdekin River catchment, Queensland, Australia. *Water Resources Research* **50**, 9067–9087.

Baird, A.H., Bhagooli, R., Ralph, P.J. & Takahashi, S. 2009. Coral bleaching: The role of the host. *Trends in Ecology & Evolution* **24**, 16–20.

Baird, A.H. & Hughes, T.P. 2000. Competitive dominance by tabular corals: An experimental analysis of recruitment and survival of understorey assemblages. *Journal of Experimental Marine Biology and Ecology* **251**, 117–132.

Baird, A.H. & Marshall, P.A. 1998. Mass bleaching of corals on the Great Barrier Reef. *Coral Reefs* **17**, 376–376.

Baird, A.H. & Marshall, P.A. 2002. Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Marine Ecology Progress Series* **237**, 133–141.

Baird, A.H., Pratchett, M.S., Hoey, A.S., Herdiana, Y. & Campbell, S.J. 2013. *Acanthaster planci* is a major cause of coral mortality in Indonesia. *Coral Reefs* **32**, 803–812.

Bak, R. 1976. The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. *Netherlands Journal of Sea Research* **10**, 285–337.

Bak, R.P.M., Lambrechts, D.Y.M., Joenje, M., Nieuwland, G. & VanVeghel, M.L.J. 1996. Long-term changes on coral reefs in booming populations of a competitive colonial ascidian. *Marine Ecology Progress Series* **133**, 303–306.

Baker, A.C., Glynn, P.W. & Riegl, B. 2008. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuarine Coastal and Shelf Science* **80**, 435–471.

Baldock, T.E., Karampour, H., Sleep, R., Vyltla, A., Albermani, F., Golshani, A., Callaghan, D.P., Roff, G. & Mumby, P.J. 2014. Resilience of branching and massive corals to wave loading under sea level rise – A coupled computational fluid dynamics-structural analysis. *Marine Pollution Bulletin* **86**, 91–101.

Balogh, R., Wolfe, K. & Byrne, M. 2019. Gonad development and spawning of the Vulnerable commercial sea cucumber, *Stichopus herrmanni,* in the southern Great Barrier Reef. *Journal of the Marine Biological Association of the United Kingdom* **99**, 487–495.

Ban, S.S., Graham, N.A.J. & Connolly, S.R. 2014a. Evidence for multiple stressor interactions and effects on coral reefs. *Global Change Biology* **20**, 681–697.

Ban, S.S., Pressey, R.L. & Graham, N.A.J. 2014b. Assessing interactions of multiple stressors when data are limited: A Bayesian belief network applied to coral reefs. *Global Environmental Change-Human and Policy Dimensions* **27**, 64–72.

Banc-Prandi, G. & Fine, M. 2019. Copper enrichment reduces thermal tolerance of the highly resistant Red Sea coral *Stylophora pistillata*. *Coral Reefs* **38**, 285–296.

Barba, J. 2010. *Demography of Parrotfish: Age, Size and Reproductive Variables*. James Cook University.

Barbosa, S.S., Byrne, M. & Kelaher, B.P. 2008. Bioerosion caused by foraging of the tropical chiton *Acanthopleura gemmata* at One Tree Reef, southern Great Barrier Reef. *Coral Reefs* **27**, 635–639.

Barfield, S.J., Aglyamova, G.V., Bay, L.K. & Matz, M.V. 2018. Contrasting effects of Symbiodinium identity on coral host transcriptional profiles across latitudes. *Molecular Ecology* **27**, 3103–3115.

Barr, Y. & Abelson, A. 2019. Feeding – cleaning trade-off: Manta ray 'decision-making' as a conservation tool. *Frontiers in Marine Science* 6.

Bartley, R., Bainbridge, Z.T., Lewis, S.E., Kroon, F.J., Wilkinson, S.N., Brodie, J.E. & Silburn, D.M. 2014. Relating sediment impacts on coral reefs to watershed sources, processes and management: A review. *Science of the Total Environment* **468**, 1138–1153.

Barton, J.A., Willis, B.L. & Hutson, K.S. 2017. Coral propagation: A review of techniques for ornamental trade and reef restoration. *Reviews in Aquaculture* **9**, 238–256.

Bates, A.E., Hilton, B.J. & Harley, C.D. 2009. Effects of temperature, season and locality on wasting disease in the keystone predatory sea star *Pisaster ochraceus*. *Diseases of Aquatic Organisms* **86**, 245–251.

Baums, I.B. 2008. A restoration genetics guide for coral reef conservation. *Molecular Ecology* **17**, 2796–2811.

Bay, L.K., Doyle, J., Logan, M. & Berkelmans, R. 2016. Recovery from bleaching is mediated by threshold densities of background thermo-tolerant symbiont types in a reef-building coral. *Royal Society Open Science* 3.

Bay, R.A. & Palumbi, S.R. 2015. Rapid acclimation ability mediated by transcriptome changes in reef-building corals. *Genome Biology and Evolution* **7**, 1602–1612.

Bayer, K., Schmitt, S. & Hentschel, U. 2008. Physiology, phylogeny and *in situ* evidence for bacterial and archaeal nitrifiers in the marine sponge *Aplysina aerophoba*. *Environmental Microbiology* **10**, 2942–2955.

Becerro, M.A., Paul, V.J. & Starmer, J. 1998. Intracolonial variation in chemical defenses of the sponge *Cacospongia* sp. and its consequences on generalist fish predators and the specialist nudibranch predator *Glossodoris pallida*. *Marine Ecology Progress Series* **168**, 187–196.

Beck, M.W., Brumbaugh, R.D., Airoldi, L. et al. 2011. Oyster reefs at risk and recommendations for conservation, restoration, and management. *Bioscience* **61**, 107–116.

Beeden, R., Maynard, J., Johnson, J., Dryden, J., Kininmonth, S. & Marshall, P. 2014a. No-anchoring areas reduce coral damage in an effort to build resilience in Keppel Bay, southern Great Barrier Reef. *Australasian Journal of Environmental Management* **21**, 311–319.

Beeden, R., Maynard, J.A., Marshall, P.A., Heron, S.F. & Willis, B.L. 2012. A framework for responding to coral disease outbreaks that facilitates adaptive management. *Environmental Management* **49**, 1–13.

Beeden, R.J., Turner, M.A., Dryden, J., Merida, F., Goudkamp, K., Malone, C., Marshall, P.A., Birtles, A. & Maynard, J.A. 2014b. Rapid survey protocol that provides dynamic information on reef condition to managers of the Great Barrier Reef. *Environmental Monitoring and Assessment* **186**, 8527–8540.

Bejarano, S., Golbuu, Y., Sapolu, T. & Mumby, P.J. 2013. Ecological risk and the exploitation of herbivorous reef fish across Micronesia. *Marine Ecology Progress Series* **482**, 197–215.

Bejarano, S., Jouffray, J.B., Chollett, I., Allen, R., Roff, G., Marshell, A., Steneck, R., Ferse, S.C.A. & Mumby, P.J. 2017. The shape of success in a turbulent world: Wave exposure filtering of coral reef herbivory. *Functional Ecology* **31**, 1312–1324.

Bejarano, S., Mumby, P.J. & Golbuu, Y. 2014. Changes in the spear fishery of herbivores associated with closed grouper season in Palau, Micronesia. *Animal Conservation* **17**, 133–143.

Bell, J.J. 2008. The functional roles of marine sponges. *Estuarine Coastal and Shelf Science* **79**, 341–353.

Bell, J.J., Davy, S.K., Jones, T., Taylor, M.W. & Webster, N.S. 2013. Could some coral reefs become sponge reefs as our climate changes? *Global Change Biology* **19**, 2613–2624.

Bell, J.J., McGrath, E., Biggerstaff, A., Bates, T., Bennett, H., Marlow, J. & Shaffer, M. 2015. Sediment impacts on marine sponges. *Marine Pollution Bulletin* **94**, 5–13.

Bell, J.J., Rovellini, A., Davy, S.K., Taylor, M.W., Fulton, E.A., Dunn, M.R., Bennett, H.M., Kandler, N.M., Luter, H.M. & Webster, N.S. 2018. Climate change alterations to ecosystem dominance: How might sponge-dominated reefs function? *Ecology* **99**, 1920–1931.

Bell, P.R.F., Lapointe, B.E. & Elmetri, I. 2007. Re-evaluation of ENCORE: Support for the eutrophication threshold model for coral reefs. *Ambio* **36**, 416–424.

Bellwood, D.R., Baird, A.H., Depczynski, M., Gonzalez-Cabello, A., Hoey, A.S., Lefevre, C.D. & Tanner, J.K. 2012a. Coral recovery may not herald the return of fishes on damaged coral reefs. *Oecologia* **170**, 567–573.

Bellwood, D.R. & Choat, J. 1990. A functional analysis of grazing in parrotfishes (family Scaridae): The ecological implications. *Environmental Biology of Fishes* **28**, 189–214.

Bellwood, D.R. & Fulton, C.J. 2008. Sediment-mediated suppression of herbivory on coral reefs: Decreasing resilience to rising sea levels and climate change? *Limnology and Oceanography* **53**, 2695–2701.

Bellwood, D.R., Goatley, C.H.R. & Bellwood, O. 2017. The evolution of fishes and corals on reefs: Form, function and interdependence. *Biological Reviews* **92**, 878–901.

Bellwood, D.R., Hoey, A.S., Bellwood, O. & Goatley, C.H.R. 2014. Evolution of long-toothed fishes and the changing nature of fish-benthos interactions on coral reefs. *Nature Communications* **5**, 3144. doi:3110.1038/ncomms4144.

Bellwood, D.R., Hoey, A.S. & Choat, J.H. 2003. Limited functional redundancy in high diversity systems: Resilience and ecosystem function on coral reefs. *Ecology Letters* **6**, 281–285.

Bellwood, D.R., Hoey, A.S. & Hughes, T.P. 2012b. Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proceedings of the Royal Society B-Biological Sciences* **279**, 1621–1629.

Bellwood, D.R. & Hughes, T.P. 2001. Regional-scale assembly rules and biodiversity of coral reefs. *Science* **292**, 1532–1534.

Bellwood, D.R., Hughes, T.P., Folke, C. & Nystrom, M. 2004. Confronting the coral reef crisis. *Nature* **429**, 827–833.

Bellwood, D.R., Hughes, T.P. & Hoey, A.S. 2006a. Sleeping functional group drives coral reef recovery. *Current Biology* **16**, 2434–2439.

Bellwood, D.R., Streit, R.P., Brandl, S.J. & Tebbett, S.B. 2019. The meaning of the term 'function' in ecology: A coral reef perspective. *Functional Ecology*, 1–14. doi:10.1111/1365-2435.13265.

Bellwood, D.R., Tebbett, S.B., Bellwood, O., Mihalitsis, M., Morais, R.A., Streit, R.P. & Fulton, C.J. 2018. The role of the reef flat in coral reef trophodynamics: Past, present, and future. *Ecology and Evolution* **8**, 4108–4119.

Bellwood, D.R., Wainwright, P.C., Fulton, C.J. & Hoey, A.S. 2006b. Functional versatility supports coral reef biodiversity. *Proceedings of the Royal Society B-Biological Sciences* **273**, 101–107.

Ben-Tzvi, O., Einbinder, S. & Brokovich, E. 2006. A beneficial association between a polychaete worm and a scleractinian coral? *Coral Reefs* **25**, 98–98.

Bender, D., Diaz-Pulido, G. & Dove, S. 2012. Effects of macroalgae on corals recovering from disturbance. *Journal of Experimental Marine Biology and Ecology* **429**, 15–19.

Bender, D., Diaz-Pulido, G. & Dove, S. 2014a. The impact of CO2 emission scenarios and nutrient enrichment on a common coral reef macroalga is modified by temporal effects. *Journal of Phycology* **50**, 203–215.

Bender, D., Diaz-Pulido, G. & Dove, S. 2014b. Warming and acidification promote cyanobacterial dominance in turf algal assemblages. *Marine Ecology Progress Series* **517**, 271–284.

Bennett, H., Bell, J.J., Davy, S.K., Webster, N.S. & Francis, D.S. 2018. Elucidating the sponge stress response; lipids and fatty acids can facilitate survival under future climate scenarios. *Global Change Biology* **24**, 3130–3144.

Bennett, H.M., Altenrath, C., Woods, L., Davy, S.K., Webster, N.S. & Bell, J.J. 2017. Interactive effects of temperature and pCO(2) on sponges: From the cradle to the grave. *Global Change Biology* **23**, 2031–2046.

Bennett, S., Wernberg, T., Harvey, E.S., Santana-Garcon, J. & Saunders, B.J. 2015. Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. *Ecology Letters* **18**, 714–723.

Bento, R., Hoey, A.S., Bauman, A.G., Feary, D.A. & Burt, J.A. 2016. The implications of recurrent disturbances within the world's hottest coral reef. *Marine Pollution Bulletin* **105**, 466–472.

Bergseth, B.J., Russ, G.R. & Cinner, J.E. 2015. Measuring and monitoring compliance in no-take marine reserves. *Fish and Fisheries* **16**, 240–258.

Bergseth, B.J., Williamson, D.H., Frisch, A.J. & Russ, G.R. 2016. Protected areas preserve natural behaviour of a targeted fish species on coral reefs. *Biological Conservation* **198**, 202–209.

Bergseth, B.J., Williamson, D.H., Russ, G.R., Sutton, S.G. & Cinner, J.E. 2017. A social-ecological approach to assessing and managing poaching by recreational fishers. *Frontiers in Ecology and the Environment* **15**, 67–73.

Bergstrom, D.M., Lucieer, A., Kiefer, K., Wasley, J., Belbin, L., Pedersen, T.K. & Chown, S.L. 2009. Indirect effects of invasive species removal devastate World Heritage Island. *Journal of Applied Ecology* **46**, 73–81.

Berkelmans, R. & van Oppen, M.J.H. 2006. The role of zooxanthellae in the thermal tolerance of corals: A 'nugget of hope' for coral reefs in an era of climate change. *Proceedings of the Royal Society B-Biological Sciences* **273**, 2305–2312.

Bersoza Hernández, A., Brumbaugh, R.D., Frederick, P., Grizzle, R., Luckenbach, M.W., Peterson, C.H. & Angelini, C. 2018. Restoring the eastern oyster: How much progress has been made in 53 years? *Frontiers in Ecology and the Environment* **16**, 463–471.

Bertucci, A., Moya, A., Tambutte, S., Allemand, D., Supuran, C.T. & Zoccola, D. 2013. Carbonic anhydrases in anthozoan corals – A review. *Bioorganic & Medicinal Chemistry* **21**, 1437–1450.

Berumen, M.L. & Pratchett, M.S. 2006. Recovery without resilience: Persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. *Coral Reefs* **25**, 647–653.

Bessell-Browne, P., Negri, A.P., Fisher, R., Clode, P.L., Duckworth, A. & Jones, R. 2017a. Impacts of turbidity on corals: The relative importance of light limitation and suspended sediments. *Marine Pollution Bulletin* **117**, 161–170.

Bessell-Browne, P., Negri, A.P., Fisher, R., Clode, P.L. & Jones, R. 2017b. Impacts of light limitation on corals and crustose coralline algae. *Scientific Reports* **7**, 11553. doi:11510.11038/s41598-11017-11783-z.

Beukers, J.S. & Jones, G.P. 1998. Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* **114**, 50–59.

Beukers-Stewart, B.D. & Jones, G.P. 2004. The influence of prey abundance on the feeding ecology of two piscivorous species of coral reef fish. *Journal of Experimental Marine Biology and Ecology* **299**, 155–184.

Beyer, H.L., Kennedy, E.V., Beger, M. et al. 2018. Risk-sensitive planning for conserving coral reefs under rapid climate change. *Conservation Letters* **11**, e12587. doi:12510.11111/conl.12587.

Bhadury, P. 2015. Effects of ocean acidification on marine invertebrates – A review. *Indian Journal of Geo-Marine Sciences* **44**, 454–464.

Bierwagen, S.L., Emslie, M.J., Heupel, M.R., Chin, A. & Simpfendorfer, C.A. 2018. Reef-scale variability in fish and coral assemblages on the central Great Barrier Reef. *Marine Biology* **165**, 144.

Biggs, B.C. 2013. Harnessing natural recovery processes to improve restoration outcomes: An experimental assessment of sponge-mediated coral reef restoration. *PLOS ONE* **8**, e64945. doi:64910.61371/journal.pone.0064945.

Binning, S.A., Roche, D.G., Grutter, A.S., Colosio, S., Sun, D., Miest, J. & Bshary, R. 2018. Cleaner wrasse indirectly affect the cognitive performance of a damselfish through ectoparasite removal. *Proceedings of the Royal Society B-Biological Sciences* **285**.

Birkeland, C. 1989. The influence of echinoderms on coral reef communities. *Echinoderm Studies* **3**, 1–79.

Birrell, C.L., McCook, L.J. & Willis, B.L. 2005. Effects of algal turfs and sediment on coral settlement. *Marine Pollution Bulletin* **51**, 408–414.

Birrell, C.L., Mccook, L.J., Willis, B.L. & Diaz-Pulido, G.A. 2008a. Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. *Oceanography and Marine Biology: An Annual Review* **46**, 25–63.

Birrell, C.L., McCook, L.J., Willis, B.L. & Harrington, L. 2008b. Chemical effects of macroalgae on larval settlement of the broadcast spawning coral *Acropora millepora*. *Marine Ecology Progress Series* **362**, 129–137.

Birtles, A., Valentine, P., Curnock, M., Mangott, A., Sobtzick, S. & Marsh, H. 2014. *Dwarf minke whale tourism monitoring program (2003–2008)*. Report to the Great Barrier Reef Marine Park Authority, Townsville. Research Publication 112. pp. 172.

Bishop, J.W. & Greenwood, J.G. 1994. Nitrogen-excretion by some demersal macrozooplankton in Heron and One Tree Reefs, Great Barrier Reef, Australia. *Marine Biology* **120**, 447–453.

Blackall, L.L., Wilson, B. & van Oppen, M.J.H. 2015. Coral – T the world's most diverse symbiotic ecosystem. *Molecular Ecology* **24**, 5330–5347.

Boaden, E. & Kingsford, M.J. 2012. Diel behaviour and trophic ecology of *Scolopsis bilineatus* (Nemipteridae). *Coral Reefs* **31**, 871–883.

Böhlke, E.B. & Randall, J.E. 2000. A review of the moray eels (Anguilliformes: Muraenidae) of the Hawaiian Islands, with description of two new species. *Proceedings of the Academy of Natural Sciences of Philadelphia* **150**, 203–278.

Bonaldo, R.M. & Bellwood, D.R. 2009. Dynamics of parrotfish grazing scars. *Marine Biology* **156**, 771–777.

Bonaldo, R.M., Hoey, A.S. & Bellwood, D.R. 2014. The ecosystem roles of parrotfishes on tropical reefs. *Oceanography and Marine Biology: An Annual Review* **52**, 81–132.

Borowitzka, M.A. 1981. Algae and grazing in coral reef ecosystems. *Endeavour* **5**, 99–106.

Borowitzka, M.A., Larkum, A.W.D. & Day, R. 1977. Seasonal aspects of productivity of coral reef algal turf communities. *Journal of Phycology* **13**, 8–8.

Bostrom-Einarsson, L., Bonin, M.C., Moon, S. & Firth, S. 2018. Environmental impact monitoring of household vinegar-injections to cull crown-of-thorns starfish, *Acanthaster* spp. *Ocean & Coastal Management* **155**, 83–89.

Bostrom-Einarsson, L. & Rivera-Posada, J. 2016. Controlling outbreaks of the coral-eating crown-of-thorns starfish using a single injection of common household vinegar. *Coral Reefs* **35**, 223–228.

Boucher, G. 1997. Species diversity and ecosystem function: A review of hypothesis and research perpectives in marine ecology. *Vie Et Milieu-Life and Environment* **47**, 307–316.

Bourne, D., Iida, Y., Uthicke, S. & Smith-Keune, C. 2008. Changes in coral-associated microbial communities during a bleaching event. *ISME Journal* **2**, 350–363.

Bourne, D. & Webster, N. 2013a. Coral reef bacterial communities. In *The Prokaryotes*. E. Rosenberg, E.F. DeLong, S. Lory, E. Stackebrandt & F. Thompson (eds). Verlag: Springer, 163–187.

Bourne, D. & Webster, N. 2013b. The Prokaryotes. In *Coral Reef Microbial Communities*. E. Rosenberg (ed.). Berlin Heidelberg, Germany: Springer.

Bourne, D.G., Morrow, K.M. & Webster, N.S. 2016. Insights into the coral microbiome: Underpinning the health and resilience of reef ecosystems. *Annual Review of Microbiology* **70**, 317–340.

Bozec, Y.M., O'Farrell, S., Bruggemann, J.H., Luckhurst, B.E. & Mumby, P.J. 2016. Tradeoffs between fisheries harvest and the resilience of coral reefs. *Proceedings of the National Academy of Sciences of the United States of America* **113**, 4536–4541.

Bozec, Y.M., Yakob, L., Bejarano, S. & Mumby, P.J. 2013. Reciprocal facilitation and non-linearity maintain habitat engineering on coral reefs. *Oikos* **122**, 428–440.

Brandl, S.J., Emslie, M.J. & Ceccarelli, D.M. 2016. Habitat degradation increases functional originality in highly diverse coral reef fish assemblages. *Ecosphere* **7**, e01557. doi:01510.01002/ecs01552.01557.

Brandl, S.J., Goatley, C.H.R., Bellwood, D.R. & Tornabene, L. 2018. The hidden half: Ecology and evolution of cryptobenthic fishes on coral reefs. *Biological reviews of the Cambridge Philosophical Society* **93**, 1846–1873.

Brandl, S.J., Tornabene, L., Goatley, C.H.R., Casey, J.M., Morais, R.A., Côté, I.M., Baldwin, C.C., Parravicini, V., Schiettekatte, N.M.D. & Bellwood, D.R. 2019. Demographic dynamics of the smallest marine vertebrates fuel coral-reef ecosystem functioning. *Science*, **364**, 1189–1192.

Branham, J.M., Reed, S.A., Bailey, J.H. & Caperon, J. 1971. Coral-eating sea stars *Acanthaster planci* in Hawaii. *Science* **172**, 1155–1157.

Brawley, S.H. & Adey, W.H. 1981. The effect of micrograzers on algal community structure in a coral reef microcosm. *Marine Biology* **61**, 167–177.

Bridge, T., Beaman, R., Done, T. & Webster, J. 2012. Predicting the location and spatial extent of submerged coral reef habitat in the Great Barrier Reef World Heritage Area, Australia. *PLOS ONE* **7**.

Briffa, M., de la Haye, K. & Munday, P.L. 2012. High CO2 and marine animal behaviour: Potential mechanisms and ecological consequences. *Marine Pollution Bulletin* **64**, 1519–1528.

Brocke, H.J., Polerecky, L., de Beer, D., Weber, M., Claudet, J. & Nugues, M.M. 2015. Organic matter degradation drives benthic cyanobacterial mat abundance on Caribbean coral reefs. *PLOS ONE* **10**, e0125445. doi:0125410.0121371/journal.pone.0125445.

Brodie, J., Fabricius, K., De'ath, G. & Okaji, K. 2005. Are increased nutrient inputs responsible for more outbreaks of crown-of-thorns starfish? An appraisal of the evidence. *Marine Pollution Bulletin* **51**, 266–278.

Brodie, J. & Waterhouse, J. 2012. A critical review of environmental management of the 'not so Great' Barrier Reef. *Estuarine Coastal and Shelf Science* **104**, 1–22.

Brodie, J., Waterhouse, J., Maynard, J. et al. 2013. *Assessment of the relative risk of water quality to ecosystems of the Great Barrier Reef.* A report to the Department of the Environment and Heritage Protection, Queensland Government, Brisbane – Report 13/28.

Brodie, J.E., Kroon, F.J., Schaffelke, B., Wolanski, E.C., Lewis, S.E., Devlin, M.J., Bohnet, I.C., Bainbridge, Z.T., Waterhouse, J. & Davis, A.M. 2012. Terrestrial pollutant runoff to the Great Barrier Reef: An update of issues, priorities and management responses. *Marine Pollution Bulletin* **65**, 81–100.

Brooker, R.M., Brandl, S.J. & Dixson, D.L. 2016a. Cryptic effects of habitat declines: Coral-associated fishes avoid coral-seaweed interactions due to visual and chemical cues. *Scientific Reports* 6.

Brooker, R.M., Hay, M.E. & Dixson, D.L. 2016b. Chemically cued suppression of coral reef resilience: Where is the tipping point? *Coral Reefs* **35**, 1263–1270.

Brown, A., Lipp, E.K. & Osenberg, C.W. 2019. Algae dictate multiple stressor effects on coral microbiomes. *Coral Reefs* **38**, 229–240.

Brown, B.E. 1997. Coral bleaching: Causes and consequences. *Coral Reefs* **16**, S129–S138.

Brown, C.J., Saunders, M.I., Possingham, H.P. & Richardson, A.J. 2014. Interactions between global and local stressors of ecosystems determine management effectiveness in cumulative impact mapping. *Diversity and Distributions* **20**, 538–546.

Brown, M.V., van de Kamp, J., Ostrowski, M. et al. 2018. Systematic, continental scale temporal monitoring of marine pelagic microbiota by the Australian Marine Microbial Biodiversity Initiative. *Scientific Data* **5**, 180130.

Browne, N.K. 2012. Spatial and temporal variations in coral growth on an inshore turbid reef subjected to multiple disturbances. *Marine Environmental Research* **77**, 71–83.

Browne, N.K., Smithers, S.G. & Perry, C.T. 2010. Geomorphology and community structure of Middle Reef, central Great Barrier Reef, Australia: An inner-shelf turbid zone reef subject to episodic mortality events. *Coral Reefs* **29**, 683–689.

Browne, N.K., Smithers, S.G. & Perry, C.T. 2012. Coral reefs of the turbid inner-shelf of the Great Barrier Reef, Australia: An environmental and geomorphic perspective on their occurrence, composition and growth. *Earth-Science Reviews* **115**, 1–20.

Browne, N.K., Smithers, S.G. & Perry, C.T. 2013. Carbonate and terrigenous sediment budgets for two inshore turbid reefs on the central Great Barrier Reef. *Marine Geology* **346**, 101–123.

Bruckner, A.W. & Borneman, E.H. 2010. Implications of coral harvest and transplantation on reefs in northwestern Dominica. *Revista De Biologia Tropical* **58**, 111–127.

Bruckner, A.W. & Bruckner, R.J. 2001. Condition of restored *Acropora palmata* fragments off Mona Island, Puerto Rico, 2 years after the Fortuna Reefer ship grounding. *Coral Reefs* **20**, 235–243.

Bruckner, A.W. & Coward, G. 2019. Abnormal density of *Culcita schmideliana* delays recovery of a reef system in the Maldives following a catastrophic bleaching event. *Marine and Freshwater Research* **70**, 292–301.

Bruckner, A.W., Coward, G., Bimson, K. & Rattanawongwan, T. 2017. Predation by feeding aggregations of *Drupella* spp. inhibits the recovery of reefs damaged by a mass bleaching event. *Coral Reefs* **36**, 1181–1187.

Bruno, J.F., Selig, E.R., Casey, K.S., Page, C.A., Willis, B.L., Harvell, C.D., Sweatman, H. & Melendy, A.M. 2007. Thermal stress and coral cover as drivers of coral disease outbreaks. *Plos Biology* **5**, 1220–1227.

Bshary, R. & Grutter, A.S. 2002. Experimental evidence that partner choice is a driving force in the payoff distribution among cooperators or mutualists: The cleaner fish case. *Ecology Letters* **5**, 130–136.

Buck, B.H., Rosenthal, H. & Saint-Paul, U. 2002. Effect of increased irradiance and thermal stress on the symbiosis of *Symbiodinium microadriaticum* and *Tridacna gigas*. *Aquatic Living Resources* **15**, 107–117.

Burgman, M.A. 2016. *Trusting Judgements: How to Get the Best Out of Experts*. Cambridge University Press.

Burkepile, D.E. & Hay, M.E. 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 16201–16206.

Burkepile, D.E. & Hay, M.E. 2010. Impact of herbivore identity on algal succession and coral growth on a Caribbean Reef. *PLOS ONE* 5.

Burkepile, D.E. & Hay, M.E. 2011. Feeding complementarity versus redundancy among herbivorous fishes on a Caribbean reef. *Coral Reefs* **30**, 351–362.

Byrne, M. 2011. Impact of ocean warming and ocean acidification on marine invertebrate life history stages: Vulnerabilities and potential for persistence in a changing ocean. *Oceanography and Marine Biology: An Annual Review* **49**, 1–42.

Byrne, M., Foo, A.S., Ross, P.M., & Putnam, H.M. 2020. Limitations to cross- and multigenerational plasticity for marine invertebrates faced with global climate change. *Global Change Biology* **26**, 80–102.

Byrne, M., Lamare, M., Winter, D., Dworjanyn, S.A. & Uthicke, S. 2013. The stunting effect of a high CO2 ocean on calcification and development in sea urchin larvae, a synthesis from the tropics to the poles. *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**, 20120439.

Cabaitan, P.C., Gomez, E.D. & Alino, P.M. 2008. Effects of coral transplantation and giant clam restocking on the structure of fish communities on degraded patch reefs. *Journal of Experimental Marine Biology and Ecology* **357**, 85–98.

Caddy, J. & Rodhouse, P. 1998. Cephalopod and groundfish landings: Evidence for ecological change in global fisheries? *Reviews in Fish Biology and Fisheries* **8**, 431–444.

Calbet, A. 2001. Mesozooplankton grazing effect on primary production: A global comparative analysis in marine ecosystems. *Limnology and Oceanography* **46**, 1824–1830.

Caldeira, K. & Wickett, M.E. 2005. Ocean model predictions of chemistry changes from carbon dioxide emissions to the atmosphere and ocean. *Journal of Geophysical Research-Oceans* **110**.

Caley, M.J., Buckley, K.A. & Jones, G.P. 2001. Separating ecological effects of habitat fragmentation, degradation, and loss on coral commensals. *Ecology* **82**, 3435–3448.

Camp, E.F., Schoepf, V., Mumby, P.J., Hardtke, L.A., Rodolfo-Metalpa, R., Smith, D.J. & Suggett, D.J. 2018a. The future of coral reefs subject to rapid climate change: Lessons from natural extreme environments. *Frontiers in Marine Science* **5**, 4. doi:10.3389/fmars.2018.00004.

Camp, E.F., Schoepf, V. & Suggett, D.J. 2018b. How can 'Super Corals' facilitate global coral reef survival under rapid environmental and climatic change? *Global Change Biology* **24**, 2755–2757.

Cantin, N.E. & Lough, J.M. 2014. Surviving coral bleaching events: *Porites* growth anomalies on the Great Barrier Reef. *PLOS ONE* **9**, e88720.

Cantin, N.E., Negri, A.P. & Willis, B.L. 2007. Photoinhibition from chronic herbicide exposure reduces reproductive output of reef-building corals. *Marine Ecology Progress Series* **344**, 81–93.

Capa, M., Faroni-Perez, L. & Hutchings, P. 2015. Sabellariidae from Lizard Island, Great Barrier Reef, including a new species of *Lygdamis* and notes on external morphology of the median organ. *Zootaxa* 4**019**, 184–206.

Capone, D.G., Dunham, S.E., Horrigan, S.G. & Duguay, L.E. 1992. Microbial nitrogen transformations in unconsolidated coral reef sediments. *Marine Ecology Progress Series* **80**, 75–88.

Carpenter, K., Lawrence, A. & Myers, R. 2016. *Lethrinus xanthochilus*. The IUCN Red List of Threatened Species. 2016: e.T16720577A16722345.

Carpenter, R.C. 1981. Grazing by *Diadema antillarum* (Philippi) and its effects on the benthic algal community. *Journal of Marine Research* **39**, 749–765.

Carpenter, R.C. 1985. Relationships between primary production and irradiance in coral reef algal communities. *Limnology and Oceanography* **30**, 784–793.

Carpenter, R.C. 1986. Partitioning herbivory and its effects on coral reef algal communities. *Ecological Monographs* **56**, 345–363.

Carpenter, R.C. 1990. Mass mortality of *Diadema Antillarum*. 1. Long-term effects on sea urchin population dynamics and coral reef algal communities. *Marine Biology* **104**, 67–77.

Carpenter, R.C. & Williams, S.L. 1993. Effects of algal turf canopy height and microscale substratum topography on profiles of flow speed in a coral forereef environment. *Limnology and Oceanography* **38**, 687–694.

Carreiro-Silva, M., McClanahan, T.R. & Kiene, W.E. 2005. The role of inorganic nutrients and herbivory in controlling microbioerosion of carbonate substratum. *Coral Reefs* **24**, 214–221.

Carrier, T.J., Wolfe, K., Lopez, K., Gall, M., Janies, D.A., Byrne, M. & Reitzel, A.M. 2018. Diet-induced shifts in the crown-of-thorns (*Acanthaster* sp.) larval microbiome. *Marine Biology* **165**, 157.

Carrillo-Baltodano, A. & Morales-Ramirez, A. 2016. Changes in abundance and composition of a Caribbean coral reef zooplankton community after 25 years. *Revista De Biologia Tropical* **64**, 1029–1040.

Casey, J.M., Baird, A.H., Brandl, S.J., Hoogenboom, M.O., Rizzari, J.R., Frisch, A.J., Mirbach, C.E. & Connolly, S.R. 2017. A test of trophic cascade theory: Fish and benthic assemblages across a predator density gradient on coral reefs. *Oecologia* **183**, 161–175.

Casey, J.M., Choat, J.H. & Connolly, S.R. 2015a. Coupled dynamics of territorial damselfishes and juvenile corals on the reef crest. *Coral Reefs* **34**, 1–11.

Casey, J.M., Connolly, S.R. & Ainsworth, T.D. 2015b. Coral transplantation triggers shift in microbiome and promotion of coral disease associated potential pathogens. *Scientific Reports* **5**, 11903. doi: 11910.11038/srep11903.

Castro, P. 1976. Brachyuran crabs symbiotic with scleractinian corals: A review of their biology. *Micronesica* **12**, 99–110.

Castro, P. 2000. Biogeography of trapeziid crabs (Brachyura, Trapeziidae) symbiotic with reef corals and other cnidarians. *Biodiversity Crisis and Crustacea* **12**, 65–75.

Castro, P., Ng, P.K.L. & Ahyong, S.T. 2004. Phylogeny and systematics of the Trapeziidae Miers, 1886 (Crustacea: Brachyura), with the description of a new family. *Zootaxa* **643**, 1–70.

Castro-Sanguino, C., Bozec, Y.M., Dempsey, A. et al. 2017. Detecting conservation benefits of marine reserves on remote reefs of the northern GBR. *PLOS ONE* **12**, e0186146. doi:0186110.0181371/journal.pone.0186146.

Ceccarelli, D.M. 2007. Modification of benthic communities by territorial damselfish: A multi-species comparison. *Coral Reefs* **26**, 853–866.

Ceccarelli, D.M., Emslie, M.J. & Richards, Z.T. 2016. Post-disturbance stability of fish assemblages measured at coarse taxonomic resolution masks change at finer scales. *PLOS ONE* **11**, e0156232. doi:0156210.0151371/journal.pone.0156232.

Ceccarelli, D.M., Hughes, T.P. & McCook, L.J. 2006. Impacts of simulated overfishing on the territoriality of coral reef damselfish. *Marine Ecology Progress Series* **309**, 255–262.

Ceccarelli, D.M., Jones, G.P. & McCook, L.J. 2001. Territorial damselfishes as determinants of the structure of benthic communities on coral reefs. *Oceanography and Marine Biology: An Annual Review* **39**, 355–389.

Ceccarelli, D.M., Jones, G.P. & McCook, L.J. 2011. Interactions between herbivorous fish guilds and their influence on algal succession on a coastal coral reef. *Journal of Experimental Marine Biology and Ecology* **399**, 60–67.

Ceccarelli, D.M., Loffler, Z., Bourne, D.G. et al. 2018. Rehabilitation of coral reefs through removal of macroalgae: State of knowledge and considerations for management and implementation. *Restoration Ecology* **26**, 827–838.

Chan, T., Sadovy, Y. & Donaldson, T.J. 2012. *Bolbometopon muricatum*. The IUCN Red List of Threatened Species 2012: e.T63571A17894276.

Charpy, L., Casareto, B.E., Langlade, M.J. & Suzuki, Y. 2012. Cyanobacteria in coral reef ecosystems: A review. *Journal of Marine Biology* **2012**, 1–9.

Chase, T.J., Pratchett, M.S., Frank, G.E. & Hoogenboom, M.O. 2018. Coral-dwelling fish moderate bleaching susceptibility of coral hosts. *PLOS ONE* **13**, e0208545.

Chase, T.J., Pratchett, M.S., Walker, S.P.W. & Hoogenboom, M.O. 2014. Small-scale environmental variation influences whether coral-dwelling fish promote or impede coral growth. *Oecologia* **176**, 1009–1022.

Chazottes, V., Hutchings, P. & Osorno, A. 2017. Impact of an experimental eutrophication on the processes of bioerosion on the reef: One Tree Island, Great Barrier Reef, Australia. *Marine Pollution Bulletin* **118**, 125–130.

Chazottes, V., Le Campion-Alsumard, T., Peyrot-Clausade, M. & Cuet, P. 2002. The effects of eutrophication-related alterations to coral reef communities on agents and rates of bioerosion (Reunion Island, Indian Ocean). *Coral Reefs* **21**, 375–390.

Cheal, A.J., Coleman, G., Delean, S., Miller, I., Osborne, K. & Sweatman, H. 2002. Responses of coral and fish assemblages to a severe but short-lived tropical cyclone on the Great Barrier Reef, Australia. *Coral Reefs* **21**, 131–142.

Cheal, A.J., Emslie, M., MacNeil, M.A., Miller, I. & Sweatman, H. 2013. Spatial variation in the functional characteristics of herbivorous fish communities and the resilience of coral reefs. *Ecological Applications* **23**, 174–188.

Cheal, A.J., MacNeil, M.A., Cripps, E., Emslie, M.J., Jonker, M., Schaffelke, B. & Sweatman, H. 2010. Coral-macroalgal phase shifts or reef resilience: Links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. *Coral Reefs* **29**, 1005–1015.

Cheal, A.J., Macneil, M.A., Emslie, M.J. & Sweatman, H. 2017. The threat to coral reefs from more intense cyclones under climate change. *Global Change Biology* **23**, 1511–1524.

Cheal, A.J., Wilson, S.K., Emslie, M.J., Dolman, A.M. & Sweatman, H. 2008. Responses of reef fish communities to coral declines on the Great Barrier Reef. *Marine Ecology Progress Series* **372**, 211–223.

Chen, C.C.M., Bourne, D.G., Drovandi, C.C., Mengersen, K., Willis, B.L., Caley, M.J. & Sato, Y. 2017. Modelling environmental drivers of black band disease outbreaks in populations of foliose corals in the genus *Montipora*. *PeerJ* **5**, e3438. doi:3410.7717/peerj.3438.

Chen, T.R., Li, S. & Yu, K.F. 2013. Macrobioerosion in *Porites* corals in subtropical northern South China Sea: A limiting factor for high-latitude reef framework development. *Coral Reefs* **32**, 101–108.

Chesher, R.H. 1969. Destruction of Pacific corals by sea star *Acanthaster planci*. *Science* **165**, 280–283.

Chisholm, J.R.M. 2000. Calcification by crustose coralline algae on the northern Great Barrier Reef, Australia. *Limnology and Oceanography* **45**, 1476–1484.

Chisholm, J.R.M. 2003. Primary productivity of reef-building crustose coralline algae. *Limnology and Oceanography* **48**, 1376–1387.

Choat, J.H. & Clements, K.D. 1998. Vertebrate herbivores in marine and terrestrial environments: A nutritional ecology perspective. *Annual Review of Ecology and Systematics* **29**, 375–403.

Choat, J.H., Clements, K.D., McIlwain, J., Abesamis, R., Myers, R., Nanola, C., Rocha, L.A., Russell, B. & Stockwell, B. 2012. *Ctenochaetus striatus*. The IUCN Red List of Threatened Species 2012: e.T178012A1520757.

Choat, J.H., Clements, K.D. & Robbins, W.D. 2002. The trophic status of herbivorous fishes on coral reefs – I: Dietary analyses. *Marine Biology* **140**, 613–623.

Choat, J.H., Robbins, W.D. & Clements, K.D. 2004. The trophic status of herbivorous fishes on coral reefs – II. Food processing modes and trophodynamics. *Marine Biology* **145**, 445–454.

Choat, J.H. & Samoilys, M. 2018. *Plectropomus leopardus*. The IUCN Red List of Threatened Species. In e.T44684A100462709.

Chong-Seng, K.M., Nash, K.L., Bellwood, D.R. & Graham, N.A.J. 2014. Macroalgal herbivory on recovering versus degrading coral reefs. *Coral Reefs* **33**, 409–419.

Chung, A.E., Wedding, L.M., Green, A.L., Friedlander, A.M., Goldberg, G., Meadows, A. & Hixon, M.A. 2019. Building coral reef resilience through spatial herbivore management. *Frontiers in Marine Science* 6.

Cinner, J.E., Huchery, C., MacNeil, M.A. et al. 2016. Bright spots among the world's coral reefs. *Nature* **535**, 416–419.

Cinner, J.E., Maire, E., Huchery, C. et al. 2018. Gravity of human impacts mediates coral reef conservation gains. *Proceedings of the National Academy of Sciences of the United States of America* **115**, E6116–E6125.

Clague, G.E., Cheney, K.L., Goldizen, A.W., McCormick, M.I., Waldie, P.A. & Grutter, A.S. 2011. Long-term cleaner fish presence affects growth of a coral reef fish. *Biology Letters* **7**, 863–865.

Clark, S. & Edwards, A.J. 1995. Coral transplantation as an aid to reef rehabilitation: Evaluation of a case study in the Maldive Islands. *Coral Reefs* **14**, 201–213.

Clark, T.D., Messmer, V., Tobin, A.J., Hoey, A.S. & Pratchett, M.S. 2017. Rising temperatures may drive fishing-induced selection of low-performance phenotypes. *Scientific Reports* **7**, 40571. doi: 40510.41038/srep40571.

Clausing, R.J., Annunziata, C., Baker, G., Lee, C., Bittick, S.J. & Fong, P. 2014. Effects of sediment depth on algal turf height are mediated by interactions with fish herbivory on a fringing reef. *Marine Ecology Progress Series* **517**, 121–129.

Clemen, R. & Winkler, R. 1999. Combining probability distributions from experts in risk analysis. *Risk Analysis* **19**, 187–204.

Clements, C.S. & Hay, M.E. 2019. Biodiversity enhances coral growth, tissue survivorship and suppression of macroalgae. *Nature Ecology & Evolution* **3**, 178–182.

Clements, K.D., German, D.P., Piche, J., Tribollet, A. & Choat, J.H. 2017. Integrating ecological roles and trophic diversification on coral reefs: Multiple lines of evidence identify parrotfishes as microphages. *Biological Journal of the Linnean Society* **120**, 729–751.

Clements, K.D., Raubenheimer, D. & Choat, J.H. 2009. Nutritional ecology of marine herbivorous fishes: Ten years on. *Functional Ecology* **23**, 79–92.

Coen, L.D. 1988. Herbivory by crabs and the control of algal epibionts on Caribbean host corals. *Oecologia* **75**, 198–203.

Coker, D.J., Pratchett, M.S. & Munday, P.L. 2009. Coral bleaching and habitat degradation increase susceptibility to predation for coral-dwelling fishes. *Behavioral Ecology* **20**, 1204–1210.

Coker, D.J., Wilson, S.K. & Pratchett, M.S. 2014. Importance of live coral habitat for reef fishes. *Reviews in Fish Biology and Fisheries* **24**, 89–126.

Cole, A.J., Pratchett, M.S. & Jones, G.P. 2008. Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish and Fisheries* **9**, 286–307.

Cole, A.J., Pratchett, M.S. & Jones, G.P. 2009. Effects of coral bleaching on the feeding response of two species of coral-feeding fish. *Journal of Experimental Marine Biology and Ecology* **373**, 11–15.

Cole, A.J., Pratchett, M.S. & Jones, G.P. 2010. Corallivory in tubelip wrasses: Diet, feeding and trophic importance. *Journal of Fish Biology* **76**, 818–835.

Colgan, M.W. 1987. Coral reef recovery on Guam (Micronesia) after catastrophic predation by *Acanthaster planci*. *Ecology* **68**, 1592–1605.

Conand, C. 2018. Recent information on worldwide illegal fisheries for sea cucumbers. *SPC Bêche-de-mer Bulletin* **38**, 68–71.

Conand, C., Polidoro, B.A., Mercier, A., Gamboa, R., Hamel, J.-F. & Purcell, S.W. 2014. The IUCN Red List assessment of aspidochirotid sea cucumbers and its implications. *SPC Bêche-de-mer Information Bulletin* **34**, 3–7.

Conklin, E.J. & Smith, J.E. 2005. Abundance and spread of the invasive red algae, *Kappaphycus* spp., in Kane'ohe Bay, Hawai'i and an experimental assessment of management options. *Biological Invasions* **7**, 1029–1039.

Connell, J.H., Hughes, T.P. & Wallace, C.C. 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecological Monographs* **67**, 461–488.

Connell, S.D. 1998. Patterns of piscivory by resident predatory reef fish at One Tree Reef, Great Barrier Reef. *Marine and Freshwater Research* **49**, 25–30.

Connell, S.D., Foster, M.S. & Airoldi, L. 2014. What are algal turfs? Towards a better description of turfs. *Marine Ecology Progress Series* **495**, 299–307.

Connell, S.D., Kroeker, K.J., Fabricius, K.E., Kline, D.I. & Russell, B.D. 2013. The other ocean acidification problem: CO2 as a resource among competitors for ecosystem dominance. *Philosophical Transactions of the Royal Society B-Biological Sciences* 368.

Connolly, S.R. & Muko, S. 2003. Space preemption, size-dependent competition, and the coexistence of clonal growth forms. *Ecology* **84**, 2979–2988.

Cooper, T.F., De 'Ath, G., Fabricius, K.E. & Lough, J.M. 2008. Declining coral calcification in massive *Porites* in two nearshore regions of the northern Great Barrier Reef. *Global Change Biology* **14**, 529–538.

Cooper, W.T., Lirman, D., VanGroningen, M.P., Parkinson, J.E., Herlan, J. & McManus, J.W. 2014. Assessing techniques to enhance early post-settlement survival of corals *in situ* for reef restoration. *Bulletin of Marine Science* **90**, 651–664.

Cornish, A. 2003. *Diadema* sea urchins and the Black-spot tuskfish. *Porcupine (the Newsletter of the Department of Ecology and Biodiversity, The University of Hong Kong)* **28**, 5–6.

Cornwall, C.E., Boyd, P.W., McGraw, C.M., Hepburn, C.D., Pilditch, C.A., Morris, J.N., Smith, A.M. & Hurd, C.L. 2014. Diffusion boundary layers ameliorate the negative effects of ocean acidification on the temperate coralline macroalga *Arthrocardia corymbosa*. *PLOS ONE* 9.

Cornwall, C.E., Diaz-Pulido, G. & Comeau, S. 2019. Impacts of ocean warming on coralline algae: Knowledge gaps and key recommendations for future research. *Frontiers in Marine Science* **6**, 186.

Costanza, R. & Mageau, M. 1999. What is a healthy ecosystem? *Aquatic Ecology* **33**, 105–115.

Cote, I.M. 2000. Evolution and ecology of cleaning symbioses in the sea. *Oceanography and Marine Biology: An Annual Review* **38**, 311–355.

Courtney, A., Spillman, C., Lemos, R., Thomas, J., Leigh, G. & Campbell, A. 2015. *Physical oceanographic influences on Queensland reef fish and scallops: Final Report FRDC 2013/020*. FRDC Final Report, 164.

Courtney, A.J., Campbell, M.J., Roya, D.P., Tonks, M.L., Chilcott, K.E. & Kyne, P.M. 2008. Round scallops and square meshes: A comparison of four codend types on the catch rates of target species and by-catch in the Queensland (Australia) saucer scallop (*Amusium balloti*) trawl fishery. *Marine and Freshwater Research* **59**, 849–864.

Couturier, L.I.E., Dudgeon, C.L., Pollock, K.H., Jaine, F.R.A., Bennett, M.B., Townsend, K.A., Weeks, S.J. & Richardson, A. 2014. Population dynamics of the reef manta ray *Manta alfredi* in eastern Australia. *Coral Reefs* **33**, 329–342.

Couturier, L.I.E., Newman, P., Jaine, F.R.A., Bennett, M.B., Venables, W.N., Cagua, E.F., Townsend, K.A., Weeks, S.J. & Richardson, A.J. 2018. Variation in occupancy and habitat use of *Mobula alfredi* at a major aggregation site. *Marine Ecology Progress Series* **599**, 125–145.

Cowan, Z.-L., Pratchett, M., Messmer, V. & Ling, S. 2017. Known predators of crown-of-thorns starfish (*Acanthaster* spp.) and their role in mitigating, if not preventing, population outbreaks. *Diversity* **9**, 7.

Craik, W., Palmer, D. & Sheldrake, R. 2017. Priorities for Australia's biosecurity system.

Crawford, C.M., Lucas, J.S. & Nash, W.J. 1988. Growth and survival during the ocean-nursery rearing of giant clams, *Tridacna gigas*. 1. Assessment of four culture methods. *Aquaculture* **68**, 103–113.

Crossman, D.J., Choat, J.H. & Clements, K.D. 2005. Nutritional ecology of nominally herbivorous fishes on coral reefs. *Marine Ecology Progress Series* **296**, 129–142.

Crossman, D.J., Choat, J.H., Clements, K.D., Hardy, T. & McConochie, J. 2001. Detritus as food for grazing fishes on coral reefs. *Limnology and Oceanography* **46**, 1596–1605.

Cumming, R.L. 1999. Predation on reef-building corals: Multiscale variation in the density of three corallivorous gastropods, *Drupella* spp. *Coral Reefs* **18**, 147–157.

Cumming, R.L. 2009. *Population Outbreaks and Large Aggregations of Drupella on the Great Barrier Reef.* Great Barrier Reef Marine Park Authority.

Curnock, M.I., Marshall, N.A., Thiault, L., Heron, S.F., Hoey, J., Williams, G., Taylor, B., Pert, P.L. & Goldberg, J. 2019. Shifts in tourists' sentiments and climate risk perceptions following mass coral bleaching of the Great Barrier Reef. *Nature Climate Change* **9**, 535.

Cvitanovic, C., Fox, R.J. & Bellwood, D.R. 2007. Herbivory by fishes on the Great Barrier Reef: A review of knowledge and understanding.

Cyronak, T., Andersson, A.J., Langdon, C. et al. 2018. Taking the metabolic pulse of the world's coral reefs. *PLOS ONE* **13**, e0190872.

Cyronak, T. & Eyre, B.D. 2016. The synergistic effects of ocean acidification and organic metabolism on calcium carbonate ($CaCO3$) dissolution in coral reef sediments. *Marine Chemistry* **183**, 1–12.

D'Olivo, J.P., McCulloch, M.T. & Judd, K. 2013. Long-term records of coral calcification across the central Great Barrier Reef: Assessing the impacts of river runoff and climate change. *Coral Reefs* **32**, 999–1012.

DAF. 2018. Sustainable fisheries expert panel. Queensland Government, Department of Agriculture and Fisheries. https://www.daf.qld.gov.au/business-priorities/fisheries/sustainable-fisheries-strategy/sustainable-fisheries-expert-panel/communique/30-31-july-2018.

Dai, C.F. & Yang, H.P. 1995. Distribution of *Spirobranchus giganteus-corniculatus* (Hove) on the coral-reefs of southern Taiwan. *Zoological Studies* **34**, 117–125.

Daily, G., Postel, S., Bawa, K. & Kaufman, L. 1997. Nature's services: Societal dependence on natural ecosystems.

Dalzell, P., Adams, T.J.H. & Polunin, N.V.C. 1996. Coastal fisheries in the Pacific islands. *Oceanography and Marine Biology: An Annual Review* **34**, 395–531.

Dart, J.K.G. 1972. Echinoids, algal lawn and coral recolonization. *Nature* **239**, 50–51.

Davies, C.H., Coughlan, A., Hallegraeff, G. et al. 2016. A database of marine phytoplankton abundance, biomass and species composition in Australian waters. *Scientific Data* **3**, 160043.

Davies, P.J. & Hutchings, P.A. 1983. Initial colonization, erosion and accretion of coral substrate. *Coral Reefs* **2**, 27–35.

Davis, K.L.F., Russ, G.R., Williamson, D.H. & Evans, R.D. 2004. Surveillance and poaching on inshore reefs of the Great Barrier Reef Marine Park. *Coastal Management* **32**, 373–387.

Dawson, J.L. & Smithers, S.G. 2014. Carbonate sediment production, transport, and supply to a coral cay at Raine Reef, northern Great Barrier Reef, Australia: A facies approach. *Journal of Sedimentary Research* **84**, 1120–1138.

Dawson, J.L., Smithers, S.G. & Hua, Q. 2014. The importance of large benthic foraminifera to reef island sediment budget and dynamics at Raine Island, northern Great Barrier Reef. *Geomorphology* **222**, 68–81.

Dawson, R.F. 1985. *Taiwanese clam boat fishing in Australian waters. Centre for the study of Australian-Asian relations, School of Modern Asian Studies. Centre for the Study of Australian-Asian Relations, School of Modern Asian Studies.* Griffith University, Research Paper 33.

Day, J. 2016. The Great Barrier Reef Marine Park: The grandfather of modern MPAs. In *Big, Bold and Blue: Lessons from Australia's Marine Protected Areas. G. Wescott & J. Fitzsimons (eds.). Victoria, Australia: CSIRO Publishing*, 65–97.

Day, J.C. 2002. Zoning – lessons from the Great Barrier Reef Marine Park. *Ocean & Coastal Management* **45**, 139–156.

Dayoub, F., Dunbabin, M. & Corke, P. 2015. Robotic detection and tracking of crown-of-thorns starfish. *International Conference on Intelligent Robots and Systems (IROS)*, 1921–1928.

de Bakker, D.M., van Duyl, F.C., Bak, R.P.M., Nugues, M.M., Nieuwland, G. & Meesters, E.H. 2017. 40 Years of benthic community change on the Caribbean reefs of Curacao and Bonaire: The rise of slimy cyanobacterial mats. *Coral Reefs* **36**, 355–367.

de Franca Doria, M., Boyd, E., Tompkins, E.L. & Adger, W.N. 2009. Using expert elicitation to define successful adaptation to climate change. *Environmental Science & Policy* **12**, 810–819.

de Goeij, J.M., van Oevelen, D., Vermeij, M.J.A., Osinga, R., Middelburg, J.J., de Goeij, A.F.P.M. & Admiraal, W. 2013. Surviving in a marine desert: The sponge loop retains resources within coral reefs. *Science* **342**, 108–110.

de Groot, R., Wilson, M. & Boumans, R. 2002. A typology for the classification description and valuation of ecosystem functions, goods and services. *Ecological Economics* **41**, 393–408.

Deaker, D.J., Agüera, A., Lin, H.A., Lawson, C., Budden, C., Dworjanyn, S.A., Mos, B. & Byrne, M. 2020a. The hidden army: corallivorous crown-of-thorns seastars can spend years as herbivorous juveniles. Biology Letters 16, 20190849.

Deaker, D.J., Mos, B., Lin, H.A., Lawson, C., Budden, C., Dworjanyn, S.A. & Byrne, B. 2020b. Diet flexibility and growth of the early herbivorous juvenile crown-of-thorns sea star, implications for its boom-bust population dynamics. PLOS ONE 15, e0236142.

de Valck, J. & Rolfe, J. 2018. Linking water quality impacts and benefits of ecosystem services in the Great Barrier Reef. *Marine Pollution Bulletin* **130**, 55–66.

De'ath, G., Fabricius, K. & Lough, J. 2013. Yes – Coral calcification rates have decreased in the last twenty-five years! *Marine Geology* **346**, 400–402.

De'ath, G., Fabricius, K.E., Sweatman, H. & Puotinen, M. 2012. The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences of the United States of America* **109**, 17995–17999.

De'ath, G., Lough, J.M. & Fabricius, K.E. 2009. Declining coral calcification on the Great Barrier Reef. *Science* **323**, 116–119.

Dean, A.J., Steneck, R.S., Tager, D. & Pandolfi, J.M. 2015. Distribution, abundance and diversity of crustose coralline algae on the Great Barrier Reef. *Coral Reefs* **34**, 581–594.

DeCarlo, T.M., Cohen, A.L., Barkley, H.C., Cobban, Q., Young, C., Shamberger, K.E., Brainard, R.E. & Golbuu, Y. 2015. Coral macrobioerosion is accelerated by ocean acidification and nutrients. *Geology* **43**, 7–10.

DeCarlo, T.M., Cohen, A.L., Wong, G.T.F., Shiah, F.K., Lentz, S.J., Davis, K.A., Shamberger, K.E.F. & Lohmann, P. 2017. Community production modulates coral reef pH and the sensitivity of ecosystem calcification to ocean acidification. *Journal of Geophysical Research-Oceans* **122**, 745–761.

DEE. 2015. Reef 2050 Long-Term Sustainability Plan. Department of the Environment and Energy, Australian Government. Commonwealth of Australia 2015. 111.

DEE. 2017. Assessment of the Queensland Coral Reef Fin Fish Fishery. Department of the Environment and Energy. Australian Government, Canberra, Australia. 39.

dela Cruz, D.W. & Harrison, P.L. 2017. Enhanced larval supply and recruitment can replenish reef corals on degraded reefs. *Scientific Reports* 7.

Delaney, M.L., Linn, L.J. & Davies, P.J. 1996. Trace and minor element ratios in *Halimeda* aragonite from the Great Barrier Reef. *Coral Reefs* **15**, 181–189.

DeMartini, E.E., Langston, R.C. & Eble, J.A. 2014. Spawning seasonality and body sizes at sexual maturity in the bluespine unicornfish, *Naso unicornis* (Acanthuridae). *Ichthyological Research* **61**, 243–251.

Depczynski, M. & Bellwood, D.R. 2003. The role of cryptobenthic reef fishes in coral reef trophodynamics. *Marine Ecology Progress Series* **256**, 183–191.

DeVantier, L.M., Reichelt, R.E. & Bradbury, R.H. 1986. Does *Spirobranchus giganteus* protect host *Porites* from predation by *Acanthaster planci*: Predator pressure as a mechanism of coevolution? *Marine Ecology Progress Series* **32**, 307–310.

Devine, B.M., Munday, P.L. & Jones, G.P. 2012. Rising CO2 concentrations affect settlement behaviour of larval damselfishes. *Coral Reefs* **31**, 229–238.

Devlin, M.J. & Brodie, J. 2005. Terrestrial discharge into the Great Barrier Reef Lagoon: Nutrient behavior in coastal waters. *Marine Pollution Bulletin* **51**, 9–22.

deVries, M.S., Stock, B.C., Christy, J.H., Goldsmith, G.R. & Dawson, T.E. 2016. Specialized morphology corresponds to a generalist diet: Linking form and function in smashing mantis shrimp crustaceans. *Oecologia* **182**, 429–442.

Di Simone, M., Horellou, A. & Conand, C. 2019. Towards a CITES listing of teatfish. *SPC Bêche-de-mer Information Bulletin* **39**, 76–78.

Diaz-Pulido, G., Anthony, K.R.N., Bender, D., Doropoulos, C., Gouezo, M., Herrero-Gimeno, M. & Reyes-Nivia, C. 2011a. Variability in the effects of ocean acidification on coral reef macroalgae. *European Journal of Phycology* **46**, 48–49.

Diaz-Pulido, G., Anthony, K.R.N., Kline, D.I., Dove, S. & Hoegh-Guldberg, O. 2012. Interactions between ocean acidification and warming on the mortality and dissolution of coralline algae. *Journal of Phycology* **48**, 32–39.

Diaz-Pulido, G., Cornwall, C., Gartrell, P., Hurd, C. & Tran, D.V. 2016. Strategies of dissolved inorganic carbon use in macroalgae across a gradient of terrestrial influence: Implications for the Great Barrier Reef in the context of ocean acidification. *Coral Reefs* **35**, 1327–1341.

Diaz-Pulido, G., Gouezo, M., Tilbrook, B., Dove, S. & Anthony, K.R.N. 2011b. High CO2 enhances the competitive strength of seaweeds over corals. *Ecology Letters* **14**, 156–162.

Diaz-Pulido, G., Harii, S., McCook, L.J. & Hoegh-Guldberg, O. 2010. The impact of benthic algae on the settlement of a reef-building coral. *Coral Reefs* **29**, 203–208.

Diaz-Pulido, G. & McCook, L.J. 2002. The fate of bleached corals: Patterns and dynamics of algal recruitment. *Marine Ecology Progress Series* **232**, 115–128.

Diaz-Pulido, G. & McCook, L. 2008. Macroalgae (Seaweeds). In *The State of the Great Barrier Reef On-line*. A. Chin (ed.). Townsville: Great Barrier Reef Marine Park Authority. 47.

Diaz-Pulido, G., McCook, L.J., Dove, S., Berkelmans, R., Roff, G., Kline, D.I., Weeks, S., Evans, R.D., Williamson, D.H. & Hoegh-Guldberg, O. 2009. Doom and boom on a resilient reef: Climate change, algal overgrowth and coral recovery. *PLOS ONE* 4.

Diaz-Pulido, G., McCook, L.J., Larkum, A.W.D., Lotze, H.K., Raven, J.A., Schaffelke, B., Smith, J.E. & Steneck, R.S. 2007. Vulnerability of macroalgae of the Great Barrier Reef to climate change. In *Climate Change and the Great Barrier Reef*. J.E. Johnson & P.A. Marshall (eds). Townsville: Great Barrier Reef Marine Park Authority, 153–192.

Diaz-Pulido, G., Nash, M.C., Anthony, K.R., Bender, D., Opdyke, B.N., Reyes-Nivia, C. & Troitzsch, U. 2014. Greenhouse conditions induce mineralogical changes and dolomite accumulation in coralline algae on tropical reefs. *Nature Communications* **5**, 3310.

Dinsdale, E.A. & Harriott, V.J. 2004. Assessing anchor damage on coral reefs: A case study in selection of environmental indicators. *Environmental Management* **33**, 126–139.

Dinsdale, E.A., Pantos, O., Smriga, S. et al. 2008. Microbial ecology of four coral atolls in the northern Line Islands. *PLOS ONE* **3**, e1584.

Dixon, G.B., Davies, S.W., Aglyamova, G.A., Meyer, E., Bay, L.K. & Matz, M.V. 2015. Genomic determinants of coral heat tolerance across latitudes. *Science* **348**, 1460–1462.

Domenici, P., Allan, B., McCormick, M.I. & Munday, P.L. 2012. Elevated carbon dioxide affects behavioural lateralization in a coral reef fish. *Biology Letters* **8**, 78–81.

Donaldson, T.J. & Dulvy, N.K. 2004. Threatened fishes of the world: *Bolbometopon muricatum* (Valenciennes 1840) (Scaridae). *Environmental Biology of Fishes* **70**, 373–373.

Doo, S.S., Fujita, K., Byrne, M. & Uthicke, S. 2014. Fate of calcifying tropical symbiont-bearing large benthic foraminifera: Living sands in a changing ocean. *Biological Bulletin* **226**, 169–186.

Doo, S.S., Hamylton, S., Finfer, J. & Byrne, M. 2017. Spatial and temporal variation in reef-scale carbonate storage of large benthic foraminifera: A case study on One Tree Reef. *Coral Reefs* **36**, 293–303.

Doropoulos, C. & Diaz-Pulido, G. 2013. High CO2 reduces the settlement of a spawning coral on three common species of crustose coralline algae. *Marine Ecology Progress Series* **475**, 93–99.

Doropoulos, C., Elzinga, J., ter Hofstede, R., van Koningsveld, M. & Babcock, R.C. 2019. Optimizing industrial-scale coral reef restoration: Comparing harvesting wild coral spawn slicks and transplanting gravid adult colonies. *Restoration Ecology*. 10.1111/rec.12918.

Doropoulos, C., Evensen, N.R., Gomez-Lemos, L.A. & Babcock, R.C. 2017a. Density-dependent coral recruitment displays divergent responses during distinct early life-history stages. *Royal Society Open Science* **4**, 170082.

Doropoulos, C., Gomez-Lemos, L.A. & Babcock, R.C. 2018. Exploring variable patterns of density-dependent larval settlement among corals with distinct and shared functional traits. *Coral Reefs* **37**, 25–29.

Doropoulos, C., Hyndes, G.A., Abecasis, D. & Verges, A. 2013. Herbivores strongly influence algal recruitment in both coral- and algal-dominated coral reef habitats. *Marine Ecology Progress Series* **486**, 153–164.

Doropoulos, C., Roff, G., Bozec, Y.M., Zupan, M., Werminghausen, J. & Mumby, P.J. 2016. Characterizing the ecological trade-offs throughout the early ontogeny of coral recruitment. *Ecological Monographs* **86**, 20–44.

Doropoulos, C., Roff, G., Visser, M.S. & Mumby, P.J. 2017b. Sensitivity of coral recruitment to subtle shifts in early community succession. *Ecology* **98**, 304–314.

Doropoulos, C., Ward, S., Diaz-Pulido, G., Hoegh-Guldberg, O. & Mumby, P.J. 2012a. Ocean acidification reduces coral recruitment by disrupting intimate larval-algal settlement interactions. *Ecology Letters* **15**, 338–346.

Doropoulos, C., Ward, S., Marshell, A., Diaz-Pulido, G. & Mumby, P.J. 2012b. Interactions among chronic and acute impacts on coral recruits: The importance of size-escape thresholds. *Ecology* **93**, 2131–2138.

Doubleday, Z.A., Prowse, T.A., Arkhipkin, A. et al. 2016. Global proliferation of cephalopods. *Current Biology* **26**, R406–407.

Dove, S.G., Kline, D.I., Pantos, O., Angly, F.E., Tyson, G.W. & Hoegh-Guldberg, O. 2013. Future reef decalcification under a business-as-usual $CO_2$ emission scenario. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 15342–15347.

Downie, R.A., Babcock, R.C., Thomson, D.P. & Vanderklift, M.A. 2013. Density of herbivorous fish and intensity of herbivory are influenced by proximity to coral reefs. *Marine Ecology Progress Series* **482**, 217–225.

Drew, E.A. 1983. *Halimeda* biomass, growth rates and sediment generation on reefs in the central Great Barrier Reef province. *Coral Reefs* **2**, 101–110.

Duckworth, A., Giofre, N. & Jones, R. 2017. Coral morphology and sedimentation. *Marine Pollution Bulletin* **125**, 289–300.

Dufault, A.M., Ninokawa, A., Bramanti, L., Cumbo, V.R., Fan, T.Y. & Edmunds, P.J. 2013. The role of light in mediating the effects of ocean acidification on coral calcification. *Journal of Experimental Biology* **216**, 1570–1577.

Dulvy, N.K., Freckleton, R.P. & Polunin, N.V.C. 2004. Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecology Letters* **7**, 410–416.

Duong, B., Blomberg, S., Cribb, T., Cowman, P., Kuris, A., McCormick, M., Warner, R., Sun, D. & Grutter, A. 2019. Parasites of coral reef fish larvae: Its role in the pelagic larval stage. *Coral Reefs*, 1–16.

Dupuy, C., Pagano, M., Got, P., Domaizon, I., Chappuis, A., Marchessaux, G. & Bouvy, M. 2016. Trophic relationships between metazooplankton communities and their plankton food sources in the Iles Eparses (Western Indian Ocean). *Marine Environmental Research* **116**, 18–31.

Duran, A., Collado-Vides, L., Palma, L. & Burkepile, D.E. 2018. Interactive effects of herbivory and substrate orientation on algal community dynamics on a coral reef. *Marine Biology* **165**, 156.

Easson, C.G., Slattery, M., Baker, D.M. & Gochfeld, D.J. 2014. Complex ecological associations: Competition and facilitation in a sponge-algal interaction. *Marine Ecology Progress Series* **507**, 153–167.

Ebisawa, A., Kanashiro, K., Kyan, T. & Motonaga, F. 1995. Aspects of reproduction and sexuality in the black-spot tuskfish, *Choerodon schoenleinii*. *Japanese Journal of Ichthyology* **42**, 121–130.

Edwards, M. & Richardson, A.J. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **430**, 881.

Egan, S., Harder, T., Burke, C., Steinberg, P., Kjelleberg, S. & Thomas, T. 2013. The seaweed holobiont: Understanding seaweed-bacteria interactions. *Fems Microbiology Reviews* **37**, 462–476.

Eisenlord, M.E., Groner, M.L., Yoshioka, R.M., Elliott, J., Maynard, J., Fradkin, S., Turner, M., Pyne, K., Rivlin, N. & van Hooidonk, R. 2016. Ochre star mortality during the 2014 wasting disease epizootic: Role of population size structure and temperature. *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**, 20150212.

Elfwing, T., Blidberg, E., Sison, M. & Tedengren, M. 2003. A comparison between sites of growth, physiological performance and stress responses in transplanted *Tridacna gigas*. *Aquaculture* **219**, 815–828.

Elmer, L.K., Kelly, L.A., Rivest, S., Steell, S.C., Twardek, W.M., Danylchuk, A.J., Arlinghaus, R., Bennett, J.R. & Cooke, S.J. 2017. Angling into the future: Ten commandments for recreational fisheries science, management, and stewardship in a good Anthropocene. *Environmental Management* **60**, 165–175.

Emslie, M.J., Cheal, A.J. & Logan, M. 2017. The distribution and abundance of reef-associated predatory fishes on the Great Barrier Reef. *Coral Reefs* **36**, 829–846.

Emslie, M.J., Logan, M. & Cheal, A.J. 2019. The distribution of planktivorous damselfishes (Pomacentridae) on the Great Barrier Reef and the relative influences of habitat and predation. *Diversity* **11**, 33.

Emslie, M.J., Logan, M., Williamson, D.H. et al. 2015. Expectations and outcomes of reserve network performance following re-zoning of the Great Barrier Reef Marine Park. *Current Biology* **25**, 983–992.

Endean, R. 1969. *Report on investigations made into aspects of the current Acanthaster planci (Crown-of-thorns) infestations of certain reefs of the Great Barrier Reef.* Brisbane, Queensland: Queensland Department of Primary Industries (Fisheries Branch), 35.

Endean, R. 1982. Crown-of-thorns starfish on the Great Barrier-Reef. *Endeavour* **6**, 10–14.

Endean, R. & Stablum, W. 1973. A study of some aspects of the crown-of-thorns starfish (*Acanthaster planci*) infestations on reefs of Australia's Great Barrier Reef. *Atoll Research Bulletin* **167**, 1–76.

Enochs, I.C. 2012. Motile cryptofauna associated with live and dead coral substrates: Implications for coral mortality and framework erosion. *Marine Biology* **159**, 709–722.

Enochs, I.C. & Manzello, D.P. 2012. Species richness of motile cryptofauna across a gradient of reef framework erosion. *Coral Reefs* **31**, 653–661.

Enochs, I.C., Manzello, D.P., Carlton, R.D., Graham, D.M., Ruzicka, R. & Colella, M.A. 2015. Ocean acidification enhances the bioerosion of a common coral reef sponge: Implications for the persistence of the Florida Reef Tract. *Bulletin of Marine Science* **91**, 271–290.

Epstein, H., Torda, G., Munday, P. & van Oppen, M. 2019a. Parental and early life stage environments drive establishment of bacterial and dinoflagellate communities in a common coral. *The ISME Journal* **13**, 1635–1638. doi: 10.1038/s41396-41019-40358-41393.

Epstein, H.E., Torda, G. & van Oppen, M.J. 2019b. Relative stability of the *Pocillopora acuta* microbiome throughout a thermal stress event. *Coral Reefs* **38**, 373–386.

Erftemeijer, P.L.A., Riegl, B., Hoeksema, B.W. & Todd, P.A. 2012. Environmental impacts of dredging and other sediment disturbances on corals: A review. *Marine Pollution Bulletin* **64**, 1737–1765.

Eriksson, H. & Byrne, M. 2015. The sea cucumber fishery in Australia's Great Barrier Reef Marine Park follows global patterns of serial exploitation. *Fish and Fisheries* **16**, 329–341.

Espinel-Velasco, N., Hoffmann, L., Agüera, A., Byrne, M., Dupont, S., Uthicke, S., Webster, N.S. & Lamare, M. 2018. Effects of ocean acidification on the settlement and metamorphosis of marine invertebrate and fish larvae: A review. *Marine Ecology Progress Series* **606**, 237–257.

Estes, J.A., Terborgh, J., Brashares, J.S. et al. 2011. Trophic downgrading of Planet Earth. *Science* **333**, 301–306.

Eurich, J.G., Shomaker, S.M., McCormick, M.I. & Jones, G.P. 2018. Experimental evaluation of the effect of a territorial damselfish on foraging behaviour of roving herbivores on coral reefs. *Journal of Experimental Marine Biology and Ecology* **506**, 155–162.

Eyre, B.D., Andersson, A.J. & Cyronak, T. 2014. Benthic coral reef calcium carbonate dissolution in an acidifying ocean. *Nature Climate Change* **4**, 969–976.

Eyre, B.D., Cyronak, T., Drupp, P., De Carlo, E.H., Sachs, J.P. & Andersson, A.J. 2018. Coral reefs will transition to net dissolving before end of century. *Science* **359**, 908–911.

Fabricius, K.E. 1997. Soft coral abundance on the central Great Barrier Reef: Effects of *Acanthaster planci*, space availability, and aspects of the physical environment. *Coral Reefs* **16**, 159–167.

Fabricius, K.E. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: Review and synthesis. *Marine Pollution Bulletin* **50**, 125–146.

Fabricius, K.E., Benayahu, Y. & Genin, A. 1995. Herbivory in asymbiotic soft corals. *Science* **268**, 90–92.

Fabricius, K.E. & De'ath, G. 2001a. Biodiversity on the Great Barrier Reef: Large-scale patterns and turbidity-related local loss of soft coral taxa. In *Oceanographic Processes of Coral Reefs: Physical and Biological Links in the Great Barrier Reef.* E. Wolanski (ed.). London: CRC Press, 127–144.

Fabricius, K.E. & De'ath, G. 2001b. Environmental factors associated with the spatial distribution of crustose coralline algae on the Great Barrier Reef. *Coral Reefs* **19**, 303–309.

Fabricius, K.E. & De'Ath, G. 2004. Identifying ecological change and its causes: A case study on coral reefs. *Ecological Applications* **14**, 1448–1465.

Fabricius, K.E. & De'ath, G. 2008. Photosynthetic symbionts and energy supply determine octocoral biodiversity in coral reefs. *Ecology* **89**, 3163–3173.

Fabricius, K.E., De'ath, g., McCook, L., Turak, E. & Williams, D.M. 2005. Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. *Marine Pollution Bulletin* **51**, 384–398.

Fabricius, K.E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G., Okazaki, R., Muehllehner, N., Glas, M.S. & Lough, J.M. 2011. Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. *Nature Climate Change* **1**, 165–169.

Fabricius, K.E., Logan, M., Weeks, S. & Brodie, J. 2014. The effects of river run-off on water clarity across the central Great Barrier Reef. *Marine Pollution Bulletin* **84**, 191–200.

Fabricius, K.E., Okaji, K. & De'ath, G. 2010. Three lines of evidence to link outbreaks of the crown-of-thorns seastar *Acanthaster planci* to the release of larval food limitation. *Coral Reefs* **29**, 593–605.

Fairclough, D.V., Clarke, K.R., Valesini, F.J. & Potter, I.C. 2008. Habitat partitioning by five congeneric and abundant *Choerodon* species (Labridae) in a large subtropical marine embayment. *Estuarine Coastal and Shelf Science* **77**, 446–456.

Fairclough, D.V. & Nakazono, A. 2004. *Choerodon schoenleinii*. The IUCN Red List of Threatened Species. e.T44669A10933431.

Falkowski, P.G., Dubinsky, Z., Muscatine, L. & Mccloskey, L. 1993. Population-control in symbiotic corals. *Bioscience* **43**, 606–611.

Falkowski, P.G., Fenchel, T. & Delong, E.F. 2008. The microbial engines that drive Earth's biogeochemical cycles. *Science* **320**, 1034–1039.

Fang, J.K.H., Mason, R.A.B., Schonberg, C.H.L., Hoegh-Guldberg, O. & Dove, S. 2017. Studying interactions between excavating sponges and massive corals by the use of hybrid cores. *Marine Ecology-an Evolutionary Perspective* 38.

Fang, J.K.H., Schonberg, C.H.L., Mello-Athayde, M.A., Achlatis, M., Hoegh-Guldberg, O. & Dove, S. 2018. Bleaching and mortality of a photosymbiotic bioeroding sponge under future carbon dioxide emission scenarios. *Oecologia* **187**, 25–35.

Farnham, E.S. & Bell, J.J. 2018. Spatial variation in a shallow-water sponge-dominated reef in Timor-Leste (East Timor). *Pacific Science* **72**, 233–244.

Farnsworth, K.D., Albantakis, L. & Caruso, T. 2017. Unifying concepts of biological function from molecules to ecosystems. *Oikos* **126**, 1367–1376.

Feary, D.A., Bauman, A.G., Guest, J. & Hoey, A.S. 2018. Trophic plasticity in an obligate corallivorous butterflyfish. *Marine Ecology Progress Series* **605**, 165–171.

Feehan, C.J. & Scheibling, R.E. 2014. Effects of sea urchin disease on coastal marine ecosystems. *Marine Biology* **161**, 1467–1485.

Fernandes, L., Day, J., Kerrigan, B. et al. 2009. A process to design a network of marine no-take areas: Lessons from the Great Barrier Reef. *Ocean & Coastal Management* **52**, 439–447.

Fernandes, L., Day, J., Lewis, A. et al. 2005. Establishing representative no-take areas in the Great Barrier Reef: Large-scale implementation of theory on marine protected areas. *Conservation Biology* **19**, 1733–1744.

Fernandes, L., Dobbs, K., Day, J. & Slegers, S. 2010. Identifying biologically and physically special or unique sites for inclusion in the protected area design for the Great Barrier Reef Marine Park. *Ocean & Coastal Management* **53**, 80–88.

Ferrari, M.C.O., McCormick, M.I., Watson, S.-A., Meekan, M.G., Munday, P.L. & Chivers, D.P. 2017. Predation in high CO2 waters: Prey fish from high-risk environments are less susceptible to ocean acidification. *Integrative and Comparative Biology* **57**, 55–62.

Ferrari, R. 2017. The hidden structure in coral reefs. *Coral Reefs* **36**, 445–445.

Ferrier-Pages, C., Godinot, C., D'Angelo, C., Wiedenmann, J. & Grover, R. 2016. Phosphorus metabolism of reef organisms with algal symbionts. *Ecological Monographs* **86**, 262–277.

Ferrier-Pages, C., Hoogenboom, M. & Houlbreque, F. 2011. The role of plankton in coral trophodynamics. In *Coral Reefs: An Ecosystem in Transition*. Z. Dubinsky & N. Stambler (eds). Dordrecht, The Netherlands: Springer, 215–229.

Ferrigno, F., Bianchi, C.N., Lasagna, R., Morri, C., Russo, G.F. & Sandulli, R. 2016. Corals in high diversity reefs resist human impact. *Ecological Indicators* **70**, 106–113.

Fichez, R., Adjeroud, M., Bozec, Y.M. et al. 2005. A review of selected indicators of particle, nutrient and metal inputs in coral reef lagoon systems. *Aquatic Living Resources* **18**, 125–147.

Fine, M. & Loya, Y. 2002. Endolithic algae: An alternative source of photoassimilates during coral bleaching. *Proceedings of the Royal Society B-Biological Sciences* **269**, 1205–1210.

Fishelson, L. 1997. Olfaction and visual detection of food and relevant morphometric characters in some species of moray eels (Muraenidae). *Israel Journal of Zoology* **43**, 367–375.

Fisher, R., O'Leary, R.A., Low-Choy, S., Mengersen, K., Knowlton, N., Brainard, R.E. & Caley, M.J. 2015. Species richness on coral reefs and the pursuit of convergent global estimates. *Current Biology* **25**, 500–505.

Fitt, W.K., Brown, B.E., Warner, M.E. & Dunne, R.P. 2001. Coral bleaching: Interpretation of thermal tolerance limits and thermal thresholds in tropical corals. *Coral Reefs* **20**, 51–65.

Forsman, Z.H., Maurin, P., Parry, M. et al. 2018. The first Hawai'i workshop for coral restoration & nurseries. *Marine Policy* **96**, 133–135.

Fox, H.E. & Caldwell, R.L. 2006. Recovery from blast fishing on coral reefs: A tale of two scales. *Ecological Applications* **16**, 1631–1635.

Fox, H.E., Pet, J.S., Dahuri, R. & Caldwell, R.L. 2003. Recovery in rubble fields: Long-term impacts of blast fishing. *Marine Pollution Bulletin* **46**, 1024–1031.

Frade, P.R., Bongaerts, P., Englebert, N., Rogers, A., Gonzalez-Rivero, M. & Hoegh-Guldberg, O. 2018. Deep reefs of the Great Barrier Reef offer limited thermal refuge during mass coral bleaching. *Nature Communications* **9**, 3447.

Frade, P.R., Roll, K., Bergauer, K. & Herndl, G.J. 2016. Archaeal and bacterial communities associated with the surface mucus of Caribbean corals differ in their degree of host specificity and community turnover over reefs. *PLOS ONE* 11.

Frisch, A.J., Baker, R., Hobbs, J.P.A. & Nankervis, L. 2008. A quantitative comparison of recreational spearfishing and linefishing on the Great Barrier Reef: Implications for management of multi-sector coral reef fisheries. *Coral Reefs* **27**, 85–95.

Frisch, A.J., Cameron, D.S., Pratchett, M.S. et al. 2016a. Key aspects of the biology, fisheries and management of Coral grouper. *Reviews in Fish Biology and Fisheries* **26**, 303–325.

Frisch, A.J., Cole, A.J., Hobbs, J.P.A., Rizzari, J.R. & Munkres, K.P. 2012. Effects of spearfishing on reef fish populations in a multi-use conservation area. *PLOS ONE* **7**, e51938.

Frisch, A.J., Ireland, M., Rizzari, J.R., Lonnstedt, O.M., Magnenat, K.A., Mirbach, C.E. & Hobbs, J.P.A. 2016b. Reassessing the trophic role of reef sharks as apex predators on coral reefs. *Coral Reefs* **35**, 459–472.

Frisch, A.J. & Rizzari, J.R. 2019. Parks for sharks: Human exclusion areas outperform no-take marine reserves. *Frontiers in Ecology and the Environment* **17**, 145–150.

Fujita, K., Hikami, M., Suzuki, A., Kuroyanagi, A., Sakai, K., Kawahata, H. & Nojiri, Y. 2011. Effects of ocean acidification on calcification of symbiont-bearing reef foraminifers. *Biogeosciences* **8**, 2089–2098.

Fujita, K., Osawa, Y., Kayanne, H., Ide, Y. & Yamano, H. 2009. Distribution and sediment production of large benthic foraminifers on reef flats of the Majuro Atoll, Marshall Islands. *Coral Reefs* **28**, 29–45.

Furnas, M.J. 1992. Pelagic *Trichodesmium* (=*Oscillatoria*) in the Great Barrier Reef Region. In *Marine Pelagic Cyanobacteria: Trichodesmium and Other Diazotrophs*. E. Carpenter, D. Capone & J. Reuter (eds). Kluwer Academic Publishers, 265–272.

Furnas, M.J. & Mitchell, A.W. 1987. Phytoplankton dynamics in the central Great Barrier Reef. 2. Primary Production. *Continental Shelf Research* **7**, 1049–1062.

Furnas, M.J. & Mitchell, A.W. 1988. Shelf-scale estimates of phytoplankton primary production in the Great Barrier Reef. In *Proceedings of the 6th International Coral Reef Symposium*, Townsville, Australia. 557–562.

Furnas, M.J., Mitchell, A.W., Skuza, M. & Brodie, J. 2005. In the other 90%: Phytoplankton responses to enhanced nutrient availability in the Great Barrier Reef Lagoon. *Marine Pollution Bulletin* **51**, 253–265.

Gabrielson, P.W., Hughey, J.R. & Diaz-Pulido, G. 2018. Genomics reveals abundant speciation in the coral reef building alga *Porolithon onkodes* (Corallinales, Rhodophyta). *Journal of Phycology* **54**, 429–434.

Gallagher, C. & Doropoulos, C. 2017. Spatial refugia mediate juvenile coral survival during coral-predator interactions. *Coral Reefs* **36**, 51–61.

Gao, K., Helbling, E.W., Häder, D.-P. & Hutchins, D.A. 2012. Responses of marine primary producers to interactions between ocean acidification, solar radiation, and warming. *Marine Ecology Progress Series* **470**, 167–189.

Garcia, S.M. & Moreno, I.D. 2003. Global overview of marine fisheries. In *Responsible Fisheries in the Marine Ecosystem*. M. Sinclair & G. Valdimarsson (eds.). Food and Agriculture Organisation of the United Nations. Cambridge: CABI Publishing, 1–24.

Gardner, T.A., Cote, I.M., Gill, J.A., Grant, A. & Watkinson, A.R. 2003. Long-term region-wide declines in Caribbean corals. *Science* **301**, 958–960.

Garren, M. & Azam, F. 2012a. Corals shed bacteria as a potential mechanism of resilience to organic matter enrichment. *ISME Journal* **6**, 1159–1165.

Garren, M. & Azam, F. 2012b. New directions in coral reef microbial ecology. *Environmental Microbiology* **14**, 833–844.

Gast, G.J., Wiegman, S., Wieringa, E., Duyl, F.C. & Bak, R.P.M. 1998. Bacteria in coral reef water types: Removal of cells, stimulation of growth and mineralization. *Marine Ecology Progress Series* **167**, 37–45.

GBRMP Act. 1975. Great Barrier Reef Marine Park Act 1975. Prepared by the Office of Parliamentary Counsel, Canberra. 223.

GBRMPA. 2004. Great Barrier Reef Marine Park Zoning Plan 2003. Great Barrier Reef Marine Park Authority Townsville, Qld. 220.

GBRMPA. 2014a. Great Barrier Reef Marine Park Authority Science Strategy and Information Needs 2014–2019. Great Barrier Reef Marine Park Authority, Townsville.

GBRMPA. 2014b. Great Barrier Reef Outlook Report 2014. Great Barrier Reef Marine Park Authority, Townsville, Australia.

GBRMPA. 2014c. Great Barrier Reef Region Strategic Assessment: Strategic assessment report. Great Barrier Reef Marine Park Authority, Townsville.

GBRMPA. 2016. Coral reef recovery. Australian Government, Great Barrier Reef Marine Park Authority. Townsville, Queensland. Available at: http://www.gbrmpa.gov.au/__data/assets/pdf_file/0006/247848/Coral-Recovery-A4-Flyer_4Print.pdf

GBRMPA. 2017. Great Barrier Reef blueprint for resilience. Great Barrier Reef Marine Park Authority, Townsville.

GBRMPA. 2018a. From Blueprint to action: Great Barrier Reef Blueprint for resilience: Progress report. Great Barrier Reef Marine Park Authority, Townsville. 36.

GBRMPA. 2018b. Reef 2050 Integrated Monitoring and Reporting Program strategy update 2018. Great Barrier Reef Marine Park Authority and Queensland Government. 16.

Geange, S.W. & Stier, A.C. 2010. Charismatic microfauna alter cyanobacterial production through a trophic cascade. *Coral Reefs* **29**, 393–397.

Germanov, E.S., Bejder, L., Chabanne, D.B.H., Dharmadi, D., Hendrawan, I.G., Marshall, A.D., Pierce, S.J., van Keulen, M. & Loneragan, N.R. 2019. Contrasting habitat use and population dynamics of reef manta rays within the Nusa Penida Marine Protected Area, Indonesia. *Frontiers in Marine Science* **6**, 215.

Gershwin, L.A., Condie, S.A., Mansbridge, J.V. & Richardson, A.J. 2014. Dangerous jellyfish blooms are predictable. *Journal of the Royal Society Interface* **11**, 20131168.

Gilbert, M., Rasmussen, J.B. & Kramer, D.L. 2005. Estimating the density and biomass of moray eels (Muraenidae) using a modified visual census method for hole-dwelling reef fauna. *Environmental Biology of Fishes* **73**, 415–426.

Gillies, C.L., Creighton, C. & McLeod, I.M. 2015. *Shellfish reef habitats: A synopsis to underpin the repair and conservation of Australia's environmentally, socially and economically important bays and estuaries.* Report to the National Environmental Science Programme, Marine Biodiversity Hub. Centre for Tropical Water and Aquatic Ecosystem Research (TropWATER) Publication, James Cook University, Townsville. 68.

Gilmour, J.P., Smith, L.D., Heyward, A.J., Baird, A.H. & Pratchett, M.S. 2013. Recovery of an isolated coral reef system following severe disturbance. *Science* **340**, 69–71.

Glasl, B., Bourne, D.G., Frade, P.R., Thomas, T., Schaffelke, B. & Webster, N.S. 2019. Microbial indicators of environmental perturbations in coral reef ecosystems. *Microbiome* **7**, 94.

Glasl, B., Bourne, D.G., Frade, P.R. & Webster, N.S. 2018a. Establishing microbial baselines to identify indicators of coral reef health. *Microbiology Australia* **39**, 42–46.

Glasl, B., Herndl, G.J. & Frade, P.R. 2016. The microbiome of coral surface mucus has a key role in mediating holobiont health and survival upon disturbance. *ISME Journal* **10**, 2280–2292.

Glasl, B., Smith, C.E., Bourne, D.G. & Webster, N.S. 2018b. Exploring the diversity-stability paradigm using sponge microbial communities. *Scientific Reports* **8**, 8425.

Glasl, B., Webster, N.S. & Bourne, D.G. 2017. Microbial indicators as a diagnostic tool for assessing water quality and climate stress in coral reef ecosystems. *Marine Biology* **164**, 91.

Gleason, M.G. 1993. Effects of disturbance on coral communities – Bleaching in Moorea, French Polynesia. *Coral Reefs* **12**, 193–201.

Gleason, M.G. 1996. Coral recruitment in Moorea, French Polynesia: The importance of patch type and temporal variation. *Journal of Experimental Marine Biology and Ecology* **207**, 79–101.

Glynn, P.W. 1973. *Acanthaster*: Effect on coral reef growth in Panama. *Science* **180**, 504–506.

Glynn, P.W. 1980. Defense by symbiotic Crustacea of host corals elicited by chemical cues from predator. *Oecologia* **47**, 287–290.

Glynn, P.W. 1983. Increased survivorship in corals harboring crustacean symbionts. *Marine Biology Letters* **4**, 105–111.

Glynn, P.W. 1984. An amphinomid worm predator of the crown-of-thorns sea star and general predation on asteroids in eastern and western Pacific coral reefs. *Bulletin of Marine Science* **35**, 54–71.

Glynn, P.W. 1996. Coral reef bleaching: Facts, hypotheses and implications. *Global Change Biology* **2**, 495–509.

Glynn, P.W. & Enochs, I.C. 2011. Invertebrates and their roles in coral reef ecosystems. In *Coral Reefs: An Ecosystem in Transition. Z. Dubinsky & N. Stambler (eds.). Dordrecht: Springer* 273–325.

Glynn, P.W. & Krupp, D.A. 1986. Feeding biology of a Hawaiian sea star corallivore, *Culcita novaeguineae* Muller & Troschel. *Journal of Experimental Marine Biology and Ecology* **96**, 75–96.

Glynn, P.W. & Manzello, D.P. 2015. Bioerosion and coral reef growth: A dynamic balance. In *Coral Reefs in the Anthropocene*. C. Birkeland (ed.). Dordrecht: Springer, 67–97.

Glynn, P.W., Perez, M. & Gilchrist, S.L. 1985. Lipid decline in stressed corals and their crustacean symbionts. *Biological Bulletin* **168**, 276–284.

Glynn, P.W., Riegl, B., Purkis, S., Kerr, J.M. & Smith, T.B. 2015. Coral reef recovery in the Galapagos Islands: The northernmost islands (Darwin and Wenman). *Coral Reefs* **34**, 421–436.

Glynn, P.W., Veron, J.E.N. & Wellington, G.M. 1996. Clipperton atoll (eastern Pacific): Oceanography, geomorphology, reef-building coral ecology and biogeography. *Coral Reefs* **15**, 71–99.

Goatley, C.H.R. & Bellwood, D.R. 2010. Biologically mediated sediment fluxes on coral reefs: Sediment removal and off-reef transportation by the surgeonfish *Ctenochaetus striatus*. *Marine Ecology Progress Series* **415**, 237–245.

Goatley, C.H.R. & Bellwood, D.R. 2012. Sediment suppresses herbivory across a coral reef depth gradient. *Biology Letters* **8**, 1016–1018.

Goatley, C.H.R., Bonaldo, R.M., Fox, R.J. & Bellwood, D.R. 2016. Sediments and herbivory as sensitive indicators of coral reef degradation. *Ecology and Society* 21.

Goatley, C.H.R., Gonzalez-Cabello, A. & Bellwood, D.R. 2017. Small cryptopredators contribute to high predation rates on coral reefs. *Coral Reefs* **36**, 207–212.

Gochfeld, D.J. 2010. Territorial damselfishes facilitate survival of corals by providing an associational defense against predators. *Marine Ecology Progress Series* **398**, 137–148.

Godoy, N., Gelcich, S., Vasquez, J.A. & Castilla, J.C. 2010. Spearfishing to depletion: Evidence from temperate reef fishes in Chile. *Ecological Applications* **20**, 1504–1511.

Goldberg, E.G., Raab, T.K., Desalles, P., Briggs, A.A., Dunbar, R.B., Millero, F.J., Woosley, R.J., Young, H.S., Micheli, F. & Mccauley, D.J. 2019. Chemistry of the consumption and excretion of the bumphead parrotfish (*Bolbometopon muricatum*), a coral reef mega-consumer. *Coral Reefs* **38**, 347–357.

Goldshmid, R., Holzman, R., Weihs, D. & Genin, A. 2004. Aeration of corals by sleep-swimming fish. *Limnology and Oceanography* **49**, 1832–1839.

Golubic, S., Friedmann, I. & Schneider, J. 1981. The lithobiontic ecological niche, with special reference to microorganisms. *Journal of Sedimentary Research* **51**, 475–478.

Golubic, S., Radtke, G. & Le Campion-Alsumard, T. 2005. Endolithic fungi in marine ecosystems. *Trends in Microbiology* **13**, 229–235.

Gomez-Lemos, L.A. & Diaz-Pulido, G. 2017. Crustose coralline algae and associated microbial biofilms deter seaweed settlement on coral reefs. *Coral Reefs* **36**, 453–462.

Gómez-Lemos, L.A., Doropoulos, C., Bayraktarov, E. & Diaz-Pulido, G. 2018. Coralline algal metabolites induce settlement and mediate the inductive effect of epiphytic microbes on coral larvae. *Scientific Reports* **8**, 17557.

Gonzalez-Gomez, R., Briones-Fourzan, P., Alvarez-Filip, L. & Lozano-Alvarez, E. 2018. Diversity and abundance of conspicuous macrocrustaceans on coral reefs differing in level of degradation. *PeerJ* **6**, e4922.

Gonzalez-Rivero, M., Yakob, L. & Mumby, P.J. 2011. The role of sponge competition on coral reef alternative steady states. *Ecological Modelling* **222**, 1847–1853.

Gordon, S.E., Goatley, C.H.R. & Bellwood, D.R. 2016a. Composition and temporal stability of turf sediments on inner-shelf coral reefs. *Marine Pollution Bulletin* **111**, 178–183.

Gordon, S.E., Goatley, C.H.R. & Bellwood, D.R. 2016b. Low-quality sediments deter grazing by the parrotfish *Scarus rivulatus* on inner-shelf reefs. *Coral Reefs* **35**, 285–291.

Gotelli, N.J., Ulrich, W. & Maestre, F.T. 2011. Randomization tests for quantifying species importance to ecosystem function. *Methods in Ecology and Evolution* **2**, 634–642.

Graham, N.A.J., Ainsworth, T.D., Baird, A.H. et al. 2011a. From microbes to people: Tractable benefits of no-take areas for coral reefs. *Oceanography and Marine Biology: An Annual Review* **49**, 105–135.

Graham, N.A.J., Chong-Seng, K.M., Huchery, C., Januchowski-Hartley, F.A. & Nash, K.L. 2014. Coral reef community composition in the context of disturbance history on the Great Barrier Reef, Australia. *PLOS ONE* **9**, e101204.

Graham, N.A.J., Jennings, S., MacNeil, M.A., Mouillot, D. & Wilson, S.K. 2015. Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* **518**, 94–97.

Graham, N.A.J., Nash, K.L. & Kool, J.T. 2011b. Coral reef recovery dynamics in a changing world. *Coral Reefs* **30**, 283–294.

Graham, N.A.J., Wilson, S.K., Carr, P., Hoey, A.S., Jennings, S. & MacNeil, M.A. 2018. Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. *Nature* **559**, 250–253.

Graham, N.A.J., Wilson, S.K., Jennings, S., Polunin, N.V.C., Robinson, J., Bijoux, J.P. & Daw, T.M. 2007. Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conservation Biology* **21**, 1291–1300.

Graham, N.A.J., Wilson, S.K., Pratchett, M.S., Polunin, N.V.C. & Spalding, M.D. 2009. Coral mortality versus structural collapse as drivers of corallivorous butterflyfish decline. *Biodiversity and Conservation* **18**, 3325–3336.

Gribble, N.A. 2003. GBR-prawn: Modelling ecosystem impacts of changes in fisheries management of the commercial prawn (shrimp) trawl fishery in the far northern Great Barrier Reef. *Fisheries Research* **65**, 493–506.

Grottoli, A.G., Martins, P.D., Wilkins, M.J. et al. 2018. Coral physiology and microbiome dynamics under combined warming and ocean acidification. *PLOS ONE* **13**, e0191156.

Grottoli, A.G., Rodrigues, L.J. & Palardy, J.E. 2006. Heterotrophic plasticity and resilience in bleached corals. *Nature* **440**, 1186–1189.

Grutter, A.S. 1996. Parasite removal rates by the cleaner wrasse *Labroides dimidiatus*. *Marine Ecology Progress Series* **130**, 61–70.

Grutter, A.S. 1997. Spatiotemporal variation and feeding selectivity in the diet of the cleaner fish *Labroides dimidiatus*. *Copeia* 1**997**, 346–355.

Grutter, A.S. 2003. Feeding ecology of the fish ectoparasite *Gnathia* sp (Crustacea: Isopoda) from the Great Barrier Reef, and its implications for fish cleaning behaviour. *Marine Ecology Progress Series* **259**, 295–302.

Grutter, A.S., Crean, A.J., Curtis, L.M., Kuris, A.M., Warner, R.R. & McCormick, M.I. 2011. Indirect effects of an ectoparasite reduce successful establishment of a damselfish at settlement. *Functional Ecology* **25**, 586–594.

Grutter, A.S., Murphy, J.M. & Choat, J.H. 2003. Cleaner fish drives local fish diversity on coral reefs. *Current Biology* **13**, 64–67.

Grutter, A.S., Pickering, J.L., McCallum, H. & McCormick, M.I. 2008. Impact of micropredatory gnathiid isopods on young coral reef fishes. *Coral Reefs* **27**, 655–661.

Grutter, A.S. & Poulin, R. 1998. Cleaning of coral reef fishes by the wrasse *Labroides dimidiatus*: Influence of client body size and phylogeny. *Copeia* 1**998**, 120–127.

Guzman, H.M. & Cortes, J. 2007. Reef recovery 20 years after the 1982–1983 El Nino massive mortality. *Marine Biology* **151**, 401–411.

Haapkyla, J., Unsworth, R.K.F., Flavell, M., Bourne, D.G., Schaffelke, B. & Willis, B.L. 2011. Seasonal rainfall and runoff promote coral disease on an inshore reef. *PLOS ONE* **6**, e16893.

Haas, A.F., Fairoz, M.F.M., Kelly, L.W. et al. 2016. Global microbialization of coral reefs. *Nature Microbiology* **1**, 16042.

Häder, D.-P. & Gao, K. 2015. Interactions of anthropogenic stress factors on marine phytoplankton. *Frontiers in Environmental Science* **3**, e00014.

Hairsine, P.B. 2017. Review: Sediment-related controls on the health of the Great Barrier Reef. *Vadose Zone Journal* 16. doi:10.2136/vzj2017.2105.0115.

Hall, M.R., Motti, C.A. & Kroon, F. 2017. *The potential role of the giant triton snail, Charonia tritonis (Gastropoda: Ranellidae) in mitigating population outbreaks of the crown-of-thorns starfish. Integrated Pest Management of Crown-of-Thorns Starfish*. Report to the National Environmental Science Programme., Reef and Rainforest Research Centre Limited, Cairns. 58.

Halpern, B.S., McLeod, K.L., Rosenberg, A.A. & Crowder, L.B. 2008. Managing for cumulative impacts in ecosystem-based management through ocean zoning. *Ocean & Coastal Management* **51**, 203–211.

Halpern, B.S., Silliman, B.R., Olden, J.D., Bruno, J.P. & Bertness, M.D. 2007. Incorporating positive interactions in aquatic restoration and conservation. *Frontiers in Ecology and the Environment* **5**, 153–160.

Hamilton, R.J., Almany, G.R., Brown, C.J., Pita, J., Peterson, N.A. & Choat, H. 2017. Logging degrades nursery habitat for an iconic coral reef fish. *Biological Conservation* **210**, 273–280.

Hamner, W.M., Colin, P.L. & Hamner, P.P. 2007. Export-import dynamics of zooplankton on a coral reef in Palau. *Marine Ecology Progress Series* **334**, 83–92.

Hamner, W.M., Jones, M.S., Carleton, J.H., Hauri, I.R. & Williams, D.M. 1988. Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. *Bulletin of Marine Science* **42**, 459–479.

Hamylton, S., Leon, J.X., Saunders, M.I. & Woodroffe, C. 2014. Simulating reef response to sea-level rise at Lizard Island: A geospatial approach. *Geomorphology* **222**, 151–161.

Hamylton, S., Pescud, A., Leon, J.X. & Callaghan, D. 2013. A geospatial assessment of the relationship between reef flat community calcium carbonate production and wave energy. *Coral Reefs* **32**, 1025–1039.

Hamylton, S.M., Duce, S., Vila-Concejo, A., Roelfsema, C.M., Phinn, S.R., Carvalho, R.C., Shaw, E.C. & Joyce, K.E. 2017. Estimating regional coral reef calcium carbonate production from remotely sensed seafloor maps. *Remote Sensing of Environment* **201**, 88–98.

Hansen, J.A., Klumpp, D.W., Alongi, D.M., Dayton, P.K. & Riddle, M.J. 1992. Detrital pathways in a coral reef lagoon. 2. Detritus deposition, benthic microbial biomass and production. *Marine Biology* **113**, 363–372.

Harborne, A.R., Mumby, P.J. & Ferrari, R. 2012. The effectiveness of different meso-scale rugosity metrics for predicting intra-habitat variation in coral-reef fish assemblages. *Environmental Biology of Fishes* **94**, 431–442.

Harborne, A.R., Rogers, A., Bozec, Y.M. & Mumby, P.J. 2017. Multiple stressors and the functioning of coral reefs. *Annual Review of Marine Science* **9**, 445–468.

Harley, C.D.G., Anderson, K.M., Demes, K.W., Jorve, J.P., Kordas, R.L., Coyle, T.A. & Graham, M.H. 2012. Effects of climate change on global seaweed communities. *Journal of Phycology* **48**, 1064–1078.

Harmelin-Vivien, M.L. 1994. The effects of storms and cyclones on coral reefs: A review. *Journal of Coastal Research* **12**, 211–231.

Harrington, L., Fabricius, K., De'Ath, G. & Negri, A. 2004. Recognition and selection of settlement substrata determine post-settlement survival in corals. *Ecology* **85**, 3428–3437.

Harris, J.L., Lewis, L.S. & Smith, J.E. 2015. Quantifying scales of spatial variability in algal turf assemblages on coral reefs. *Marine Ecology Progress Series* **532**, 41–57.

Harris, P.T., Bridge, T.C.L., Beaman, R.J., Webster, J.M., Nichol, S.L. & Brooke, B.P. 2013. Submerged banks in the Great Barrier Reef, Australia, greatly increase available coral reef habitat. *Ices Journal of Marine Science* **70**, 284–293.

Harvell, D., Jordan-Dahlgren, E., Merkel, S., Rosenberg, E., Raymundo, L., Smith, G., Weil, E. & Willis, B. 2007. Coral disease, environmental drivers, and the balance between coral and microbial associates. *Oceanography* **20**, 172–195.

Harvey, B.J., Nash, K.L., Blanchard, J.L. & Edwards, D.P. 2018. Ecosystem-based management of coral reefs under climate change. *Ecology and Evolution* **8**, 6354–6368.

Hata, H. & Kato, M. 2004. Monoculture and mixed-species algal farms on a coral reef are maintained through intensive and extensive management by damselfishes. *Journal of Experimental Marine Biology and Ecology* **313**, 285–296.

Hatcher, B.G. 1988. Coral reef primary productivity – a beggars banquet. *Trends in Ecology & Evolution* **3**, 106–111.

Hatcher, B.G. & Larkum, A.W.D. 1983. An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. *Journal of Experimental Marine Biology and Ecology* **69**, 61–84.

He, Q., Bertness, M.D. & Altieri, A.H. 2013. Global shifts towards positive species interactions with increasing environmental stress. *Ecology Letters* **16**, 695–706.

Head, C.E.I., Bonsall, M.B., Koldewey, H., Pratchett, M.S., Speight, M. & Rogers, A.D. 2015. High prevalence of obligate coral-dwelling decapods on dead corals in the Chagos Archipelago, central Indian Ocean. *Coral Reefs* **34**, 905–915.

Heinrich, D.D.U., Watson, S.-A., Rummer, J.L., Brandl, S.J., Simpfendorfer, C.A., Heupel, M.R. & Munday, P.L. 2016. Foraging behaviour of the epaulette shark *Hemiscyllium ocellatum* is not affected by elevated CO2. *ICES Journal of Marine Science* **73**, 633–640.

Hemming, V., Burgman, M.A., Hanea, A.M., McBride, M.F. & Wintle, B.C. 2018. A practical guide to structured expert elicitation using the IDEA protocol. *Methods in Ecology and Evolution* **9**, 169–180.

Hempson, T.N., Graham, N.A.J., MacNeil, A.M., Hoey, A.S. & Almany, G.R. 2018a. Mesopredator trophodynamics on thermally stressed coral reefs. *Coral Reefs* **37**, 135–144.

Hempson, T.N., Graham, N.A.J., MacNeil, M.A., Bodin, N. & Wilson, S.K. 2018b. Regime shifts shorten food chains for mesopredators with potential sublethal effects. *Functional Ecology* **32**, 820–830.

Hempson, T.N., Graham, N.A.J., MacNeil, M.A., Hoey, A.S. & Wilson, S.K. 2018c. Ecosystem regime shifts disrupt trophic structure. *Ecological Applications* **28**, 191–200.

Hempson, T.N., Graham, N.A.J., MacNeil, M.A., Williamson, D.H., Jones, G.P. & Almany, G.R. 2017. Coral reef mesopredators switch prey, shortening food chains, in response to habitat degradation. *Ecology and Evolution* **7**, 2626–2635.

Hernaman, V., Probert, P.K. & Robbins, W.D. 2009. Trophic ecology of coral reef gobies: Interspecific, ontogenetic, and seasonal comparison of diet and feeding intensity. *Marine Biology* **156**, 317–330.

Hernandez-Agreda, A., Gates, R.D. & Ainsworth, T.D. 2017. Defining the Core Microbiome in Corals' Microbial Soup. *Trends in Microbiology* **25**, 125–140.

Heupel, M.R., Williams, A.J., Welch, D.J., Ballagh, A., Mapstone, B.D., Carlos, G., Davies, C. & Simpfendorfer, C.A. 2009. Effects of fishing on tropical reef associated shark populations on the Great Barrier Reef. *Fisheries Research* **95**, 350–361.

Hewson, I., Button, J.B., Gudenkauf, B.M., Miner, B., Newton, A.L., Gaydos, J.K., Wynne, J., Groves, C.L., Hendler, G. & Murray, M. 2014. Densovirus associated with sea-star wasting disease and mass mortality. *Proceedings of the National Academy of Sciences* **111**, 17278–17283.

Heyward, A.J. & Negri, A.P. 1999. Natural inducers for coral larval metamorphosis. *Coral Reefs* **18**, 273–279.

Heyward, A.J., Smith, L.D., Rees, M. & Field, S.N. 2002. Enhancement of coral recruitment by *in situ* mass culture of coral larvae. *Marine Ecology Progress Series* **230**, 113–118.

Hiatt, R.W. & Strasburg, D.W. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecological Monographs* **30**, 66–127.

Hill, B.J. & Wassenberg, T.J. 2000. The probable fate of discards from prawn trawlers fishing near coral reefs – A study in the northern Great Barrier Reef, Australia. *Fisheries Research* **48**, 277–286.

Hixon, M.A. & Beets, J.P. 1993. Predation, prey refuges, and the structure of coral reef fish assemblages. *Ecological Monographs* **63**, 77–101.

Hixon, M.A. & Carr, M.H. 1997. Synergistic predation, density dependence, and population regulation in marine fish. *Science* **277**, 946–949.

Hixon, M.A. & Menge, B.A. 1991. Species diversity: Prey refuges modify the interactive effects of predation and competition. *Theoretical Population Biology* **39**, 178–200.

Hobbs, J.P.A. & Frisch, A.J. 2010. Coral disease in the Indian Ocean: Taxonomic susceptibility, spatial distribution and the role of host density on the prevalence of white syndrome. *Diseases of Aquatic Organisms* **89**, 1–8.

Hobbs, J.P.A., Frisch, A.J., Newman, S.J. & Wakefield, C.B. 2015. Selective impact of disease on coral communities: Outbreak of White Syndrome causes significant total mortality of *Acropora* plate corals. *PLOS ONE* **10**, e0132528.

Hobson, E.S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fishery Bulletin* **72**, 915–1031.

Hock, K., Wolff, N.H., Condie, S.A., Anthony, K.R.N. & Mumby, P.J. 2014. Connectivity networks reveal the risks of crown-of-thorns starfish outbreaks on the Great Barrier Reef. *Journal of Applied Ecology* **51**, 1188–1196.

Hock, K., Wolff, N.H., Ortiz, J.C., Condie, S.A., Anthony, K.R.N., Blackwell, P.G. & Mumby, P.J. 2017. Connectivity and systemic resilience of the Great Barrier Reef. *Plos Biology* **15**, e2003355.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* **50**, 839–866.

Hoegh-Guldberg, O. 2005. Low coral cover in a high-CO2 world. *Journal of Geophysical Research-Oceans* **110**, C09S06.

Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J. et al. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* **318**, 1737–1742.

Hoey, A.S. & Bellwood, D.R. 2008. Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs* **27**, 37–47.

Hoey, A.S. & Bellwood, D.R. 2009. Limited functional redundancy in a high diversity system: Single species dominates key ecological process on coral reefs. *Ecosystems* **12**, 1316–1328.

Hoey, A.S. & Bellwood, D.R. 2010a. Among-habitat variation in herbivory on *Sargassum* spp. on a mid-shelf reef in the northern Great Barrier Reef. *Marine Biology* **157**, 189–200.

Hoey, A.S. & Bellwood, D.R. 2010b. Cross-shelf variation in browsing intensity on the Great Barrier Reef. *Coral Reefs* **29**, 499–508.

Hoey, A.S. & Bellwood, D.R. 2010c. Damselfish territories as a refuge for macroalgae on coral reefs. *Coral Reefs* **29**, 107–118.

Hoey, A.S. & Bellwood, D.R. 2011. Suppression of herbivory by macroalgal density: A critical feedback on coral reefs? *Ecology Letters* **14**, 267–273.

Hoey, A.S., Brandl, S.J. & Bellwood, D.R. 2013. Diet and cross-shelf distribution of rabbitfishes (f. Siganidae) on the northern Great Barrier Reef: Implications for ecosystem function. *Coral Reefs* **32**, 973–984.

Hoey, A.S., Howells, E., Johansen, J.L., Hobbs, J.-P.A., Messmer, V., McCowan, D.M., Wilson, S.K. & Pratchett, M.S. 2016a. Recent advances in understanding the effects of climate change on coral reefs. *Diversity* **8**, 12.

Hoey, J., Campbell, M.L., Hewitt, C.L., Gould, B. & Bird, R. 2016b. *Acanthaster planci* invasions: Applying biosecurity practices to manage a native boom and bust coral pest in Australia. *Management of Biological Invasions* **7**, 213–220.

Holbrook, S.J., Schmitt, R.J. & Brooks, A.J. 2008. Resistance and resilience of a coral reef fish community to changes in coral cover. *Marine Ecology Progress Series* **371**, 263–271.

Holbrook, S.J., Schmitt, R.J., Messmer, V., Brooks, A.J., Srinivasan, M., Munday, P.L. & Jones, G.P. 2015. Reef fishes in biodiversity hotspots are at greatest risk from loss of coral species. *PLOS ONE* **10**, e0124054.

Holzman, R. & Genin, A. 2003. Zooplanktivory by a nocturnal coral-reef fish: Effects of light, flow, and prey density. *Limnology and Oceanography* **48**, 1367–1375.

Holzman, R., Reidenbach, M.A., Monismith, S.G., Koseff, J.R. & Genin, A. 2005. Near-bottom depletion of zooplankton over a coral reef – II: Relationships with zooplankton swimming ability. *Coral Reefs* **24**, 87–94.

Hoogenboom, M., Rottier, C., Sikorski, S. & Ferrier-Pages, C. 2015. Among-species variation in the energy budgets of reef-building corals: Scaling from coral polyps to communities. *Journal of Experimental Biology* **218**, 3866–3877.

Hooper, D.U., Chapin, F.S., Ewel, J.J. et al. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* **75**, 3–35.

Hopcroft, R.R. & Roff, J.C. 1995. Zooplankton growth rates: Extraordinary production by the larvacean *Oikopleura dioica* in tropical waters. *Journal of Plankton Research* **17**, 205–220.

Howells, E.J., Beltran, V.H., Larsen, N.W., Bay, L.K., Willis, B.L. & van Oppen, M.J.H. 2012. Coral thermal tolerance shaped by local adaptation of photosymbionts. *Nature Climate Change* **2**, 116–120.

Howells, E.J., Berkelmans, R., van Oppen, M.J.H., Willis, B.L. & Bay, L.K. 2013. Historical thermal regimes define limits to coral acclimatization. *Ecology* **94**, 1078–1088.

Hughes, T.P. 1994. Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. *Science* **265**, 1547–1551.

Hughes, T.P., Anderson, K.D., Connolly, S.R. et al. 2018a. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* **359**, 80–83.

Hughes, T.P., Barnes, M.L., Bellwood, D.R. et al. 2017a. Coral reefs in the Anthropocene. *Nature* **546**, 82–90.

Hughes, T.P., Bellwood, D.R., Folke, C.S., McCook, L.J. & Pandolfi, J.M. 2007a. No-take areas, herbivory and coral reef resilience. *Trends in Ecology & Evolution* **22**, 1–3.

Hughes, T.P. & Connell, J.H. 1999. Multiple stressors on coral reefs: A long-term perspective. *Limnology and Oceanography* **44**, 932–940.

Hughes, T.P., Kerry, J.T., Alvarez-Noriega, M. et al. 2017b. Global warming and recurrent mass bleaching of corals. *Nature* **543**, 373–377.

Hughes, T.P., Kerry, J.T., Baird, A.H. et al. 2019a. Global warming impairs stock–recruitment dynamics of corals. *Nature* **568**, 387–390.

Hughes, T.P., Kerry, J.T., Baird, A.H. et al. 2018b. Global warming transforms coral reef assemblages. *Nature* **556**, 492–496.

Hughes, T.P., Kerry, J.T., Connolly, S.R. et al. 2019b. Ecological memory modifies the cumulative impact of recurrent climate extremes. *Nature Climate Change* **9**, 40–43.

Hughes, T.P., Kerry, J.T. & Simpson, T. 2018c. Large-scale bleaching of corals on the Great Barrier Reef. *Ecology* **99**, 501–501.

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S. & Willis, B. 2007b. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology* **17**, 360–365.

Hunsicker, M.E. & Essington, T.E. 2008. Evaluating the potential for trophodynamic control of fish by the longfin inshore squid (*Loligo pealeii*) in the Northwest Atlantic Ocean. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 2524–2535.

Huntley, M.E. & Lopez, M.D. 1992. Temperature-dependent production of marine copepods: A global synthesis. *The American Naturalist* **140**, 201–242.

Hutchings, P.A. 1983. Cryptofaunal communities of coral reefs. In *Perspectives in Coral Reefs*. D.J. Barnes (ed.). Townsville: Australian Institute of Marine Science, 200–208.

Hutchings, P.A. 1986. Biological destruction of coral reefs – A review. *Coral Reefs* **4**, 239–252.

Hutchings, P.A. 2008. Role of polychaetes in bioerosion of coral substrates. In *Current Developments in Bioerosion*. M. Wisshak & L. Tapanila (eds). Erlangen Earth Conference Series. Berlin, Heidelberg: Springer, 249–264.

Hutchings, P.A. 2011. Bioerosion. In *Encyclopedia of Modern Coral Reefs: Structure, Form and Process*. D. Hopley (ed.). Netherlands: Springer, 139–156.

Hutchings, P.A. & Kiene, W.E. 1986. Bioerosion of coral reefs. *Oceanus* **29**, 71–71.

Hutchings, P.A., Kiene, W.E., Cunningham, R.B. & Donnelly, C. 1992. Spatial and temporal patterns of non-colonial boring organisms (polychaetes, sipunculans and bivalve mollusks) in *Porites* at Lizard Island, Great Barrier Reef. *Coral Reefs* **11**, 23–31.

Hutchings, P.A., Kingsford, M. & Hoegh-Guldberg, O. 2019. *The Great Barrier Reef: Biology, Environment and Management*, 2nd edition. CSIRO Publishing.

Hutchings, P.A. & Kupriyanova, E. 2015. Polychaetes and allies of Lizard Island. *Zootaxa* 4**019**, 2.

Hutson, K.S., Cable, J., Grutter, A.S., Paziewska-Harris, A. & Barber, I. 2018. Aquatic parasite cultures and their applications. *Trends in Parasitology* **34**, 1082–1096.

Hutchings, P.A., Peyrot-Clausade, M. & Osnorno, A. 2005. Influence of land runoff on rates and agents of bioerosion of coral substrates. *Marine Pollution Bulletin* **51**, 438–447.

Huynh, T.T., Pereira, P., Mulcahy, R., Cullen, P., Seymour, J., Carrette, T. & Little, M. 2003. Severity of Irukandji syndrome and nematocyst identification from skin scrapings. *Medical Journal of Australia* **178**, 38–41.

IMOS. 2018. IMOS Science and Technology Advisory Committee (STAC) Meeting Report. National Research Infrastructure for Australia (NCRIS) and the Integrated Marine Observing System (IMOS). 4–5 September 2018. 34 pp.

IPCC. 2007. Climate change 2007: Impacts, adaptation and vulnerability. *Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. M.L. Parry et al. (eds). Cambridge, UK: Cambridge University Press.

IPCC. 2019. *Global warming of 1.5°C: An IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty*. V. Masson-Delmotte, P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J.B.R. Matthews, Y. Chen, X. Zhou, M.I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, and T. Waterfield (eds.). *Intergovernmental Panel on Climate Change*. , 630 pp.

Jackson, J.B.C., Kirby, M.X., Berger, W.H. et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**, 629–637.

Jacoby, C.A. & Greenwood, J.G. 1988. Spatial, temporal, and behavioral patterns in emergence of zooplankton in the lagoon of Heron Reef, Great Barrier Reef, Australia. *Marine Biology* **97**, 309–328.

Jain, M., Flynn, D.F.B., Prager, C.M. et al. 2014. The importance of rare species: A trait-based assessment of rare species contributions to functional diversity and possible ecosystem function in tall-grass prairies. *Ecology and Evolution* **4**, 104–112.

Jaine, F.R.A., Couturier, L.I.E., Weeks, S.J., Townsend, K.A., Bennett, M.B., Fiora, K. & Richardson, A.J. 2012. When giants turn up: Sighting trends, environmental influences and habitat use of the manta ray *Manta alfredi* at a coral reef. *PLOS ONE* **7**, e46170.

Jarrold, M.D., Humphrey, C., McCormick, M.I. & Munday, P.L. 2017. Diel CO2 cycles reduce severity of behavioural abnormalities in coral reef fish under ocean acidification. *Scientific Reports* **7**, 10153.

Jarrold, M.D. & Munday, P.L. 2018. Diel CO2 cycles do not modify juvenile growth, survival and otolith development in two coral reef fish under ocean acidification. *Marine Biology* **165**, 49.

Jax, K. 2005. Function and "functioning" in ecology: What does it mean? *Oikos* **111**, 641–648.

Jenkins, W.G., Demopoulos, A.W.J. & Sikkel, P.C. 2018. Effects of host injury on susceptibility of marine reef fishes to ectoparasitic gnathiid isopods. *Symbiosis* **75**, 113–121.

Jiao, N., Herndl, G.J., Hansell, D.A., Benner, R., Kattner, G., Wilhelm, S.W., Kirchman, D.L., Weinbauer, M.G., Luo, T., Chen, F. & Azam, F. 2010. Microbial production of recalcitrant dissolved organic matter: Long-term carbon storage in the global ocean. *Nature Reviews Microbiology* **8**, 593–599.

Johansen, J.L. & Jones, G.P. 2013. Sediment-induced turbidity impairs foraging performance and prey choice of planktivorous coral reef fishes. *Ecological Applications* **23**, 1504–1517.

Johansen, J.L., Messmer, V., Coker, D.J., Hoey, A.S. & Pratchett, M.S. 2014. Increasing ocean temperatures reduce activity patterns of a large commercially important coral reef fish. *Global Change Biology* **20**, 1067–1074.

Johansen, J.L., Pratchett, M.S., Messmer, V., Coker, D.J., Tobin, A.J. & Hoey, A.S. 2015. Large predatory coral trout species unlikely to meet increasing energetic demands in a warming ocean. *Scientific Reports* **5**, 13830.

Johansson, C.L., Francis, D.S. & Uthicke, S. 2016. Food preferences of juvenile corallivorous crown-of-thorns (*Acanthaster planci*) sea stars. *Marine Biology* **163**, 49.

Johansson, C.L., van de Leemput, I.A., Depczynski, M., Hoey, A.S. & Bellwood, D.R. 2013. Key herbivores reveal limited functional redundancy on inshore coral reefs. *Coral Reefs* **32**, 963–972.

Johns, K.A., Emslie, M.J., Hoey, A.S., Osborne, K., Jonker, M.J. & Cheal, A.J. 2018. Macroalgal feedbacks and substrate properties maintain a coral reef regime shift. *Ecosphere* **9**, e02349.

Johns, K.A., Osborne, K.O. & Logan, M. 2014. Contrasting rates of coral recovery and reassembly in coral communities on the Great Barrier Reef. *Coral Reefs* **33**, 553–563.

Johnson, C.R., Sutton, D.C., Olson, R.R. & Giddins, R. 1991. Settlement of crown-of-thorns starfish – role of bacteria on surfaces of coralline algae and a hypothesis for deep-water recruitment. *Marine Ecology Progress Series* **71**, 143–162.

Johnson, M.D., Rodriguez Bravo, L.M., O'Connor, S.E., Varley, N.F. & Altieri, A.H. 2019. pH variability exacerbates effects of ocean acidification on a Caribbean crustose coralline alga. *Frontiers in Marine Science* **6**, 150.

Jones, A.M., Brown, C. & Gardner, S. 2011. Tool use in the tuskfish *Choerodon schoenleinii*? *Coral Reefs* **30**, 865–865.

Jones, R., Bessell-Browne, P., Fisher, R., Klonowski, W. & Slivkoff, M. 2016. Assessing the impacts of sediments from dredging on corals. *Marine Pollution Bulletin* **102**, 9–29.

Jonker, M.M., Johns, K.K. & Osborne, K.K. 2008. Surveys of benthic reef communities using underwater digital photography and counts of juvenile corals. Long-term Monitoring of the Great Barrier Reef. Standard Operational Procedure No. 10. Townsville: Australian Institute of Marine Science. 75 pp.

Jordán, F., Okey, T., Bauer, B. & Libralato, S. 2008. Identifying important species: Linking structure and function in ecological networks. *Ecological Modelling* **216**, 75–80.

Kamali, E., Valinassab, T. & Emadi, H. 2006. Age determination of John's snapper (*Lutjanus johni*) using otolith sections. *Iranian Scientific Fisheries Journal* **15**, 109–118.

Kamya, P.Z., Byrne, M., Mos, B. & Dworjanyn, S.A. 2018. Enhanced performance of juvenile crown-of-thorns starfish in a warm-high CO2 ocean exacerbates poor growth and survival of their coral prey. *Coral Reefs* **37**, 751–762.

Karkarey, R., Alcoverro, T., Kumar, S. & Arthur, R. 2017. Coping with catastrophe: Foraging plasticity enables a benthic predator to survive in rapidly degrading coral reefs. *Animal Behaviour* **131**, 13–22.

Keesing, J.K., Halford, A.R. & Hall, K.C. 2018. Mortality rates of small juvenile crown-of-thorns starfish *Acanthaster planci* on the Great Barrier Reef: Implications for population size and larval settlement thresholds for outbreaks. *Marine Ecology Progress Series* **597**, 179–190.

Keesing, J.K., Thomson, D.P., Haywood, M.D.E. & Babcock, R.C. 2019. Two time losers: Selective feeding by crown-of-thorns starfish on corals most affected by successive coral bleaching episodes on western Australian coral reefs. *Marine Biology* **166**, 72.

Kellogg, C.A. 2004. Tropical Archaea: Diversity associated with the surface microlayer of corals. *Marine Ecology Progress Series* **273**, 81–88.

Kelly, L.W., Williams, G.J., Barott, K.L. et al. 2014. Local genomic adaptation of coral reef-associated microbiomes to gradients of natural variability and anthropogenic stressors. *Proceedings of the National Academy of Sciences of the United States of America* **111**, 10227–10232.

Kennedy, E.V., Ordonez, A. & Diaz-Pulido, G. 2018. Coral bleaching in the southern inshore Great Barrier Reef: A case study from the Keppel Islands. *Marine and Freshwater Research* **69**, 191–197.

Kennedy, E.V., Ordonez, A., Lewis, B.E. & Diaz-Pulido, G. 2017. Comparison of recruitment tile materials for monitoring coralline algae responses to a changing climate. *Marine Ecology Progress Series* **569**, 129–144.

Kennedy, E.V., Perry, C.T., Halloran, P.R. et al. 2013. Avoiding coral reef functional collapse requires local and global action. *Current Biology* **23**, 912–918.

Kerry, J.T. & Bellwood, D.R. 2012. The effect of coral morphology on shelter selection by coral reef fishes. *Coral Reefs* **31**, 415–424.

Kerry, J.T. & Bellwood, D.R. 2015a. Do tabular corals constitute keystone structures for fishes on coral reefs? *Coral Reefs* **34**, 41–50.

Kerry, J.T. & Bellwood, D.R. 2015b. The functional role of tabular structures for large reef fishes: Avoiding predators or solar irradiance? *Coral Reefs* **34**, 693–702.

Kerry, J.T. & Bellwood, D.R. 2016. Competition for shelter in a high-diversity system: Structure use by large reef fishes. *Coral Reefs* **35**, 245–252.

Kerry, J.T. & Bellwood, D.R. 2017. Environmental drivers of sheltering behaviour in large reef fishes. *Marine Pollution Bulletin* **125**, 254–259.

Kiene, W. & Hutchings, P. 1994. Bioerosion experiments at Lizard Island, Great Barrier Reef. *Coral Reefs* **13**, 91–98.

Kimes, N.E., Van Nostrand, J.D., Weil, E., Zhou, J.Z. & Morris, P.J. 2010. Microbial functional structure of *Montastraea faveolata*, an important Caribbean reef-building coral, differs between healthy and yellow-band diseased colonies. *Environmental Microbiology* **12**, 541–556.

Kingsford, M.J., Seymour, J.E. & O'Callaghan, M.D. 2012. Abundance patterns of cubozoans on and near the Great Barrier Reef. *Hydrobiologia* **690**, 257–268.

Kininmonth, S., Lemm, S., Malone, C. & Hatley, T. 2014. Spatial vulnerability assessment of anchor damage within the Great Barrier Reef World Heritage Area, Australia. *Ocean & Coastal Management* **100**, 20–31.

Kinsey, D.W. 1983. Standards of performance in coral reef primary production and carbon turnover. In *Perspectives on Coral Reefs*. D.J. Barnes (ed.). Townsville: Australian Institute of Marine Science, 209–220.

Kirby, M.X. 2004. Fishing down the coast: Historical expansion and collapse of oyster fisheries along continental margins. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 13096–13099.

Kirby, R.R., Beaugrand, G., Lindley, J.A., Richardson, A.J., Edwards, M. & Reid, P.C. 2007. Climate effects and benthic-pelagic coupling in the North Sea. *Marine Ecology Progress Series* **330**, 31–38.

Kleypas, J.A., Buddemeier, R.W., Archer, D., Gattuso, J.P., Langdon, C. & Opdyke, B.N. 1999. Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* **284**, 118–120.

Klumpp, D.W., Bayne, B.L. & Hawkins, A.J.S. 1992. Nutrition of the giant clam *Tridacna gigas* (L). 1. Contribution of filter feeding and photosynthates to respiration and growth. *Journal of Experimental Marine Biology and Ecology* **155**, 105–122.

Klumpp, D.W. & Lucas, J.S. 1994. Nutritional ecology of the giant clams *Tridacna tevoroa* and *T. derasa* from Tonga – Influence of light on filter feeding and photosynthesis. *Marine Ecology Progress Series* **107**, 147–156.

Klumpp, D.W. & McKinnon, A.D. 1989. Temporal and spatial patterns in primary production of a coral reef epilithic algal community. *Journal of Experimental Marine Biology and Ecology* **131**, 1–22.

Klumpp, D.W. & McKinnon, A.D. 1992. Community structure, biomass and productivity of epilithic algal communities on the Great Barrier Reef – dynamics at different spatial scales. *Marine Ecology Progress Series* **86**, 77–89.

Klumpp, D.W., McKinnon, A.D. & Mundy, C.N. 1988. Motile cryptofauna of a coral reef – abundance, distribution and trophic potential. *Marine Ecology Progress Series* **45**, 95–108.

Klumpp, D.W. & Polunin, N.V.C. 1990. Algal production, grazers and habitat partitioning on a coral reef: Positive correlation between grazing rate and food availability. In *Trophic Relationships in the Marine Environment: Proceedings of the 24th European Marine Biology Symposium*. Aberdeen University Press, Aberdeen. 372–388.

Klumpp, D.W. & Pulfrich, A. 1989. Trophic significance of herbivorous macroinvertebrates on the central Great Barrier Reef. *Coral Reefs* **8**, 135–144.

Knol, A.B., Slottje, P., van der Sluijs, J.P. & Lebret, E. 2010. The use of expert elicitation in environmental health impact assessment: A seven step procedure. *Environmental Health* **9**, 19.

Knowlton, N. 2001. The future of coral reefs. *Proceedings of the National Academy of Sciences of the United States of America* **98**, 5419–5425.

Knowlton, N. 2012. Iconic coral reef degraded despite substantial protection. *Proceedings of the National Academy of Sciences of the United States of America* **109**, 17734–17735.

Kohda, M., Hotta, T., Takeyama, T., Awata, S., Tanaka, H., Asai, J.-Y. & Jordan, A.L. 2019. If a fish can pass the mark test, what are the implications for consciousness and self-awareness testing in animals? *Plos Biology* **17**, e3000021.

Kohn, A.J. 2015. Ecology of *Conus* on Seychelles reefs at mid-twentieth century: Comparative habitat use and trophic roles of co-occurring congeners. *Marine Biology* **162**, 2391–2407.

Konow, N., Price, S., Abom, R., Bellwood, D. & Wainwright, P. 2017. Decoupled diversification dynamics of feeding morphology following a major functional innovation in marine butterflyfishes. *Proceedings of the Royal Society B-Biological Sciences* **284**, 20170906.

Koop, K., Booth, D., Broadbent, A. et al. 2001. ENCORE: The effect of nutrient enrichment on coral reefs. Synthesis of results and conclusions. *Marine Pollution Bulletin* **42**, 91–120.

Kramer, M.J., Bellwood, D.R. & Bellwood, O. 2012. Cryptofauna of the epilithic algal matrix on an inshore coral reef, Great Barrier Reef. *Coral Reefs* **31**, 1007–1015.

Kramer, M.J., Bellwood, O. & Bellwood, D.R. 2013. The trophic importance of algal turfs for coral reef fishes: The crustacean link. *Coral Reefs* **32**, 575–583.

Kramer, M.J., Bellwood, O., Fulton, C.J. & Bellwood, D.R. 2015. Refining the invertivore: Diversity and specialisation in fish predation on coral reef crustaceans. *Marine Biology* **162**, 1779–1786.

Krause, E., Wichels, A., Gimenez, L., Lunau, M., Schilhabel, M.B. & Gerdts, G. 2012. Small changes in pH have direct effects on marine bacterial community composition: A microcosm approach. *PLOS ONE* **7**, e47035.

Krediet, C.J., Ritchie, K.B., Paul, V.J. & Teplitski, M. 2013. Coral-associated micro-organisms and their roles in promoting coral health and thwarting diseases. *Proceedings of the Royal Society B-Biological Sciences* **280**, 20122328.

Krone, R., Paster, M. & Schuhmacher, H. 2011. Effect of the surgeonfish *Ctenochaetus striatus* (Acanthuridae) on the processes of sediment transport and deposition on a coral reef in the Red Sea. *Facies* **57**, 215–221.

Kroon, F.J., Kuhnert, P.M., Henderson, B.L., Wilkinson, S.N., Kinsey-Henderson, A., Abbott, B., Brodie, J.E. & Turner, R.D.R. 2012. River loads of suspended solids, nitrogen, phosphorus and herbicides delivered to the Great Barrier Reef lagoon. *Marine Pollution Bulletin* **65**, 167–181.

Krumm, D.K. 1999. Bivalve bioerosion in oligocene corals from Puerto Rico and Jamaica. *Bulletin of the Geological Society of Denmark* **45**, 179–180.

Ladd, M.C., Burkepile, D.E. & Shantz, A.A. 2019. Near-term impacts of coral restoration on target species, coral reef community structure, and ecological processes. *Restoration Ecology* **27**, 1166–1176. doi: 10.1111/rec.12939.

Ladd, M.C., Miller, M.W., Hunt, J.H., Sharp, W.C. & Burkepile, D.E. 2018. Harnessing ecological processes to facilitate coral restoration. *Frontiers in Ecology and the Environment* **16**, 239–247.

LaJeunesse, T.C., Parkinson, J.E., Gabrielson, P.W., Jeong, H.J., Reimer, J.D., Voolstra, C.R. & Santos, S.R. 2018. Systematic revision of Symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. *Current Biology* **28**, 2570–2580.e2576.

Lam, V.Y.Y., Chaloupka, M., Thompson, A., Doropoulos, C. & Mumby, P.J. 2018. Acute drivers influence recent inshore Great Barrier Reef dynamics. *Proceedings of the Royal Society B: Biological Sciences* **285**, 20182063.

Lamb, J.B., True, J.D., Piromvaragorn, S. & Willis, B.L. 2014. Scuba diving damage and intensity of tourist activities increases coral disease prevalence. *Biological Conservation* **178**, 88–96.

Lamb, J.B., Wenger, A.S., Devlin, M.J., Ceccarelli, D.M., Williamson, D.H. & Willis, B.L. 2016. Reserves as tools for alleviating impacts of marine disease. *Philosophical Transactions of the Royal Society B-Biological Sciences* **371**, 20150210.

Lamb, J.B., Williamson, D.H., Russ, G.R. & Willis, B.L. 2015. Protected areas mitigate diseases of reef-building corals by reducing damage from fishing. *Ecology* **96**, 2555–2567.

Lamb, J.B. & Willis, B.L. 2011. Using coral disease prevalence to assess the effects of concentrating tourism activities on offshore reefs in a tropical Marine Park. *Conservation Biology* **25**, 1044–1052.

Lamb, J.B., Willis, B.L., Fiorenza, E.A. et al. 2018. Plastic waste associated with disease on coral reefs. *Science* **359**, 460–462.

Lane, D.J.W. 2012. *Acanthaster planci* impact on coral communities at permanent transect sites on Bruneian reefs, with a regional overview and a critique on outbreak causes. *Journal of the Marine Biological Association of the United Kingdom* **92**, 803–809.

Langer, M.R., Silk, M.T. & Lipps, J.H. 1997. Global ocean carbonate and carbon dioxide production: The role of reef foraminifera. *Journal of Foraminiferal Research* **27**, 271–277.

Larkum, A.W.D., Kennedy, I.R. & Muller, W.J. 1988. Nitrogen fixation on a coral reef. *Marine Biology* **98**, 143–155.

Lassig, B.R. 1983. The effects of a cyclonic storm on coral reef fish assemblages. *Environmental Biology of Fishes* **9**, 55–63.

Lau, P. & Parry Jones, R. 1999. The Hong Kong trade in live reef fish for food. *Live Reef Fish* **38**, 27–30.

Laxton, J.H. 1974a. Aspects of ecology of coral-eating starfish *Acanthaster planci*. *Biological Journal of the Linnean Society* **6**, 19–45.

Laxton, J.H. 1974b. Preliminary study of biology and ecology of blue atarfish *Linckia laevigata* (L) on Australian Great Barrier Reef and an interpretation of its role in coral reef ecosystem. *Biological Journal of the Linnean Society* **6**, 47–64.

Lazar, B. & Loya, Y. 1991. Bioerosion of coral reefs – a chemical approach. *Limnology and Oceanography* **36**, 377–383.

Leahy, S.M., Russ, G.R. & Abesamis, R.A. 2016. Primacy of bottom-up effects on a butterflyfish assemblage. *Marine and Freshwater Research* **67**, 1175–1185.

Lecchini, D., Planes, S. & Galzin, R. 2007. The influence of habitat characteristics and conspecifics on attraction and survival of coral reef fish juveniles. *Journal of Experimental Marine Biology and Ecology* **341**, 85–90.

Lee, S., Ferse, S., Ford, A., Wild, C. & Mangubhai, S. 2017. Effect of sea cucumber density on the health of reef-flat sediments. In *Fiji's Sea Cucumber Fishery: Advances in Science for Improved Management*. S. Mangubhai, W. Lalavanua & S.W. Purcell (eds). Report No. 01/17. Suva, Fiji: Wildlife Conservation Society.

Leggat, W., Buck, B.H., Grice, A. & Yellowlees, D. 2003. The impact of bleaching on the metabolic contribution of dinoflagellate symbionts to their giant clam host. *Plant Cell and Environment* **26**, 1951–1961.

Leigh, G.M., Campbell, A.B., Lunow, C.P. & O'Neill, M.F. 2014. *Stock assessment of the Queensland east coast common coral trout (Plectropomus leopardus) fishery*. Technical report. Queensland Department of Agriculture, Fisheries and Forestry.

Lesser, M.P., Stochaj, W.R., Tapley, D.W. & Shick, J.M. 1990. Bleaching in coral reef anthozoans – effects of irradiance, ultraviolet-radiation, and temperature on the activities of protective enzymes against active oxygen. *Coral Reefs* **8**, 225–232.

LeTissier, M.D.A. & Brown, B.E. 1996. Dynamics of solar bleaching in the intertidal reef coral Goniastrea aspera at Ko Phuket, Thailand. *Marine Ecology Progress Series* **136**, 235–244.

Letourneur, Y., Briand, M.J. & Graham, N.A.J. 2017. Coral reef degradation alters the isotopic niche of reef fishes. *Marine Biology* **164**, 224.

Lewis, B., Kennedy, E.V. & Diaz-Pulido, G. 2017. Seasonal growth and calcification of a reef-building crustose coralline alga on the Great Barrier Reef. *Marine Ecology Progress Series* **568**, 73–86.

Lewis, S.E., Brodie, J.E., Bainbridge, Z.T., Rohde, K.W., Davis, A.M., Masters, B.L., Maughan, M., Devlin, M.J., Mueller, J.F. & Schaffelke, B. 2009. Herbicides: A new threat to the Great Barrier Reef. *Environmental Pollution* **157**, 2470–2484.

Lewis, S.E., Schaffelke, B., Shaw, M. et al. 2012. Assessing the additive risks of PSII herbicide exposure to the Great Barrier Reef. *Marine Pollution Bulletin* **65**, 280–291.

Lewis, S.E., Wust, R.A.J., Webster, J.M., Collins, J., Wright, S.A. & Jacobsen, G. 2015. Rapid relative sea-level fall along north-eastern Australia between 1200 and 800 cal. yr BP: An appraisal of the oyster evidence. *Marine Geology* **370**, 20–30.

Linares, C., Pratchett, M.S. & Coker, D.J. 2011. Recolonisation of *Acropora hyacinthus* following climate-induced coral bleaching on the Great Barrier Reef. *Marine Ecology Progress Series* **438**, 97–104.

Littler, M.M. & Littler, D.S. 2007. Assessment of coral reefs using herbivory/nutrient assays and indicator groups of benthic primary producers: A critical synthesis, proposed protocols, and critique of management strategies. *Aquatic Conservation-Marine and Freshwater Ecosystems* **17**, 195–215.

Liu, H., Zhang, C.L., Yang, C., Chen, S., Cao, Z., Zhang, Z. & Tian, J. 2017. Marine Group II dominates planktonic Archaea in water column of the northeastern South China Sea. *Frontiers in Microbiology* **8**, 1098.

Llopiz, J.K. 2013. Latitudinal and taxonomic patterns in the feeding ecologies of fish larvae: A literature synthesis. *Journal of Marine Systems* **109**, 69–77.

Loffler, Z., Bellwood, D.R. & Hoey, A.S. 2015a. Among-habitat algal selectivity by browsing herbivores on an inshore coral reef. *Coral Reefs* **34**, 597–605.

Loffler, Z., Bellwood, D.R. & Hoey, A.S. 2015b. Associations among coral reef macroalgae influence feeding by herbivorous fishes. *Coral Reefs* **34**, 51–55.

Loffler, Z. & Hoey, A.S. 2018. Canopy-forming macroalgal beds (*Sargassum*) on coral reefs are resilient to physical disturbance. *Journal of Ecology* **106**, 1156–1164.

Lonborg, C., Doyle, J., Furnas, M., Menendez, P., Benthuysen, J.A. & Carreira, C. 2017. Seasonal organic matter dynamics in the Great Barrier Reef lagoon: Contribution of carbohydrates and proteins. *Continental Shelf Research* **138**, 95–105.

Londono-Cruz, E., Cantera, J.R., Toro-Farmer, G. & Orozco, C. 2003. Internal bioerosion by macroborers in *Pocillopora* spp. in the tropical eastern Pacific. *Marine Ecology Progress Series* **265**, 289–295.

Longenecker, K., Langston, R., Bolick, H., Kondio, U. & Mulrooney, M. 2014. Six-year baseline information: Size structure and reproduction of exploited reef fishes before establishing a management plan at Kamiali Wildlife Management Area, Papua New Guinea. Bishop Museum Technical Report 63. Honolulu, Hawaii.

Lopez-Legentil, S., Erwin, P.M., Pawlik, J.R. & Song, B. 2010. Effects of sponge bleaching on ammonia-oxidizing Archaea: Distribution and relative expression of ammonia monooxygenase genes associated with the barrel sponge *Xestospongia muta*. *Microbial Ecology* **60**, 561–571.

Lopez-Legentil, S., Song, B., McMurray, S.E. & Pawlik, J.R. 2008. Bleaching and stress in coral reef ecosystems: hsp70 expression by the giant barrel sponge *Xestospongia muta*. *Molecular Ecology* **17**, 1840–1849.

Lopez-Victoria, M., Zea, S. & Wei, E. 2006. Competition for space between encrusting excavating Caribbean sponges and other coral reef organisms. *Marine Ecology Progress Series* **312**, 113–121.

Lough, J. 2007. Chapter 2: Climate and climate change on the Great Barrier Reef. In *Climate Change and the Great Barrier Reef: A Vulnerability Assessment*. T. The Great Barrier Reef Marine Park Authority (ed.). 84.

Lovelock, C.E. & Ellison, J. 2007. Vulnerability of mangroves and tidal wetlands of the Great Barrier Reef to climate change. In *Climate Change and the Great Barrier Reef: A Vulnerability Assessment. Part II: Species and Species Groups*. J.E. Johnson & P.A. Marshall (eds.).Townsville: Great Barrier Reef Marine Park Authority, 239–269.

Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H. & van Woesik, R. 2001. Coral bleaching: The winners and the losers. *Ecology Letters* **4**, 122–131.

Lucas, J.S. 1982. Quantitative studies of feeding and nutrition during larval development of the coral reef asteroid *Acanthaster planci* (L). *Journal of Experimental Marine Biology and Ecology* **65**, 173–193.

Lucas, J.S., Nash, W.J., Crawford, C.M. & Braley, R.D. 1989. Environmental influences on growth and survival during the ocean-nursery rearing of giant clams, *Tridacna gigas* (L. *). Aquaculture* **80**, 45–61.

Lukoschek, V. & McCormick, M.I. 2000. A review of multi-species foraging associations in fishes and their ecological significance. In *Proceedings of the 9th International Coral Reef Symposium*. 467–474.

Mace, G.M., Reyers, B., Alkemade, R., Biggs, R., Chapin III, F.S., Cornell, S.E., Díaz, S., Jennings, S., Leadley, P. & Mumby, P.J. 2014. Approaches to defining a planetary boundary for biodiversity. *Global Environmental Change* **28**, 289–297.

MacNeil, M.A., Mellin, C., Matthews, S., Wolff, N.H., McClanahan, T.R., Devlin, M., Drovandi, C., Mengersen, K. & Graham, N.A.J. 2019. Water quality mediates resilience on the Great Barrier Reef. *Nature Ecology & Evolution* **3**, 620–627.

Madin, E.M.P., Madin, J.S. & Booth, D.J. 2011. Landscape of fear visible from space. *Scientific Reports* **1**, 14.

Madin, J.S. 2005. Mechanical limitations of reef corals during hydrodynamic disturbances. *Coral Reefs* **24**, 630–635.

Madin, J.S., Baird, A.H., Dornelas, M. & Connolly, S.R. 2014. Mechanical vulnerability explains size-dependent mortality of reef corals. *Ecology Letters* **17**, 1008–1015.

Madin, J.S. & Connolly, S.R. 2006. Ecological consequences of major hydrodynamic disturbances on coral reefs. *Nature* **444**, 477–480.

Madin, J.S., Hughes, T.P. & Connolly, S.R. 2012. Calcification, storm damage and population resilience of tabular corals under climate change. *PLOS ONE* **7**, e46637.

Magnusson, M., Heimann, K. & Negri, A.P. 2008. Comparative effects of herbicides on photosynthesis and growth of tropical estuarine microalgae. *Marine Pollution Bulletin* **56**, 1545–1552.

Magnusson, M., Heimann, K., Ridd, M. & Negri, A.P. 2012. Chronic herbicide exposures affect the sensitivity and community structure of tropical benthic microalgae. *Marine Pollution Bulletin* **65**, 363–372.

Maire, E., Villeger, S., Graham, N.A.J. et al. 2018. Community-wide scan identifies fish species associated with coral reef services across the Indo-Pacific. *Proceedings of the Royal Society B-Biological Sciences* 285.

Maldonado, M., Aguilar, R., Bannister, R.J. et al. 2015. Sponge grounds as key marine habitats: A synthetic review of types, structure, functional roles, and conservation concerns. In *Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots*. S. Rossi, L. Bramanti, A. Gori & C. Orejas Saco del Valle (eds). Cham: Springer International Publishing, 1–39.

Mallela, J. & Perry, C. 2007. Calcium carbonate budgets for two coral reefs affected by different terrestrial runoff regimes, Rio Bueno, Jamaica. *Coral Reefs* **26**, 129–145.

Manzello, D.P. 2010. Coral growth with thermal stress and ocean acidification: Lessons from the eastern tropical Pacific. *Coral Reefs* **29**, 749–758.

Manzello, D.P., Eakin, C.M. & Glynn, P.W. 2017. Effects of global warming and ocean acidification on carbonate budgets of Eastern Pacific coral reefs. *Coral Reefs of the Eastern Tropical Pacific: Persistence and Loss in a Dynamic Environment* **8**, 517–533.

Manzello, D.P., Enochs, I.C., Kolodziej, G., Carlton, R. & Valentino, L. 2018. Resilience in carbonate production despite three coral bleaching events in 5 years on an inshore patch reef in the Florida Keys. *Marine Biology* **165**, 99.

Mapstone, B.D., Davies, C.R., Little, L.R. et al. 2004. The effects of line fishing on the Great Barrier Reef and evaluations of alternative potential management strategies. In *CRC Reef Research Centre Technical Report No 52*, Townsville, Australia.

Marnane, M.J. & Bellwood, D.R. 2002. Diet and nocturnal foraging in cardinalfishes (Apogonidae) at One Tree Reef, Great Barrier Reef, Australia. *Marine Ecology Progress Series* **231**, 261–268.

Marshall, A.D. & Bennett, M.B. 2010a. The frequency and effect of shark-inflicted bite injuries to the reef manta ray *Manta alfredi*. *African Journal of Marine Science* **32**, 573–580.

Marshall, A.D. & Bennett, M.B. 2010b. Reproductive ecology of the reef manta ray *Manta alfredi* in southern Mozambique. *Journal of Fish Biology* **77**, 169–190.

Marshall, J.F. & Davies, P.J. 1988. Halimeda bioherms of the northern Great Barrier Reef. *Coral Reefs* **6**, 139–148.

Marshall, N., Barnes, M.L., Birtles, A. et al. 2018. Measuring what matters in the Great Barrier Reef. *Frontiers in Ecology and the Environment* **16**, 271–277.

Marshall, N.J., Land, M.F. & Cronin, T.W. 1994. The 6-eyed stomatopod. *Endeavour* **18**, 17–26.

Marshall, P.A. & Baird, A.H. 2000. Bleaching of corals on the Great Barrier Reef: Differential susceptibilities among taxa. *Coral Reefs* **19**, 155–163.

Marshell, A. & Mumby, P.J. 2012. Revisiting the functional roles of the surgeonfish *Acanthurus nigrofuscus* and *Ctenochaetus striatus*. *Coral Reefs* **31**, 1093–1101.

Marshell, A. & Mumby, P.J. 2015. The role of surgeonfish (Acanthuridae) in maintaining algal turf biomass on coral reefs. *Journal of Experimental Marine Biology and Ecology* **473**, 152–160.

Martin, T.G., Burgman, M.A., Fidler, F., Kuhnert, P.M., Low-Choy, S., Mcbride, M. & Mengersen, K. 2012. Eliciting expert knowledge in conservation science. *Conservation Biology* **26**, 29–38.

Marulanda-Gomez, A., Lopez-Victoria, M. & Zea, S. 2017. Current status of coral takeover by an encrusting excavating sponge in a Caribbean reef. *Marine Ecology-an Evolutionary Perspective* **38**, e12379.

Mason, B., Beard, M. & Miller, M.W. 2011. Coral larvae settle at a higher frequency on red surfaces. *Coral Reefs* **30**, 667–676.

Matsuda, S. 1989. Succession and growth rates of encrusting crustose coralline algae (Rhodophyta, Cryptonemiales) in the upper forereef environment off Ishigaki Island, Ryukyu Islands. *Coral Reefs* **7**, 185–195.

Matz, M.V., Treml, E.A., Aglyamova, G.V. & Bay, L.K. 2018. Potential and limits for rapid genetic adaptation to warming in a Great Barrier Reef coral. *Plos Genetics* **14**, e1007220.

Maynard, J.A., Anthony, K.R.N., Harvell, C.D., Burgman, M.A., Beeden, R., Sweatman, H., Heron, S.F., Lamb, J.B. & Willis, B.L. 2011. Predicting outbreaks of a climate-driven coral disease in the Great Barrier Reef. *Coral Reefs* **30**, 485–495.

Maynard, J.A., Anthony, K.R.N., Marshall, P.A. & Masiri, I. 2008. Major bleaching events can lead to increased thermal tolerance in corals. *Marine Biology* **155**, 173–182.

Maynard, J.A., Beeden, R., Puotinen, M., Johnson, J.E., Marshall, P., van Hooidonk, R., Heron, S.F., Devlin, M., Lawrey, E., Dryden, J., Ban, N., Wachenfeld, D. & Planes, S. 2016. Great Barrier Reef no-take areas Iinclude a range of disturbance regimes. *Conservation Letters* **9**, 191–199.

McClanahan, T., Polunin, N. & Done, T. 2002. Ecological states and the resilience of coral reefs. *Conservation Ecology* **6**, 18.

McClanahan, T.R. 1988. Coexistence in a sea urchin guild and its implications to coral reef diversity and degradation. *Oecologia* **77**, 210–218.

McClanahan, T.R., Baird, A.H., Marshall, P.A. & Toscano, M.A. 2004. Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. *Marine Pollution Bulletin* **48**, 327–335.

McClanahan, T.R., Graham, N.A.J. & Darling, E.S. 2014. Coral reefs in a crystal ball: Predicting the future from the vulnerability of corals and reef fishes to multiple stressors. *Current Opinion in Environmental Sustainability* **7**, 59–64.

McClanahan, T.R., Maina, J. & Ateweberhan, M. 2015. Regional coral responses to climate disturbances and warming is predicted by multivariate stress model and not temperature threshold metrics. *Climatic Change* **131**, 607–620.

McCook, L.J., Ayling, T., Cappo, M. et al. 2010. Adaptive management of the Great Barrier Reef: A globally significant demonstration of the benefits of networks of marine reserves. *Proceedings of the National Academy of Sciences of the United States of America* **107**, 18278–18285.

McCook, L.J., Jompa, J. & Diaz-Pulido, G. 2001. Competition between corals and algae on coral reefs: A review of evidence and mechanisms. *Coral Reefs* **19**, 400–417.

McCormack, C., Roelofs, A., Gaffney, P., Andersen, C., Smith, T., Young, B., Olyott, L. & Dunning, M. 2005. *Ecological assessment of the Queensland coral fishery: A report to the Australian Government Department of the Environment and Heritage on the ecologically sustainable management of the Queensland Coral Fishery.* Queensland Government, Department of Primary Industries and Fisheries. 59.

McCoy, S.J. & Kamenos, N.A. 2015. Coralline algae (Rhodophyta) in a changing world: Integrating ecological, physiological, and geochemical responses to global change. *Journal of Phycology* **51**, 6–24.

McCulloch, M., Falter, J., Trotter, J. & Montagna, P. 2012. Coral resilience to ocean acidification and global warming through pH up-regulation. *Nature Climate Change* **2**, 623–633.

McKinley, A. & Johnston, E.L. 2010. Impacts of contaminant sources on marine fish abundance and species richness: A review and meta-analysis of evidence from the field. *Marine Ecology Progress Series* **420**, 175–191.

McKinnon, A.D., Doyle, J., Duggan, S., Logan, M., Lonborg, C. & Brinkman, R. 2015. Zooplankton growth, respiration and grazing on the Australian margins of the tropical Indian and Pacific Oceans. *PLOS ONE* **10**, e0140012.

McKinnon, A.D., Duggan, S. & De'ath, G. 2005. Mesozooplankton dynamics in nearshore waters of the Great Barrier Reef. *Estuarine Coastal and Shelf Science* **63**, 497–511.

McKinnon, A.D., Meekan, M.G., Carleton, J.H., Furnas, M.J., Duggan, S. & Skirving, W. 2003. Rapid changes in shelf waters and pelagic communities on the southern Northwest Shelf, Australia, following a tropical cyclone. *Continental Shelf Research* **23**, 93–111.

McKinnon, A.D., Richardson, A.J., Burford, M. & Furnas, M. 2007. Vulnerability of Great Barrier Reef plankton to climate change. In *Climate Change and the Great Barrier Reef : A Vulnerability Assessment.* E.J. Johnson & P.A. Marshall (eds). Townsville: Great Barrier Reef Marine Park Authority, 121–152.

McKinnon, A.D. & Thorrold, S.R. 1993. Zooplankton community structure and copepod egg production in coastal waters of the central Great Barrier Reef Lagoon. *Journal of Plankton Research* **15**, 1387–1411.

McMahon, A., Santos, I.R., Schulz, K.G., Scott, A., Silverman, J., Davis, K.L. & Maher, D.T. 2019. Coral reef calcification and production after the 2016 bleaching event at Lizard Island, *Great Barrier Reef. Journal of Geophysical Research: Oceans.* **124**, 4003–4016. doi: 10.1029/2018JC014698.

McWilliam, M., Hoogenboom, M.O., Baird, A.H., Kuo, C.Y., Madin, J.S. & Hughes, T.P. 2018. Biogeographical disparity in the functional diversity and redundancy of corals. *Proceedings of the National Academy of Sciences of the United States of America* **115**, 3084–3089.

Mellin, C., Kulbicki, M. & Ponton, D. 2007. Seasonal and ontogenetic patterns of habitat use in coral reef fish juveniles. *Estuarine Coastal and Shelf Science* **75**, 481–491.

Mellin, C., MacNeil, M.A., Cheal, A.J., Emslie, M.J. & Caley, M.J. 2016. Marine protected areas increase resilience among coral reef communities. *Ecology Letters* **19**, 629–637.

Mellin, C., Matthews, S., Anthony, K.R.N. et al. 2019. Spatial resilience of the Great Barrier Reef under cumulative disturbance impacts. *Global Change Biology*. doi: 10.1111/gcb.14625.

Messmer, V., Jones, G.P., Munday, P.L., Holbrook, S.J., Schmitt, R.J. & Brooks, A.J. 2011. Habitat biodiversity as a determinant of fish community structure on coral reefs. *Ecology* **92**, 2285–2298.

Messmer, V., Pratchett, M.S., Hoey, A.S., Tobin, A.J., Coker, D.J., Cooke, S.J. & Clark, T.D. 2017. Global warming may disproportionately affect larger adults in a predatory coral reef fish. *Global Change Biology* **23**, 2230–2240.

Meyer, C.G. 2007. The impacts of spear and other recreational fishers on a small permanent Marine Protected Area and adjacent pulse fished area. *Fisheries Research* **84**, 301–307.

Micheli, F. & Halpern, B.S. 2005. Low functional redundancy in coastal marine assemblages. *Ecology Letters* **8**, 391–400.

Miller, I., Cheal, A.J., Emslie, M.J., Logan, M. & Sweatman, H. 2012. Ongoing effects of no-take marine reserves on commercially exploited coral trout populations on the Great Barrier Reef. *Marine Environmental Research* **79**, 167–170.

Miller, I., Sweatman, H., Cheal, A., Emslie, M., Johns, K., Jonker, M. & Osborne, K. 2015. Origins and implications of a primary crown-of-thorns starfish outbreak in the southern Great Barrier Reef. *Journal of Marine Biology* 2**015**, 10.

Miller, K.J. & Ayre, D.J. 2004. The role of sexual and asexual reproduction in structuring high latitude populations of the reef coral *Pocillopora damicornis*. *Heredity* **92**, 557–568.

Mills, L.S., Soulé, M.E. & Doak, D.F. 1993. The keystone-species concept in ecology and conservation. *Bioscience* **43**, 219–224.

Moberg, F. & Folke, C. 1999. Ecological goods and services of coral reef ecosystems. *Ecological Economics* **29**, 215–233.

Moltschaniwskyj, N.A. & Doherty, P.J. 1995. Cross-shelf distribution patterns of tropical juvenile cephalopods sampled with light-traps. *Marine and Freshwater Research* **46**, 707–714.

Mongin, M., Baird, M.E., Hadley, S. & Lenton, A. 2016a. Optimising reef-scale $CO_2$ removal by seaweed to buffer ocean acidification. *Environmental Research Letters* **11**, 034023.

Mongin, M., Baird, M.E., Tilbrook, B. et al. 2016b. The exposure of the Great Barrier Reef to ocean acidification. *Nature Communications* **7**, 10732.

Montecino-Latorre, D., Eisenlord, M.E., Turner, M., Yoshioka, R., Harvell, C.D., Pattengill-Semmens, C.V., Nichols, J.D. & Gaydos, J.K. 2016. Devastating transboundary impacts of sea star wasting disease on subtidal asteroids. *PLOS ONE* **11**, e0163190.

Montgomery, W.L. & Galzin, R. 1993. Seasonality in gonads, fat deposits and condition of tropical surgeonfishes (Teleostei, Acanthuridae). *Marine Biology* **115**, 529–536.

Mora, C., Graham, N.A.J. & Nystrom, M. 2016. Ecological limitations to the resilience of coral reefs. *Coral Reefs* **35**, 1271–1280.

Morgan, K.M., Perry, C.T., Smithers, S.G., Johnson, J.A. & Daniell, J.J. 2016. Evidence of extensive reef development and high coral cover in nearshore environments: Implications for understanding coral adaptation in turbid settings. *Scientific Reports* **6**, 29616.

Morgan, M.G. 2014. Use (and abuse) of expert elicitation in support of decision making for public policy. *Proceedings of the National Academy of Sciences* **111**, 7176–7184.

Morgan, M.G., Pitelka, L.F. & Shevliakova, E. 2001. Elicitation of expert judgments of climate change impacts on forest ecosystems. *Climatic Change* **49**, 279–307.

Morrison, T.H. 2017. Evolving polycentric governance of the Great Barrier Reef. *Proceedings of the National Academy of Sciences of the United States of America* **114**, E3013–E3021.

Motro, R., Ayalon, I. & Genin, A. 2005. Near-bottom depletion of zooplankton over coral reefs: III: Vertical gradient of predation pressure. *Coral Reefs* **24**, 95–98.

Mouchka, M.E., Hewson, I. & Harvell, C.D. 2010. Coral-associated bacterial assemblages: Current knowledge and the potential for climate-driven impacts. *Integrative and Comparative Biology* **50**, 662–674.

Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, C.E.T., Renaud, J. & Thuiller, W. 2013. Rare species support vulnerable functions in high-diversity ecosystems. *Plos Biology* **11**, e1001569.

Mouillot, D., Villeger, S., Parravicini, V. et al. 2014. Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences of the United States of America* **111**, 13757–13762.

Moutardier, G., Gereva, S., Mills, S.C., Adjeroud, M., Beldade, R., Ham, J., Kaku, R. & Dumas, P. 2015. Lime juice and vinegar injections as a cheap and natural alternative to control COTS outbreaks. *PLOS ONE* **10**, e0137605.

Mumby, P.J. 2006. The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecological Applications* **16**, 747–769.

Mumby, P.J. 2009a. Herbivory versus corallivory: Are parrotfish good or bad for Caribbean coral reefs? *Coral Reefs* **28**, 683–690.

Mumby, P.J. 2009b. Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. *Coral Reefs* **28**, 761–773.

Mumby, P.J. 2016. Stratifying herbivore fisheries by habitat to avoid ecosystem overfishing of coral reefs. *Fish and Fisheries* **17**, 266–278.

Mumby, P.J. 2017. Embracing a world of subtlety and nuance on coral reefs. *Coral Reefs* **36**, 1003–1011.

Mumby, P.J., Bejarano, S., Golbuu, Y., Steneck, R.S., Arnold, S.N., van Woesik, R. & Friedlander, A.M. 2013a. Empirical relationships among resilience indicators on Micronesian reefs. *Coral Reefs* **32**, 213–226.

Mumby, P.J., Broad, K., Brumbaugh, D.R., Dahlgren, C.P., Harborne, A.R., Hastings, A., Holmes, K.E., Kappel, C.V., Micheli, F. & Sanchirico, J.N. 2008. Coral reef habitats as surrogates of species, ecological functions, and ecosystem services. *Conservation Biology* **22**, 941–951.

Mumby, P.J., Dahlgren, C.P., Harborne, A.R. et al. 2006a. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* **311**, 98–101.

Mumby, P.J., Hedley, J.D., Zychaluk, K., Harborne, A.R. & Blackwell, P.G. 2006b. Revisiting the catastrophic die-off of the urchin *Diadema antillarum* on Caribbean coral reefs: Fresh insights on resilience from a simulation model. *Ecological Modelling* **196**, 131–148.

Mumby, P.J. & Steneck, R.S. 2018. Paradigm lost: Dynamic nutrients and missing detritus on coral reefs. *Bioscience* **68**, 487–495.

Mumby, P.J., Steneck, R.S., Adjeroud, M. & Arnold, S.N. 2016. High resilience masks underlying sensitivity to algal phase shifts of Pacific coral reefs. *Oikos* **125**, 644–655.

Mumby, P.J., Steneck, R.S. & Hastings, A. 2013b. Evidence for and against the existence of alternate attractors on coral reefs. *Oikos* **122**, 481–491.

Mumby, P.J., Wolff, N.H., Bozec, Y.M., Chollett, I. & Halloran, P. 2014. Operationalizing the resilience of coral reefs in an era of climate change. *Conservation Letters* **7**, 176–187.

Munday, P.L. 2004. Habitat loss, resource specialization, and extinction on coral reefs. *Global Change Biology* **10**, 1642–1647.

Munday, P.L., Cheal, A.J., Dixson, D.L., Rummer, J.L. & Fabricius, K.E. 2014. Behavioural impairment in reef fishes caused by ocean acidification at $CO_2$ seeps. *Nature Climate Change* **4**, 487–492.

Munday, P.L., Dixson, D.L., McCormick, M.I., Meekan, M., Ferrari, M.C.O. & Chivers, D.P. 2010. Replenishment of fish populations is threatened by ocean acidification. *Proceedings of the National Academy of Sciences of the United States of America* **107**, 12930–12934.

Munday, P.L., Donelson, J.M., Dixson, D.L. & Endo, G.G.K. 2009a. Effects of ocean acidification on the early life history of a tropical marine fish. *Proceedings of the Royal Society B-Biological Sciences* **276**, 3275–3283.

Munday, P.L., Leis, J.M., Lough, J.M., Paris, C.B., Kingsford, M.J., Berumen, M.L. & Lambrechts, J. 2009b. Climate change and coral reef connectivity. *Coral Reefs* **28**, 379–395.

Munday, P.L., McCormick, M.I. & Nilsson, G.E. 2012. Impact of global warming and rising $CO_2$ levels on coral reef fishes: What hope for the future? *Journal of Experimental Biology* **215**, 3865–3873.

Munday, P.L., Pratchett, M.S., Dixson, D.L., Donelson, J.M., Endo, G.G.K., Reynolds, A.D. & Knuckey, R. 2013a. Elevated $CO_2$ affects the behavior of an ecologically and economically important coral reef fish. *Marine Biology* **160**, 2137–2144.

Munday, P.L., Warner, R.R., Monro, K., Pandolfi, J.M. & Marshall, D.J. 2013b. Predicting evolutionary responses to climate change in the sea. *Ecology Letters* **16**, 1488–1500.

Murie, C.J.G. & Marshall, A.D. 2016. *Mobula kuhlii* cleaning station identified at an inshore reef in southern Mozambique. *PeerJ PrePrints* **4**, e1724v1721.

Muscatine, L. & Porter, J.W. 1977. Reef corals – mutualistic symbioses adapted to nutrient-poor environments. *Bioscience* **27**, 454–460.

Musso, B.M. 1994. Internal bioerosion of in situ living and dead corals on the Great Barrier Reef. *PhD thesis*, James Cook University of North Queensland.

Myers, R.F. 1999. *Micronesian Reef Fishes: A Comprehensive Guide to the Coral Reef Fishes of Micronesia, 3rd revised and Expanded Edition*. Barrigada, Guam: Coral Graphics, 297.

Myers, S.A., Blackmore, M.J., Smith, T.F. & Carter, R.W. 2012. Climate change and stewardship: Strategies to build community resilience in the Capricorn Coast. *Australasian Journal of Environmental Management* **19**, 164–181.

Naeem, S., Duffy, J.E. & Zavaleta, E. 2012. The functions of biological diversity in an age of extinction. *Science* **336**, 1401–1406.

Negri, A., Vollhardt, C., Humphrey, C., Heyward, A., Jones, R., Eaglesham, G. & Fabricius, K. 2005. Effects of the herbicide diuron on the early life history stages of coral. *Marine Pollution Bulletin* **51**, 370–383.

Negri, A.P., Flores, F., Rothig, T. & Uthicke, S. 2011. Herbicides increase the vulnerability of corals to rising sea surface temperature. *Limnology and Oceanography* **56**, 471–485.

Neilson, B.J., Wall, C.B., Mancini, F.T. & Gewecke, C.A. 2018. Herbivore biocontrol and manual removal successfully reduce invasive macroalgae on coral reefs. *PeerJ* 6.

Nelson, W.A. 2009. Calcified macroalgae – critical to coastal ecosystems and vulnerable to change: A review. *Marine and Freshwater Research* **60**, 787–801.

Neo, M.L., Eckman, W., Vicentuan, K., Teo, S.L.M. & Todd, P.A. 2015. The ecological significance of giant clams in coral reef ecosystems. *Biological Conservation* **181**, 111–123.

Neo, M.L., Wabnitz, C.C.C., Braley, R.D. et al. 2017. Giant clams (Bivalvia: Cardiidae: Tridacninae): A comprehensive update of species and their distribution, current threats and conservation status. *Oceanography and Marine Biology: An Annual Review* **55**, 87–387.

Neumann, A.C. 1966. Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge, *Cliona lampa*. *Limnology and Oceanography* **11**, 92–108.

Newman, M.J.H., Paredes, G.A., Sala, E. & Jackson, J.B.C. 2006. Structure of Caribbean coral reef communities across a large gradient of fish biomass. *Ecology Letters* **9**, 1216–1227.

Newton, K., Cote, I.M., Pilling, G.M., Jennings, S. & Dulvy, N.K. 2007. Current and future sustainability of island coral reef fisheries. *Current Biology* **17**, 655–658.

Nijman, V., Spaan, D. & Nekaris, K.A.-I. 2016. Large-scale trade in legally protected marine mollusc shells from Java and Bali, Indonesia. *PLOS ONE* **10**, e0140593.

Noda, M., Kawabata, K., Gushima, K. & Kakuda, S. 1992. Importance of zooplankton patches in foraging ecology of the planktivorous reef fish *Chromis chrysurus* (Pomacentridae) at Kuchinoerabu Island, Japan. *Marine Ecology Progress Series* **87**, 251–263.

Norman, M.D. 1992. Ocellate octopuses (Cephalopoda: Octopodidae) of the Great Barrier Reef, Australia: Description of two new species and redescription of *Octopus polyzenia*, Gray, 1849. *Memoirs of the Museum of Victoria* **52**, 309–344.

Norman, M.D. & Finn, J. 2001. Revision of the *Octopus horridus* species-group, including erection of a new subgenus and description of two member species from the Great Barrier Reef, Australia. *Invertebrate Taxonomy* **15**, 13–35.

Norstrom, A.V., Nystrom, M., Lokrantz, J. & Folke, C. 2009. Alternative states on coral reefs: Beyond coral-macroalgal phase shifts. *Marine Ecology Progress Series* **376**, 295–306.

O'Leary, R.A., Fisher, R., Choy, S.L., Mengersen, K. & Caley, M.J. 2011. What is an expert? *19th International Congress on Modelling and Simulation (Modsim) 2011*, 2149–2155.

O'Mahoney, J., Simes, R., Redhill, D., Heaton, K., Atkinson, C., Hayward, E. & Nguyen, M. 2017. At what price? The economic, social and icon value of the Great Barrier Reef. Brisbane, Australia: Deloitte Access Economics. , 92 pp

O'Shea, O.R., Kingsford, M.J. & Seymour, J. 2010. Tide-related periodicity of manta rays and sharks to cleaning stations on a coral reef. *Marine and Freshwater Research* **61**, 65–73.

Ober, G.T., Diaz-Pulido, G. & Thornber, C. 2016. Ocean acidification influences the biomass and diversity of reef-associated turf algal communities. *Marine Biology* **163**, 204.

Obura, D.O. 2001. Can differential bleaching and mortality among coral species offer useful indicators for assessment and management of reefs under stress? *Bulletin of Marine Science* **69**, 421–442.

Ogden, J.C. & Lobel, P. 1978. The role of herbivorous fishes and urchins in coral reef communities. *Environmental Biology of Fishes* **3**, 49–63.

Ohman, M.C., Munday, P.L., Jones, G.P. & Caley, M.J. 1998. Settlement strategies and distribution patterns of coral-reef fishes. *Journal of Experimental Marine Biology and Ecology* **225**, 219–238.

Okubo, N., Taniguchi, H. & Motokawa, T. 2005. Successful methods for transplanting fragments of *Acropora formosa* and *Acropora hyacinthus. Coral Reefs* **24**, 333–342.

Oliver, S.P., Hussey, N.E., Turner, J.R. & Beckett, A.J. 2011. Oceanic sharks clean at coastal seamount. *PLOS ONE* **6**, e14755.

Ollivier, Q.R., Hammill, E., Booth, D.J., Madin, E.M.P., Hinchliffe, C., Harborne, A.R., Lovelock, C.E., Macreadie, P.I. & Atwood, T.B. 2018. Benthic meiofaunal community response to the cascading effects of herbivory within an algal halo system of the Great Barrier Reef. *PLOS ONE* **13**, e0193932.

Olson, R. 1987. *In situ* culturing as a test of the larval starvation hypothesis for the crown-of-thorns starfish, *Acanthaster planci. Limnology and Oceanography* **32**, 895–904.

Ordonez, A., Doropoulos, C. & Diaz-Pulido, G. 2014. Effects of ocean acidification on population dynamics and community structure of crustose coralline algae. *Biological Bulletin* **226**, 255–268.

Orr, J.C., Fabry, V.J., Aumont, O. et al. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* **437**, 681–686.

Ortiz, J.-C., Bozec, Y.M., Wolff, N.H., Doropoulos, C. & Mumby, P.J. 2014. Global disparity in the ecological benefits of reducing carbon emissions for coral reefs. *Nature Climate Change* **4**, 1090–1094.

Ortiz, J.-C., Wolff, N.H., Anthony, K.R.N., Devlin, M., Lewis, S. & Mumby, P.J. 2018. Impaired recovery of the Great Barrier Reef under cumulative stress. *Science Advances* **4**, eaar6127.

Osborne, K., Thompson, A.A., Cheal, A.J., Emslie, M.J., Johns, K.A., Jonker, M.J., Logan, M., Miller, I.R. & Sweatman, H.P.A. 2017. Delayed coral recovery in a warming ocean. *Global Change Biology* **23**, 3869–3881.

Osorno, A., Peyrot-Clausade, M. & Hutchings, P. 2005. Patterns and rates of erosion in dead *Porites* across the Great Barrier Reef (Australia) after 2 years and 4 years of exposure. *Coral Reefs* **24**, 292–303.

Pacala, S.W. & Kinzig, A.P. 2013. Introduction to theory and the common ecosystem model. In *The Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions.* D. Tilman, A.P. Kinzig & S. Pacala (eds). Princeton: Princeton University Press, 169–174.

Padilla-Gamino, J.L., Hanson, K.M., Stat, M. & Gates, R.D. 2012. Phenotypic plasticity of the coral *Porites rus*: Acclimatization responses to a turbid environment. *Journal of Experimental Marine Biology and Ecology* **434**, 71–80.

Page, C.A., Baker, D.M., Harvell, C.D., Golbuu, Y., Raymundo, L., Neale, S.J., Rosell, K.B., Rypien, K.L., Andras, J.P. & Willis, B.L. 2009. Influence of marine reserves on coral disease prevalence. *Diseases of Aquatic Organisms* **87**, 135–150.

Page, H.N., Andersson, A.J., Jokiel, P.L., Rodgers, K.S., Lebrato, M., Yeakel, K., Davidson, C., D'Angelo, S. & Bahr, K.D. 2016. Differential modification of seawater carbonate chemistry by major coral reef benthic communities. *Coral Reefs* **35**, 1311–1325.

Paine, R.T. 1969. A note on trophic complexity and community stability. *The American Naturalist* **103**, 91–93.

Paine, R.T. 1995. A conversation on refining the concept of keystone species. *Conservation Biology* **9**, 962–964.

Palacios, M.D., Warren, D.T. & McCormick, M.I. 2016a. Sensory cues of a top-predator indirectly control a reef fish mesopredator. *Oikos* **125**, 201–209.

Palacios, M.M., Killen, S.S., Nadler, L.E., White, J.R. & McCormick, M.I. 2016b. Top predators negate the effect of mesopredators on prey physiology. *Journal of Animal Ecology* **85**, 1078–1086.

Palardy, J.E., Rodrigues, L.J. & Grottoli, A.G. 2008. The importance of zooplankton to the daily metabolic carbon requirements of healthy and bleached corals at two depths. *Journal of Experimental Marine Biology and Ecology* **367**, 180–188.

Pandolfi, J.M., Connolly, S.R., Marshall, D.J. & Cohen, A.L. 2011. Projecting coral reef futures under global warming and ocean acidification. *Science* **333**, 418–422.

Patton, W.K. 1983. The evolution and distribution of coral-inhabiting decapod crustaceans. *Bulletin of Marine Science* **33**, 782–782.

Patton, W.K. 1994. Distribution and ecology of animals associated with branching corals (*Acropora* spp) from the Great Barrier Reef, Australia. *Bulletin of Marine Science* **55**, 193–211.

Pavlowich, T. & Kapuscinski, A.R. 2017. Understanding spearfishing in a coral reef fishery: Fishers' opportunities, constraints, and decision-making. *PLOS ONE* **12**, e0181617.

Pawlik, J.R. 2011. The chemical ecology of sponges on caribbean reefs: Natural products shape natural systems. *Bioscience* **61**, 888–898.

Pawlik, J.R., Loh, T.L. & McMurray, S.E. 2018. A review of bottom-up vs. top-down control of sponges on Caribbean fore-reefs: What's old, what's new, and future directions. *PeerJ* **6**, e4343.

Pearson, R.G. 1977. Impact of foreign vessels poaching giant clams. *Australian Fisheries* **36**, 8–11.

Pearson, R.G. 1981. Recovery and recolonization of coral reefs. *Marine Ecology Progress Series* **4**, 105–122.

Pearson, R.G. & Endean, R. 1969. A preliminary study of the coral predator *Acanthaster planci* (L.) (Asteroidea) on the Great Barrier Reef. Fisheries Notes, Queensland Fisheries Branch. 27–55.

Pecl, G.T. & Jackson, G.D. 2008. The potential impacts of climate change on inshore squid: Biology, ecology and fisheries. *Reviews in Fish Biology and Fisheries* **18**, 373–385.

Penfold, R., Grutter, A.S., Kuris, A.M., McCormick, M.I. & Jones, C.M. 2008. Interactions between juvenile marine fish and gnathiid isopods: Predation versus micropredation. *Marine Ecology Progress Series* **357**, 111–119.

Perry, C.T., Alvarez-Filip, L., Graham, N.A., Mumby, P.J., Wilson, S.K., Kench, P.S., Manzello, D.P., Morgan, K.M., Slangen, A.B. & Thomson, D.P. 2018. Loss of coral reef growth capacity to track future increases in sea level. *Nature* **558**, 396.

Perry, C.T., Edinger, E.N., Kench, P.S., Murphy, G.N., Smithers, S.G., Steneck, R.S. & Mumby, P.J. 2012a. Estimating rates of biologically driven coral reef framework production and erosion: A new census-based carbonate budget methodology and applications to the reefs of Bonaire. *Coral Reefs* **31**, 853–868.

Perry, C.T. & Harborne, A.R. 2016. Bioerosion on modern reefs: Impacts and responses under changing ecological and environmental conditions. *Coral Reefs at the Crossroads* **6**, 69–101.

Perry, C.T., Smithers, S.G., Gulliver, P. & Browne, N.K. 2012b. Evidence of very rapid reef accretion and reef growth under high turbidity and terrigenous sedimentation. *Geology* **40**, 719–722.

Perry, C.T., Spencer, T. & Kench, P. 2008. Carbonate budgets and reef production states: A geomorphic perspective on the ecological phase-shift concept. *Coral Reefs* **27**, 853–866.

Petchey, O.L. & Gaston, K.J. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters* **5**, 402–411.

Pigot, A.L., Bregman, T., Sheard, C., Daly, B., Etienne, R.S. & Tobias, J.A. 2016. Quantifying species contributions to ecosystem processes: A global assessment of functional trait and phylogenetic metrics across avian seed-dispersal networks. *Proceedings of the Royal Society B: Biological Sciences* **283**, 20161597.

Pineda, M.C., Strehlow, B., Kamp, J., Duckworth, A., Jones, R. & Webster, N.S. 2017a. Effects of combined dredging-related stressors on sponges: A laboratory approach using realistic scenarios. *Scientific Reports* **7**, 5155.

Pineda, M.C., Strehlow, B., Sternel, M., Duckworth, A., den Haan, J., Jones, R. & Webster, N.S. 2017b. Effects of sediment smothering on the sponge holobiont with implications for dredging management. *Scientific Reports* **7**, 5156.

Pineda, M.C., Strehlow, B., Sternel, M., Duckworth, A., Jones, R. & Webster, N.S. 2017c. Effects of suspended sediments on the sponge holobiont with implications for dredging management. *Scientific Reports* **7**, 4925.

Piraino, S. & Fanelli, G. 1999. Keystone species: What are we talking about? *Conservation Ecology* **3**, R4.

Piraino, S., Fanelli, G. & Boero, F. 2002. Variability of species' roles in marine communities: Change of paradigms for conservation priorities. *Marine Biology* **140**, 1067–1074.

Platten, J.R., Tibbetts, I.R. & Sheaves, M.J. 2002. The influence of increased line-fishing mortality on the sex ratio and age of sex reversal of the venus tusk fish. *Journal of Fish Biology* **60**, 301–318.

Polasky, S., Carpenter, S.R., Folke, C. & Keeler, B. 2011. Decision-making under great uncertainty: Environmental management in an era of global change. *Trends in Ecology & Evolution* **26**, 398–404.

Pollock, F.J., Katz, S.M., Bourne, D.G. & Willis, B.L. 2013. *Cymo melanodactylus* crabs slow progression of white syndrome lesions on corals. *Coral Reefs* **32**, 43–48.

Pollock, F.J., Lamb, J.B., Field, S.N., Heron, S.F., Schaffelke, B., Shedrawi, G., Bourne, D.G. & Willis, B.L. 2016. Sediment and turbidity associated with offshore dredging increase coral disease prevalence on nearby reefs. *PLOS ONE* **11**, e102498.

Poloczanska, E.S., Brown, C.J., Sydeman, W.J. et al. 2013. Global imprint of climate change on marine life. *Nature Climate Change* **3**, 919.

Ponder, W., Hutchings, P. & Chapman, R. 2002. *Overview of the conservation of Australian marine invertebrates*. In A report for Environment Australia, Australian Museum, Sydney, NSW. 588.

Porter, M.L., Zhang, Y.F., Desai, S., Caldwell, R.L. & Cronin, T.W. 2010. Evolution of anatomical and physiological specialization in the compound eyes of stomatopod crustaceans. *Journal of Experimental Biology* **213**, 3473–3486.

Pörtner, H.O. & Farrell, A.P. 2008. Physiology and climate change. *Science* **322**, 690–692.

Powell, A., Jones, T., Smith, D.J., Jompa, J. & Bell, J.J. 2015. Spongivory in the Wakatobi Marine National Park, Southeast Sulawesi, Indonesia. *Pacific Science* **69**, 487–508.

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J. & Paine, R.T. 1996. Challenges in the quest for keystones: Identifying keystone species is difficult—but essential to understanding how loss of species will affect ecosystems. *Bioscience* **46**, 609–620.

Pratchett, M., Thompson, C., Hoey, A., Cowman, P. & Wilson, S. 2018. Effects of coral bleaching and coral loss on the structure and function of reef fish assemblages. In *Coral Bleaching. Ecological Studies (Analysis and Synthesis)*. M. van Oppen & J. Lough (eds). Cham: Springer, 265–293.

Pratchett, M.S. 2001. Influence of coral symbionts on feeding preferences of crown-of-thorns starfish *Acanthaster planci* in the western Pacific. *Marine Ecology Progress Series* **214**, 111–119.

Pratchett, M.S. 2007. Feeding preferences of *Acanthaster planci* (Echinodermata: Asteroidea) under controlled conditions of food availability. *Pacific Science* **61**, 113–120.

Pratchett, M.S., Anderson, K.D., Hoogenboom, M.O., Widman, E., Baird, A.H., Pandolfi, J.M., Edmunds, P.J. & Lough, J.M. 2015. Spatial, temporal and taxonomic variation in coral growth – implications for the structure and function of coral reef ecosystems. *Oceanography and Marine Biology: An Annual Review* **53**, 215–295.

Pratchett, M.S., Berumen, M.L., Marnane, M.J., Eagle, J.V. & Pratchett, D.J. 2008a. Habitat associations of juvenile versus adult butterflyfishes. *Coral Reefs* **27**, 541–551.

Pratchett, M.S., Caballes, C.F., Rivera-Posada, J.A. & Sweatman, H.P.A. 2014. Limits to understanding and managing outbreaks of crown-of-thorns starfish (*Acanthaster* spp.). *Oceanography and Marine Biology: An Annual Review* **52**, 133–199.

Pratchett, M.S., Caballes, C.F., Wilmes, J.C. et al. 2017a. Thirty years of research on crown-of-thorns Starfish (1986–2016): Scientific advances and emerging opportunities. *Diversity* **9**, 41.

Pratchett, M.S., Cameron, D.S., Donelson, J. et al. 2017b. Effects of climate change on coral grouper (*Plectropomus* spp.) and possible adaptation options. *Reviews in Fish Biology and Fisheries* **27**, 297–316.

Pratchett, M.S., Munday, P.L., Wilson, S.K., Graham, N.A.J., Cinner, J.E., Bellwood, D.R., Jones, G.P., Polunin, N.V.C. & McClanahan, T.R. 2008b. Effects of climate-induced coral bleaching on coral-reef fishes – Ecological and economic consequences. *Oceanography and Marine Biology: An Annual Review* **46**, 251–296.

Pratchett, M.S., Wilson, S.K., Berumen, M.L. & McCormick, M.I. 2004. Sublethal effects of coral bleaching on an obligate coral feeding butterflyfish. *Coral Reefs* **23**, 352–356.

Prazeres, M., Uthicke, S. & Pandolfi, J.M. 2015. Ocean acidification induces biochemical and morphological changes in the calcification process of large benthic foraminifera. *Proceedings of the Royal Society B-Biological Sciences* **282**, 20142782.

Proksch, P. 1994. Defensive roles for secondary metabolites from marine sponges and sponge-feeding nudibranchs. *Toxicon* **32**, 639–655.

Przeslawski, R., Ahyong, S., Byrne, M., Worheide, G. & Hutchings, P. 2008. Beyond corals and fish: The effects of climate change on noncoral benthic invertebrates of tropical reefs. *Global Change Biology* **14**, 2773–2795.

Przeslawski, R., Byrne, M. & Mellin, C. 2015. A review and meta-analysis of the effects of multiple abiotic stressors on marine embryos and larvae. *Global Change Biology* **21**, 2122–2140.

Puk, L.D., Ferse, S.C.A. & Wild, C. 2016. Patterns and trends in coral reef macroalgae browsing: A review of browsing herbivorous fishes of the Indo-Pacific. *Reviews in Fish Biology and Fisheries* **26**, 53–70.

Purcell, J.E. & Arai, M.N. 2001. Interactions of pelagic cnidarians and ctenophores with fish: A review. *Hydrobiologia* **451**, 27–44.

Purcell, S.W. & Bellwood, D.R. 1993. A functional analysis of food procurement in two surgeonfish species, *Acanthurus nigrofuscus* and *Ctenochaetus striatus* (Acanthuridae). *Environmental Biology of Fishes* **37**, 139–159.

Purcell, S.W., Conand, C., Uthicke, S. & Byrne, M. 2016a. Ecological roles of exploited sea cucumbers. *Oceanography and Marine Biology: An Annual Review* **54**, 367–386.

Purcell, S.W., Eriksson, H. & Byrne, M. 2016b. Rotational zoning systems in multispecies sea cucumber fisheries. *SPC Bêche-de-mer Bulletin* **36**, 3–8.

Purcell, S.W., Mercier, A., Conand, C., Hamel, J.F., Toral-Granda, M.V., Lovatelli, A. & Uthicke, S. 2013. Sea cucumber fisheries: Global analysis of stocks, management measures and drivers of overfishing. *Fish and Fisheries* **14**, 34–59.

Purcell, S.W., Polidoro, B.A., Hamel, J.-F., Gamboa, R.U. & Mercier, A. 2014. The cost of being valuable: Predictors of extinction risk in marine invertebrates exploited as luxury seafood. *Proceedings of the Royal Society B-Biological Sciences* **281**, 20133296.

Putnam, H.M., Edmunds, P.J. & Fan, T.Y. 2010. Effect of a fluctuating thermal regime on adult and larval reef corals. *Invertebrate Biology* **129**, 199–209.

QGSO. 2019. Shark control program: Sharks caught by type, Queensland, 2007–08 to 2017–18. http://www.qgso.qld.gov.au/products/tables/shark-control-program-caught-type/index.php. In Queensland Government Statistician's Office.

Quigley, K.M., Bay, L.K. & Willis, B.L. 2018. Leveraging new knowledge of *Symbiodinium* community regulation in corals for conservation and reef restoration. *Marine Ecology Progress Series* **600**, 245–253.

Ramsby, B.D., Hoogenboom, M.O., Smith, H.A., Whalan, S. & Webster, N.S. 2018a. The bioeroding sponge *Cliona orientalis* will not tolerate future projected ocean warming. *Scientific Reports* **8**, 8302.

Ramsby, B.D., Hoogenboom, M.O., Whalan, S. & Webster, N.S. 2018b. Elevated seawater temperature disrupts the microbiome of an ecologically important bioeroding sponge. *Molecular Ecology* **27**, 2124–2137.

Ramsby, B.D., Hoogenboom, M.O., Whalan, S., Webster, N.S. & Thompson, A. 2017. A decadal analysis of bioeroding sponge cover on the inshore Great Barrier Reef. *Scientific Reports* **7**, 2706.

Rasheed, M., Badran, M.I., Richter, C. & Huettel, M. 2002. Effect of reef framework and bottom sediment on nutrient enrichment in a coral reef of the Gulf of Aqaba, Red Sea. *Marine Ecology Progress Series* **239**, 277–285.

Rasher, D.B., Hoey, A.S. & Hay, M.E. 2013. Consumer diversity interacts with prey defenses to drive ecosystem function. *Ecology* **94**, 1347–1358.

Razak, T.B., Mumby, P.J., Nguyen, A.D., Zhao, J.-X., Lough, J.M., Cantin, N.E. & Roff, G. 2017. Use of skeletal Sr/Ca ratios to determine growth patterns in a branching coral *Isopora palifera*. *Marine Biology* **164**, 96.

Reaka-Kudla, M. 1997. The global biodiversity of coral reefs: A comparison with rainforests. In *Biodiversity II: Understanding and Protecting Our Biological Resources*. M. Reaka-Kudla, D.E. Wilson & E.O. Wilson (eds). Washington, DC: Joseph Henry Press, 83–108.

Renzi, J.J., He, Q. & Silliman, B.R. 2019. Harnessing positive species interactions to enhance coastal wetland restoration. *Frontiers in Ecology and Evolution* **7**, 131.

Revelante, N. & Gilmartin, M. 1982. Dynamics of phytoplankton in the Great Barrier Reef lagoon. *Journal of Plankton Research* **4**, 47–76.

Revelante, N., Williams, W.T. & Bunt, J.S. 1982. Temporal and spatial distribution of diatoms, dinoflagellates and *Trichodesmium* in waters of the Great Barrier Reef. *Journal of Experimental Marine Biology and Ecology* **63**, 27–45.

Reyes-Nivia, C., Diaz-Pulido, G. & Dove, S. 2014. Relative roles of endolithic algae and carbonate chemistry variability in the skeletal dissolution of crustose coralline algae. *Biogeosciences* **11**, 4615–4626.

Reyes-Nivia, C., Diaz-Pulido, G., Kline, D., Guldberg, O.H. & Dove, S. 2013. Ocean acidification and warming scenarios increase microbioerosion of coral skeletons. *Global Change Biology* **19**, 1919–1929.

Rhyne, A.L., Tlusty, M.F., Szczebak, J.T. & Holmberg, R.J. 2017. Expanding our understanding of the trade in marine aquarium animals. *PeerJ* **5**, e2949.

Rice, M.M., Ezzat, L. & Burkepile, D.E. 2019. Corallivory in the Anthropocene: Interactive effects of anthropogenic stressors and corallivory on coral reefs. *Frontiers in Marine Science* **5**, 525.

Richards, Z.T. & Day, J.C. 2018. Biodiversity of the Great Barrier Reef – how adequately is it protected? *PeerJ* **6**, e4747.

Richardson, A.J. & Schoeman, D. 2019. Sea animals are more vulnerable to warming than are land ones. *Nature* **569**, 50–51.

Richardson, A.J. & Schoeman, D.S. 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. *Science* **305**, 1609–1612.

Richardson, L.E., Graham, N.A.J., Pratchett, M.S., Eurich, J.G. & Hoey, A.S. 2018. Mass coral bleaching causes biotic homogenization of reef fish assemblages. *Global Change Biology* **24**, 3117–3129.

Richardson, L.L. 1998. Coral diseases: What is really known? *Trends in Ecology & Evolution* **13**, 438–443.

Riegl, B. & Riegl, A. 1996. Studies on coral community structure and damage as a basis for zoning marine reserves. *Biological Conservation* **77**, 269–277.

Riegl, B. & Velimirov, B. 1991. How many damaged corals in Red Sea reef systems – A quantitative survey. *Hydrobiologia* **216**, 249–256.

Rinkevich, B., Wolodarsky, Z. & Loya, Y. 1991. Coral-crab association – A compact domain of a multilevel trophic system. *Hydrobiologia* **216**, 279–284.

Risch, D., Norris, T., Curnock, M. & Friedlaender, A. 2019. Common and Antarctic minke whales: Conservation status and future research directions. *Frontiers in Marine Science* **6**, 247.

Ritchie, E.G. & Johnson, C.N. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* **12**, 982–998.

Ritson-Williams, R. & Paul, V.J. 2007. Marine benthic invertebrates use multimodal cues for defense against reef fish. *Marine Ecology Progress Series* **340**, 29–39.

Rizzari, J.R., Bergseth, B.J. & Frisch, A.J. 2015. Impact of conservation areas on trophic interactions between apex predators and herbivores on coral reefs. *Conservation Biology* **29**, 418–429.

Rizzari, J.R., Frisch, A.J., Hoey, A.S. & McCormick, M.I. 2014. Not worth the risk: Apex predators suppress herbivory on coral reefs. *Oikos* **123**, 829–836.

Robbins, W.D., Hisano, M., Connolly, S.R. & Choat, J.H. 2006. Ongoing collapse of coral-reef shark populations. *Current Biology* **16**, 2314–2319.

Robertson, D.R. 1983. On the spawning behavior and spawning cycles of eight surgeonfishes (Acanthuridae) from the Indo-Pacific. *Environmental Biology of Fishes* **9**, 193–223.

Roche, R.C., Pratchett, M.S., Carr, P., Turner, J.R., Wagner, D., Head, C. & Sheppard, C.R.C. 2015. Localized outbreaks of *Acanthaster planci* at an isolated and unpopulated reef atoll in the Chagos Archipelago. *Marine Biology* **162**, 1695–1704.

Rocker, M.M., Francis, D.S., Fabricius, K.E., Willis, B.L. & Bay, L.K. 2017. Variation in the health and biochemical condition of the coral *Acropora tenuis* along two water quality gradients on the Great Barrier Reef, Australia. *Marine Pollution Bulletin* **119**, 106–119.

Rodhouse, P.G., Pierce, G.J., Nichols, O.C. et al. 2014. Environmental effects on cephalopod population dynamics: Implications for management of fisheries. In *Advances in Marine Biology*. E.A.G. Vidal (ed.). Elsevier. **67**, 99–233.

Roelofs, A. 2008. Ecological Risk Assessment of the Queensland Marine Aquarium Fish Fishery. *Department of Primary Industries and Fisheries*, Brisbane, Australia: Department of Primary Industries and Fisheries. 18 pp.

Roff, G., Bejarano, S., Priest, M., Marshell, A., Chollett, I., Steneck, R.S., Doropoulos, C., Golbuu, Y. & Mumby, P.J. 2019. Seascapes as drivers of coral reef ecosystem function. *Ecological Monographs* **89**, e01336.

Roff, G., Brown, C.J., Priest, M.A. & Mumby, P.J. 2018. Decline of coastal apex shark populations over the past half century. *Communications Biology* **1**, 223.

Roff, G., Doropoulos, C., Rogers, A., Bozec, Y.M., Krueck, N.C., Aurellado, E., Priest, M., Birrell, C. & Mumby, P.J. 2016. The ecological role of sharks on coral reefs. *Trends in Ecology & Evolution* **31**, 395–407.

Roff, G., Doropoulos, C., Zupan, M., Rogers, A., Steneck, R.S., Golbuu, Y. & Mumby, P.J. 2015. Phase shift facilitation following cyclone disturbance on coral reefs. *Oecologia* **178**, 1193–1203.

Roff, G., Hoegh-Guldberg, O. & Fine, M. 2006. Intra-colonial response to acroporid 'White syndrome' lesions in tabular *Acropora* spp. (Scleractinia). *Coral Reefs* **25**, 255–264.

Roff, G., Kvennefors, E.C.E., Fine, M., Ortiz, J., Davy, J.E. & Hoegh-Guldberg, O. 2011. The ecology of 'Acroporid White Syndrome', a coral disease from the southern Great Barrier Reef. *PLOS ONE* **6**, e26829.

Roff, G., Kvennefors, E.C.E., Ulstrup, K.E., Fine, M. & Hoegh-Guldberg, O. 2008. Coral disease physiology: The impact of Acroporid white syndrome on *Symbiodinium*. *Coral Reefs* **27**, 373–377.

Roff, G. & Mumby, P.J. 2012. Global disparity in the resilience of coral reefs. *Trends in Ecology & Evolution* **27**, 404–413.

Rogers, A., Blanchard, J.L. & Mumby, P.J. 2014. Vulnerability of coral reef fisheries to a loss of structural complexity. *Current Biology* **24**, 1000–1005.

Rogers, A., Blanchard, J.L. & Mumby, P.J. 2018a. Fisheries productivity under progressive coral reef degradation. *Journal of Applied Ecology* **55**, 1041–1049.

Rogers, A., Blanchard, J.L., Newman, S.P., Dryden, C.S. & Mumby, P.J. 2018b. High refuge availability on coral reefs increases the vulnerability of reef-associated predators to overexploitation. *Ecology* **99**, 450–463.

Rogers, A., Harborne, A.R., Brown, C.J. et al. 2015. Anticipative management for coral reef ecosystem services in the 21st century. *Global Change Biology* **21**, 504–514.

Rogers, J.G.D., Plaganyi, E.E. & Babcock, R.C. 2017. Aggregation, Allee effects and critical thresholds for the management of the crown-of-thorns starfish *Acanthaster planci*. *Marine Ecology Progress Series* **578**, 99–114.

Rohner, C.A., Pierce, S.J., Marshall, A.D., Weeks, S.J., Bennett, M.B. & Richardson, A.J. 2013. Trends in sightings and environmental influences on a coastal aggregation of manta rays and whale sharks. *Marine Ecology Progress Series* **482**, 153–168.

Roper, C.F.E. & Hochberg, F.G. 1987. Cephalopods of Lizard Island, Great Barrier Reef, Australia. *Occasional Papers from the Museum of Victoria* **3**, 15–20.

Rosa, R., Lopes, A.R., Pimentel, M. et al. 2014. Ocean cleaning stations under a changing climate: Biological responses of tropical and temperate fish-cleaner shrimp to global warming. *Global Change Biology* **20**, 3068–3079.

Rosa, R., Pissarra, V., Borges, F.O. et al. 2019. Global patterns of species richness in coastal cephalopods. *Frontiers in Marine Science* 6.

Rosewater, J. 1965. The family Tridacnidae in the Indo-Pacific. *Indo-Pacific Mollusca* **1**, 347–396.

Roth, F., Saalmann, F., Thomson, T., Coker, D.J., Villalobos, R., Jones, B.H., Wild, C. & Carvalho, S. 2018. Coral reef degradation affects the potential for reef recovery after disturbance. *Marine Environmental Research* **142**, 48–58.

Rotjan, R.D. & Lewis, S.M. 2008. Impact of coral predators on tropical reefs. *Marine Ecology Progress Series* **367**, 73–91.

Rowley, S. 2008. A critical evaluation of the symbiotic association between tropical tube-dwelling Polychaetes and their Hermatypic coral hosts, with a focus on *Spirobranchus giganteus* (Pallas, 1766). *The Plymouth Student Scientist* **1**, 19.

Ruiz-Morenol, D., Willis, B.L., Page, A.C., Weil, E., Croquer, A., Vargas-Angel, B., Jordan-Garzae, A.G., Jordan-Dahlgren, E., Raymundo, L. & Harvell, C.D. 2012. Global coral disease prevalence associated with sea temperature anomalies and local factors. *Diseases of Aquatic Organisms* **100**, 249–261.

Runge, M.C., Converse, S.J. & Lyons, J.E. 2011. Which uncertainty? Using expert elicitation and expected value of information to design an adaptive program. *Biological Conservation* **144**, 1214–1223.

Rusch, A. & Gaidos, E. 2013. Nitrogen-cycling bacteria and archaea in the carbonate sediment of a coral reef. *Geobiology* **11**, 472–484.

Rusch, A., Hannides, A.K. & Gaidos, E. 2009. Diverse communities of active Bacteria and Archaea along oxygen gradients in coral reef sediments. *Coral Reefs* **28**, 15–26.

Russ, G.R. 2003. Grazer biomass correlates more strongly with production than with biomass of algal turfs on a coral reef. *Coral Reefs* **22**, 63–67.

Russ, G.R., Questel, S.L.A., Rizzari, J.R. & Alcala, A.C. 2015. The parrotfish-coral relationship: Refuting the ubiquity of a prevailing paradigm. *Marine Biology* **162**, 2029–2045.

Russell, F.S. 1935. The zooplankton: IV. The occurrence and seasonal distribution of the Tunicata, Mollusca and Coelenterata (Siphonophora). Great Barrier Reef Expedition (1928–29). *Scientific Reports* **2**, 203–276.

Salm, R. 1978. Conservation of marine resources in Seychelles. *IUCN Report to Government of Seychelles*, Morges, Switzerland.

Sammarco, P.W. 1985. The Great Barrier vs the Caribbean comparisons of grazers, coral recruitment patterns and reef recovery. In *Fifth International Coral Reefs Congress, Antenne Museum-EPHE*, Tahiti. 391–397.

Sammarco, P.W. 1996. Comments on coral reef regeneration, bioerosion, biogeography, and chemical ecology: Future directions. *Journal of Experimental Marine Biology and Ecology* **200**, 135–168.

Sammarco, P.W. & Crenshaw, H. 1984. Plankton community dynamics of the central Great Barrier Reef lagoon – analysis of data from Ikeda *et al*. *Marine Biology* **82**, 167–180.

Samyn, Y. & Tallon, I. 2005. Zoogeography of the shallow-water holothuroids of the western Indian Ocean. *Journal of Biogeography* **32**, 1523–1538.

Sarkar, S., Ghosh, A.K. & Rao, G.M.N. 2016. Coralline algae and benthic foraminifera from the long formation (middle Miocene) of the Little Andaman Island, India: Biofacies analysis, systematics and palaeoenvironmental implications. *Journal of the Geological Society of India* **87**, 69–84.

Sato, Y., Bell, S.C., Nichols, C., Fry, K., Menendez, P. & Bourne, D.G. 2018. Early-phase dynamics in coral recovery following cyclone disturbance on the inshore Great Barrier Reef, Australia. *Coral Reefs* **37**, 431–443.

Sato, Y., Bourne, D.G. & Willis, B.L. 2009. Dynamics of seasonal outbreaks of black band disease in an assemblage of *Montipora* species at Pelorus Island (Great Barrier Reef, Australia). *Proceedings of the Royal Society B-Biological Sciences* **276**, 2795–2803.

Sato, Y., Bourne, D.G. & Willis, B.L. 2011. Effects of temperature and light on the progression of black band disease on the reef coral, *Montipora hispida*. *Coral Reefs* **30**, 753–761.

Sato, Y., Civiello, M., Bell, S.C., Willis, B.L. & Bourne, D.G. 2016. Integrated approach to understanding the onset and pathogenesis of black band disease in corals. *Environmental Microbiology* **18**, 752–765.

Savage, C. 2019. Seabird nutrients are assimilated by corals and enhance coral growth rates. *Scientific Reports* **9**, 4284.

Scanlan, D.J. & West, N.J. 2002. Molecular ecology of the marine cyanobacterial genera Prochlorococcus and Synechococcus. *FEMS Microbiology Ecology* **40**, 1–12.

Schaffelke, B. & Klumpp, D.W. 1997. Biomass and productivity of tropical macroalgae on three nearshore fringing reefs in the central Great Barrier Reef, Australia. *Botanica Marina* **40**, 373–383.

Schaffelke, B., Mellors, J. & Duke, N.C. 2005. Water quality in the Great Barrier Reef region: Responses of mangrove, seagrass and macroalgal communities. *Marine Pollution Bulletin* **51**, 279–296.

Schleussner, C.F., Lissner, T.K., Fischer, E.M. et al. 2016. Differential climate impacts for policy-relevant limits to global warming: The case of 1.5 degrees C and 2 degrees C. *Earth System Dynamics* **7**, 327–351.

Schmidt, C., Kucera, M. & Uthicke, S. 2014. Combined effects of warming and ocean acidification on coral reef Foraminifera *Marginopora vertebralis* and *Heterostegina depressa*. *Coral Reefs* **33**, 805–818.

Schmidt, C., Titelboim, D., Brandt, J., Herut, B., Abramovich, S., Almogi-Labin, A. & Kucera, M. 2016. Extremely heat tolerant photo-symbiosis in a shallow marine benthic foraminifera. *Scientific Reports* **6**, 30930.

Schmitt, D. & Gischler, E. 2017. Recent sedimentary facies of Roatan (Bay Islands, Honduras), a Caribbean oceanic barrier reef system. *Facies* **63**, 5.

Schneider, K., Silverman, J., Kravitz, B., Rivlin, T., Schneider-Mor, A., Barbosa, S., Byrne, M. & Caldeira, K. 2013. Inorganic carbon turnover caused by digestion of carbonate sands and metabolic activity of holothurians. *Estuarine Coastal and Shelf Science* **133**, 217–223.

Schneider, K., Silverman, J., Woolsey, E., Eriksson, H., Byrne, M. & Caldeira, K. 2011. Potential influence of sea cucumbers on coral reef CaCO3 budget: A case study at One Tree Reef. *Journal of Geophysical Research-Biogeosciences* **116**, G04032.

Schönberg, C.H.L. 2000. Bioeroding sponges common to the Central Australian Great Barrier Reef: Descriptions of three new species, two new records, and additions to two previously described species. *Senckenbergiana Maritima* **30**, 161–221.

Schönberg, C.H.L. 2001. Small-scale distribution of great barrier reef bioeroding sponges in shallow water. *Ophelia* **55**, 39–54.

Schönberg, C.H.L. 2016. Happy relationships between marine sponges and sediments – a review and some observations from Australia. *Journal of the Marine Biological Association of the United Kingdom* **96**, 493–514.

Schönberg, C.H.L., Fang, J.K.H., Carreiro-Silva, M., Tribollet, A. & Wisshak, M. 2017. Bioerosion: The other ocean acidification problem. *Ices Journal of Marine Science* **74**, 895–925.

Scott, C.M., Mehrotra, R., Hein, M.Y., Moerland, M.S. & Hoeksema, B.W. 2017a. Population dynamics of corallivores (*Drupella* and *Acanthaster*) on coral reefs of Koh Tao, a diving destination in the Gulf of Thailand. *Raffles Bulletin of Zoology* **65**, 68–79.

Scott, F.J. & Russ, G.R. 1987. Effects of grazing on species composition of the epilithic algal community on coral reefs of the central Great Barrier Reef. *Marine Ecology Progress Series* **39**, 293–304.

Scott, M., Heupel, M., Tobin, A. & Pratchett, M. 2017b. A large predatory reef fish species moderates feeding and activity patterns in response to seasonal and latitudinal temperature variation. *Scientific Reports* **7**, 12966.

Shaver, E.C., Burkepile, D.E. & Silliman, B.R. 2018. Local management actions can increase coral resilience to thermally-induced bleaching. *Nature Ecology & Evolution* **2**, 1075–1079.

Shaver, E.C. & Silliman, B.R. 2017. Time to cash in on positive interactions for coral restoration. *PeerJ* **5**, e3499.

Shaw, E.C., Hamylton, S.M. & Phinn, S.R. 2016. Incorporating benthic community changes into hydrochemical-based projections of coral reef calcium carbonate production under ocean acidification. *Coral Reefs* **35**, 739–750.

Shaw, M., Negri, A., Fabricius, K. & Mueller, J.F. 2009. Predicting water toxicity: Pairing passive sampling with bioassays on the Great Barrier Reef. *Aquatic Toxicology* **95**, 108–116.

Shea, S. & Liu, M. 2010. *Labroides dimidiatus*. The IUCN Red List of Threatened Species 2010: e.T187396A8523800.

Shima, J.S., Osenberg, C.W. & St Mary, C.M. 2008. Quantifying site quality in a heterogeneous landscape: Recruitment of a reef fish. *Ecology* **89**, 86–94.

Shima, J.S., Osenberg, C.W. & Stier, A.C. 2010. The vermetid gastropod *Dendropoma maximum* reduces coral growth and survival. *Biology Letters* **6**, 815–818.

Shore, A. & Caldwell, J.M. 2019. Modes of coral disease transmission: How do diseases spread between individuals and among populations? *Marine Biology* **166**, 45.

Siboni, N., Abrego, D., Evenhuis, C., Logan, M. & Motti, C.A. 2015. Adaptation to local thermal regimes by crustose coralline algae does not affect rates of recruitment in coral larvae. *Coral Reefs* **34**, 1243–1253.

Siboni, N., Abrego, D., Seneca, F., Motti, C.A., Andreakis, N., Tebben, J., Blackall, L.L. & Harder, T. 2012a. Using bacterial extract along with differential gene expression in *Acropora millepora* larvae to decouple the processes of attachment and metamorphosis. *PLOS ONE* **7**, e37774.

Siboni, N., Ben-Dov, E., Sivan, A. & Kushmaro, A. 2012b. Geographic specific coral-associated ammonia-oxidizing Archaea in the northern Gulf of Eilat (Red Sea). *Microbial Ecology* **64**, 18–24.

Sievers, M., Brown, C.J., Tulloch, V.J.D., Pearson, R.M., Haig, J.A., Turschwell, M.P. & Connolly, R.M. 2019. The role of vegetated coastal wetlands for marine megafauna conservation. *Trends in Ecology & Evolution*, 2531.

Sikkel, P.C., Richardson, M.A., Sun, D., Narvaez, P., Feeney, W.E. & Grutter, A.S. 2019. Changes in abundance of fish-parasitic gnathiid isopods associated with warm-water bleaching events on the northern Great Barrier Reef. *Coral Reefs* **38**, 721–730.

Silveira, C.B., Cavalcanti, G.S., Walter, J.M., Silva-Lima, A.W., Dinsdale, E.A., Bourne, D.G., Thompson, C.C. & Thompson, F.L. 2017. Microbial processes driving coral reef organic carbon flow. *Fems Microbiology Reviews* **41**, 575–595.

Silverman, J., Kline, D.I., Johnson, L., Rivlin, T., Schneider, K., Erez, J., Lazar, B. & Caldeira, K. 2012. Carbon turnover rates in the One Tree Island reef: A 40-year perspective. *Journal of Geophysical Research-Biogeosciences* **117**, G03023.

Silverman, J., Schneider, K., Kline, D.I., Rivlin, T., Rivlin, A., Hamylton, S., Lazar, B., Erez, J. & Caldeira, K. 2014. Community calcification in Lizard Island, Great Barrier Reef: A 33 year perspective. *Geochimica Et Cosmochimica Acta* **144**, 72–81.

Simister, R., Taylor, M.W., Tsai, P., Fan, L., Bruxner, T.J., Crowe, M.L. & Webster, N. 2012. Thermal stress responses in the bacterial biosphere of the Great Barrier Reef sponge, *Rhopaloeides odorabile*. *Environmental Microbiology* **14**, 3232–3246.

Skerratt, J.H., Mongin, M., Baird, M.E., Wild-Allen, K.A., Robson, B.J., Schaffelke, B., Davies, C.H., Richardson, A.J., Margvelashvili, N., Soja-Wozniak, M. & Steven, A.D.L. 2019. Simulated nutrient and plankton dynamics in the Great Barrier Reef (2011–2016). *Journal of Marine Systems* **192**, 51–74.

Smalley, T. 1984. Possible effects of intraspecific competition on the population structure of a solitary vermetid mollusc. *Marine Ecology Progress Series* **14**, 139–144.

Smith, J.E., Price, N.N., Nelson, C.E. & Haas, A.F. 2013. Coupled changes in oxygen concentration and pH caused by metabolism of benthic coral reef organisms. *Marine Biology* **160**, 2437–2447.

Smith, L.D. & Hughes, T.P. 1999. An experimental assessment of survival, re-attachment and fecundity of coral fragments. *Journal of Experimental Marine Biology and Ecology* **235**, 147–164.

Soares, M.C., Oliveira, R.F., Ros, A.F.H., Grutter, A.S. & Bshary, R. 2011. Tactile stimulation lowers stress in fish. *Nature Communications* **2**, 534.

Spady, B.L., Munday, P.L. & Watson, S.-A. 2018. Predatory strategies and behaviours in cephalopods are altered by elevated CO2. *Global Change Biology* **24**, 2585–2596.

Spady, B.L., Watson, S.-A., Chase, T.J. & Munday, P.L. 2014. Projected near-future CO2 levels increase activity and alter defensive behaviours in the tropical squid *Idiosepius pygmaeus*. *Biology Open* **3**, 1063–1070.

Srivastava, D.S. & Vellend, M. 2005. Biodiversity-ecosystem function research: Is it relevant to conservation? *Annual Review of Ecology, Evolution, and Systematics* **36**, 267–294.

Stat, M., Pochon, X., Franklin, E.C., Bruno, J.F., Casey, K.S., Selig, E.R. & Gates, R.D. 2013. The distribution of the thermally tolerant symbiont lineage (*Symbiodinium* clade D) in corals from Hawaii: Correlations with host and the history of ocean thermal stress. *Ecology and Evolution* **3**, 1317–1329.

Stella, J.S., Jones, G.P. & Pratchett, M.S. 2010. Variation in the structure of epifaunal invertebrate assemblages among coral hosts. *Coral Reefs* **29**, 957–973.

Stella, J.S., Munday, P.L. & Jones, G.P. 2011a. Effects of coral bleaching on the obligate coral-dwelling crab *Trapezia cymodoce*. *Coral Reefs* **30**, 719–727.

Stella, J.S., Munday, P.L., Walker, S.P.W., Pratchett, M.S. & Jones, G.P. 2014. From cooperation to combat: Adverse effect of thermal stress in a symbiotic coral-crustacean community. *Oecologia* **174**, 1187–1195.

Stella, J.S., Pratchett, M.S., Hutchings, P.A. & Jones, G.P. 2011b. Coral-associated invertebrates: Diversity, ecological importance and vulnerability to disturbance. *Oceanography and Marine Biology: An Annual Review* **49**, 43–104.

Steneck, R.S., Bellwood, D.R. & Hay, M.E. 2017. Herbivory in the marine realm. *Current Biology* **27**, R484–R489.

Stevens, J.D., Bonfil, R., Dulvy, N.K. & Walker, P.A. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *Ices Journal of Marine Science* **57**, 476–494.

Stewart, H.L., Holbrook, S.J., Schmitt, R.J. & Brooks, A.J. 2006. Symbiotic crabs maintain coral health by clearing sediments. *Coral Reefs* **25**, 609–615.

Stier, A.C., McKeon, C.S., Osenberg, C.W. & Shima, J.S. 2010. Guard crabs alleviate deleterious effects of vermetid snails on a branching coral. *Coral Reefs* **29**, 1019–1022.

Stier, A.C., Stallings, C.D., Samhouri, J.F., Albins, M.A. & Almany, G.R. 2017. Biodiversity effects of the predation gauntlet. *Coral Reefs* **36**, 601–606.

Stier, A.C. & White, J.W. 2014. Predator density and the functional responses of coral reef fish. *Coral Reefs* **33**, 235–240.

Stimson, J. 1990. Stimulation of fat-body production in the polyps of the coral *Pocillopora damicornis* by the presence of mutualistic crabs of the genus *Trapezia*. *Marine Biology* **106**, 211–218.

Stimson, J., Cunha, T. & Philippoff, J. 2007. Food preferences and related behavior of the browsing sea urchin *Tripneustes gratilla* (Linnaeus) and its potential for use as a biological control agent. *Marine Biology* **151**, 1761–1772.

Stoeckl, N., Birtles, A., Farr, M., Mangott, A., Curnock, M. & Valentine, P. 2010a. Live-aboard dive boats in the Great Barrier Reef: Regional economic impact and the relative values of their target marine species. *Tourism Economics* **16**, 995–1018.

Stoeckl, N., Birtles, A., Valentine, P., Farr, M., Curnock, M., Mangott, A. & Sobtzick, S. 2010b. *Understanding the social and economic values of key marine species in the Great Barrier Reef. MTSRF Project 4.8.6(a).* Final project report to the Marine and Tropical Sciences Research Facility (MTSRF). James Cook University, Townsville. 76 pp.

Stoeckl, N., Hicks, C.C., Mills, M., Fabricius, K., Esparon, M., Kroon, F., Kaur, K. & Costanza, R. 2011. The economic value of ecosystem services in the Great Barrier Reef: Our state of knowledge. *Ecological Economics Reviews* 1**219**, 113–133.

Strathmann, R.R., Cameron, R.A. & Strathmann, M.F. 1984. *Spirobranchus giganteus* (Pallas) breaks a rule for suspension-feeders. *Journal of Experimental Marine Biology and Ecology* **79**, 245–249.

Strehlow, B.W., Pineda, M.C., Duckworth, A., Kendrick, G.A., Renton, M., Wahab, M.A.A., Webster, N.S. & Clode, P.L. 2017. Sediment tolerance mechanisms identified in sponges using advanced imaging techniques. *PeerJ* **5**, e3904.

Streit, R., Hoey, A. & Bellwood, D. 2015. Feeding characteristics reveal functional distinctions among browsing herbivorous fishes on coral reefs. *Coral Reefs* **34**, 1037–1047.

Stuart-Smith, R.D., Bates, A.E., Lefcheck, J.S. et al. 2013. Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature* **501**, 539.

Stuart-Smith, R.D., Brown, C.J., Ceccarelli, D.M. & Edgar, G.J. 2018. Ecosystem restructuring along the Great Barrier Reef following mass coral bleaching. *Nature* **560**, 92–96.

Sun, D., Blomberg, S.P., Cribb, T.H., McCormick, M.I. & Grutter, A.S. 2012. The effects of parasites on the early life stages of a damselfish. *Coral Reefs* **31**, 1065–1075.

Sun, D., Cheney, K.L., Werminghausen, J., Meekan, M.G., McCormick, M.I., Cribb, T.H. & Grutter, A.S. 2015. Presence of cleaner wrasse increases the recruitment of damselfishes to coral reefs. *Biology Letters* **11**, 20150456.

Suzuki, A., Kawahata, H., Ayukai, T. & Goto, K. 2001. The oceanic CO2 system and carbon budget in the Great Barrier Reef, Australia. *Geophysical Research Letters* **28**, 1243–1246.

Sweatman, H. 2008. No-take reserves protect coral reefs from predatory starfish. *Current Biology* **18**, R598–R599.

Sweatman, H. & Cappo, M. 2018. Do no-take zones reduce the likelihood of outbreaks of the Crown-of-thorns starfish? Integrated Pest Management of Crown-of-Thorns Starfish. *Report to the National Environmental Science Program*. Reef and Rainforest Research Centre Limited, Cairns. 38 pp.

Sweatman, H., Cheal, A., Emslie, M., Johns, K., Jonker, M., Miller, I. & Osborne, K. 2015. Effects of marine park zoning on coral reefs of the Capricorn-Bunker Group – Report on surveys in October 2015. *Report to the National Environmental Science Program*. Reef and Rainforest Research Centre Limited, Cairns. 15 pp.

Sweatman, H. & Robertson, D.R. 1994. Grazing halos and predation on juvenile Caribbean surgeonfishes. *Marine Ecology Progress Series* **111**, 1–6.

Szmant, A.M. & Gassman, N.J. 1990. The effects of prolonged bleaching on the tissue biomass and reproduction of the reef coral *Montastrea annularis*. *Coral Reefs* **8**, 217–224.

Tambutte, S., Holcomb, M., Ferrier-Pages, C., Reynaud, S., Tambutte, E., Zoccola, D. & Allemand, D. 2011. Coral biomineralization: From the gene to the environment. *Journal of Experimental Marine Biology and Ecology* **408**, 58–78.

Tanner, J.E., Hughes, T.P. & Connell, J.H. 1996. The role of history in community dynamics: A modelling approach. *Ecology* **77**, 108–117.

Tavares, D.C., Moura, J.F., Acevedo-Trejos, E. & Merico, A. 2019. Traits shared by marine megafauna and their relationships with ecosystem functions and services. *Frontiers in Marine Science* **6**, 262.

Taylor, M.W., Radax, R., Steger, D. & Wagner, M. 2007. Sponge-associated microorganisms: Evolution, ecology, and biotechnological potential. *Microbiology and Molecular Biology Reviews* **71**, 295–347.

Taylor, M.W., Tsai, P., Simister, R.L., Deines, P., Botte, E., Ericson, G., Schmitt, S. & Webster, N.S. 2013. 'Sponge-specific' bacteria are widespread (but rare) in diverse marine environments. *Isme Journal* **7**, 438–443.

Taylor, S.M. & Bennett, M.B. 2008. Cephalopod dietary specialization and ontogenetic partitioning of the Australian weasel shark *Hemigaleus australiensis* White, Last & Compagno. *Journal of Fish Biology* **72**, 917–936.

Tebbett, S.B., Goatley, C.H.R. & Bellwood, D.R. 2017a. Algal turf sediments and sediment production by parrotfishes across the continental shelf of the northern Great Barrier Reef. *PLOS ONE* **12**, e0170854.

Tebbett, S.B., Goatley, C.H.R. & Bellwood, D.R. 2017b. Clarifying functional roles: Algal removal by the surgeonfishes *Ctenochaetus striatus* and *Acanthurus nigrofuscus*. *Coral Reefs* **36**, 803–813.

Tebbett, S.B., Goatley, C.H.R. & Bellwood, D.R. 2017c. The effects of algal turf sediments and organic loads on feeding by coral reef surgeonfishes. *PLOS ONE* **12**, e0169479.

Tebbett, S.B., Goatley, C.H.R. & Bellwood, D.R. 2017d. Fine sediments suppress detritivory on coral reefs. *Marine Pollution Bulletin* **114**, 934–940.

Tebbett, S.B., Goatley, C.H.R., Huertas, V., Mihalitsis, M. & Bellwood, D.R. 2018. A functional evaluation of feeding in the surgeonfish *Ctenochaetus striatus*: The role of soft tissues. *Royal Society Open Science* **5**, 171111.

Tebbett, S.B., Streit, R.P. & Bellwood, D.R. 2019. Expansion of a colonial ascidian following consecutive mass coral bleaching at Lizard Island, Australia. *Marine Environmental Research* **144**, 125–129.

Thompson, A.A. & Dolman, A.M. 2010. Coral bleaching: One disturbance too many for near-shore reefs of the Great Barrier Reef. *Coral Reefs* **29**, 637–648.

Thompson, C.A., Matthews, S., Hoey, A.S. & Pratchett, M.S. 2019. Changes in sociality of butterflyfishes linked to population declines and coral loss. *Coral Reefs* **38**, 527–537. https://doi.org/10.1007/s00338-00019-01792-x.

Thompson, J.R., Rivera, H.E., Closek, C.J. & Medina, M. 2015. Microbes in the coral holobiont: Partners through evolution, development, and ecological interactions. *Frontiers in Cellular and Infection Microbiology* **4**, 176.

Thomsen, M.S., Altieri, A.H., Angelini, C. et al. 2018. Secondary foundation species enhance biodiversity. *Nature Ecology & Evolution* **2**, 634–639.

Tootell, J.S. & Steele, M.A. 2016. Distribution, behavior, and condition of herbivorous fishes on coral reefs track algal resources. *Oecologia* **181**, 13–24.

Torda, G., Donelson, J.M., Aranda, M. et al. 2017. Rapid adaptive responses to climate change in corals. *Nature Climate Change* **7**, 627–636.

Torda, G., Lundgren, P., Willis, B.L. & van Oppen, M.J.H. 2013a. Genetic assignment of recruits reveals short- and long-distance larval dispersal in *Pocillopora damicornis* on the Great Barrier Reef. *Molecular Ecology* **22**, 5821–5834.

Torda, G., Lundgren, P., Willis, B.L. & van Oppen, M.J.H. 2013b. Revisiting the connectivity puzzle of the common coral *Pocillopora damicornis. Molecular Ecology* **22**, 5805–5820.

Tout, J., Jeffries, T.C., Webster, N.S., Stocker, R., Ralph, P.J. & Seymour, J.R. 2014. Variability in microbial community composition and function between different niches within a coral reef. *Microbial Ecology* **67**, 540–552.

Tribble, G.W., Atkinson, M.J., Sansone, F.J. & Smith, S.V. 1994. Reef metabolism and endo-upwelling in perspective. *Coral Reefs* **13**, 199–201.

Tribollet, A. 2008. The boring microflora in modern coral reef ecosystems: A review of its roles. In *Current Developments in Bioerosion*. M. Wisshak & L. Tapanila (eds). Erlangen Earth Conference Series. Berlin, Heidelberg: Springer.

Tribollet, A., Atkinson, M.J. & Langdon, C. 2006. Effects of elevated pCO(2) on epilithic and endolithic metabolism of reef carbonates. *Global Change Biology* **12**, 2200–2208.

Tribollet, A., Decherf, G., Hutchings, P.A. & Peyrot-Clausade, M. 2002. Large-scale spatial variability in bioerosion of experimental coral substrates on the Great Barrier Reef (Australia): Importance of microborers. *Coral Reefs* **21**, 424–432.

Tribollet, A. & Golubic, S. 2005. Cross-shelf differences in the pattern and pace of bioerosion of experimental carbonate substrates exposed for 3 years on the northern Great Barrier Reef, Australia. *Coral Reefs* **24**, 422–434.

Triki, Z., Wismer, S., Levorato, E. & Bshary, R. 2018. A decrease in the abundance and strategic sophistication of cleaner fish after environmental perturbations. *Global Change Biology* **24**, 481–489.

Trip, E.L., Choat, J.H., Wilson, D.T. & Robertson, D.R. 2008. Inter-oceanic analysis of demographic variation in a widely distributed Indo-Pacific coral reef fish. *Marine Ecology Progress Series* **373**, 97–109.

Tsatsaros, J.H., Brodie, J.E., Bohnet, I.C. & Valentine, P. 2013. Water quality degradation of coastal waterways in the Wet Tropics, Australia. *Water Air and Soil Pollution* **224**, 1443.

Tudhope, A.W. & Risk, M.J. 1985. Rate of dissolution of carbonate sediments by microboring organisms, Davies Reef, Australia. *Journal of Sedimentary Petrology* **55**, 440–447.

Turner, J.A., Babcock, R.C., Hovey, R. & Kendrick, G.A. 2017. Deep thinking: A systematic review of mesophotic coral ecosystems. *Ices Journal of Marine Science* **74**, 2309–2320.

Turner, S.J. 1994. The biology and population outbreaks of the corallivorous gastropod *Drupella* on Indo-Pacific reefs. *Oceanography and Marine Biology: An Annual Review* **32**, 461–530.

Uthicke, S. 1999. Sediment bioturbation and impact of feeding activity of *Holothuria* (*Halodeima*) *atra* and *Stichopus chloronotus*, two sediment feeding holothurians, at Lizard Island, Great Barrier Reef. *Bulletin of Marine Science* **64**, 129–141.

Uthicke, S. 2001. Nutrient regeneration by abundant coral reef holothurians. *Journal of Experimental Marine Biology and Ecology* **265**, 153–170.

Uthicke, S., Fabricius, K., De'ath, G., Negri, A., Warne, M., Smith, R., Noonan, S., Johansson, C., Gorsuch, H. & Anthony, K. 2016. Multiple and cumulative impacts on the GBR: Assessment of current status and development of improved approaches for management. *Report to the National Environmental Science Programme.* Reef and Rainforest Research Centre Limited, Cairns. 144 pp.

Uthicke, S., Furnas, M. & Lonborg, C. 2014. Coral reefs on the edge? Carbon chemistry on inshore reefs of the Great Barrier Reef. *PLOS ONE* **9**, e109092.

Uthicke, S. & Klumpp, D.W. 1998. Microphytobenthos community production at a near-shore coral reef: Seasonal variation and response to ammonium recycled by holothurians. *Marine Ecology Progress Series* **169**, 1–11.

Uthicke, S., Liddy, M., Patel, F., Logan, M., Johansson, C. & Lamare, M. 2018. Effects of larvae density and food concentration on crown-of-thorns seastar (*Acanthaster* cf. *solaris*) development in an automated flow-through system. *Scientific Reports* **8**, 642.

Uthicke, S., Schaffelke, B. & Byrne, M. 2009. A boom-bust phylum? Ecological and evolutionary consequences of density variations in echinoderms. *Ecological Monographs* **79**, 3–24.

Uthicke, S., Welch, D. & Benzie, J.A.H. 2004. Slow growth and lack of recovery in overfished holothurians on the Great Barrier Reef: Evidence from DNA fingerprints and repeated large scale surveys. *Conservation Biology* **18**, 1395–1404.

Vail, A.L., Manica, A. & Bshary, R. 2013. Referential gestures in fish collaborative hunting. *Nature Communications* **4**, 1765.

Valls, A., Coll, M. & Christensen, V. 2015. Keystone species: Toward an operational concept for marine biodiversity conservation. *Ecological Monographs* **85**, 29–47.

van Dam, J.W., Negri, A.P., Mueller, J.F., Altenburger, R. & Uthicke, S. 2012. Additive pressures of elevated sea surface temperatures and herbicides on symbiont-bearing foraminifera. *PLOS ONE* **7**, e33900.

van Dam, J.W., Negri, A.P., Uthicke, S. & Mueller, J.F. 2011. Chemical pollution on coral reefs: Exposure and ecological effects (Chapter 9). In *Ecological Impacts of Toxic Chemicals*. F. Sanchez-Bayo, P.J. van den Brink & R.M. Mann (eds). Amsterdam, Netherlands: Bentham Science Publishers, 187–211.

van Dam, J.W., Uthicke, S., Beltran, V.H., Mueller, J.F. & Negri, A.P. 2015. Combined thermal and herbicide stress in functionally diverse coral symbionts. *Environmental Pollution* **204**, 271–279.

van de Koppel, J., van der Heide, T., Altieri, A.H., Eriksson, B.K., Bouma, T.J., Olff, H. & Silliman, B.R. 2015. Long-distance interactions regulate the structure and resilience of coastal ecosystems. *Annual Review of Marine Science* **7**, 139–158.

van de Leemput, I.A., Hughes, T.P., van Nes, E.H. & Scheffer, M. 2016. Multiple feedbacks and the prevalence of alternate stable states on coral reefs. *Coral Reefs* **35**, 857–865.

van de Water, J.A.J.M., Lamb, J.B., Heron, S.F., van Oppen, M.J.H. & Willis, B.L. 2016. Temporal patterns in innate immunity parameters in reef-building corals and linkages with local climatic conditions. *Ecosphere* **7**, e01505.

van de Water, J.A.J.M., Lamb, J.B., van Oppen, M.J.H., Willis, B.L. & Bourne, D.G. 2015. Comparative immune responses of corals to stressors associated with offshore reef-based tourist platforms. *Conservation Physiology* **3**, cov032.

van Hooidonk, R., Maynard, J., Tamelander, J., Gove, J., Ahmadia, G., Raymundo, L., Williams, G., Heron, S.F. & Planes, S. 2016. Local-scale projections of coral reef futures and implications of the Paris Agreement. *Scientific Reports* **6**, 39666.

van Oppen, M.J.H., Gates, R.D., Blackall, L.L. et al. 2017. Shifting paradigms in restoration of the world's coral reefs. *Global Change Biology* **23**, 3437–3448.

van Oppen, M.J.H., Oliver, J.K., Putnam, H.M. & Gates, R.D. 2015. Building coral reef resilience through assisted evolution. *Proceedings of the National Academy of Sciences of the United States of America* **112**, 2307–2313.

van Woesik, R., Sakai, K., Ganase, A. & Loya, Y. 2011. Revisiting the winners and the losers a decade after coral bleaching. *Marine Ecology Progress Series* **434**, 67–76.

Vargas-Ángel, B., Richards, C.L., Vroom, P.S., Price, N.N., Schils, T., Young, C.W., Smith, J., Johnson, M.D. & Brainard, R.E. 2015. Baseline assessment of net calcium carbonate accretion rates on US Pacific reefs. *PLOS ONE* **10**, e0142196.

Vaughan, D.B., Grutter, A.S., Costello, M.J. & Hutson, K.S. 2017. Cleaner fishes and shrimp diversity and a re-evaluation of cleaning symbioses. *Fish and Fisheries* **18**, 698–716.

Vaughan, D.B., Grutter, A.S., Ferguson, H.W., Jones, R. & Hutson, K.S. 2018. Cleaner shrimp are true cleaners of injured fish. *Marine Biology* **165**, 118.

Venera-Ponton, D.E., Diaz-Pulido, G., McCook, L.J. & Rangel-Campo, A. 2011. Macroalgae reduce growth of juvenile corals but protect them from parrotfish damage. *Marine Ecology Progress Series* **421**, 109–115.

Vercelloni, J., Clifford, S., Caley, M.J. et al. 2018. Using virtual reality to estimate aesthetic values of coral reefs. *Royal Society Open Science* **5**, 172226.

Vermeij, M.J.A., Dailer, M.L. & Smith, C.M. 2011. Crustose coralline algae can suppress macroalgal growth and recruitment on Hawaiian coral reefs. *Marine Ecology Progress Series* **422**, 1–7.

Vermeij, M.J.A., van Moorselaar, I., Engelhard, S., Hornlein, C., Vonk, S.M. & Visser, P.M. 2010. The effects of nutrient enrichment and herbivore abundance on the ability of turf algae to overgrow coral in the Caribbean. *PLOS ONE* **5**, e14312.

Veron, J.E.N. 1986. Distribution of reef-building corals. *Oceanus* **29**, 27–31.

Vicente, V.P. 1990. Response of sponges with autotrophic endosymbionts during the coral bleaching episode in Puerto Rico. *Coral Reefs* **8**, 199–202.

Vidal-Ramirez, F. & Dove, S. 2016. Diurnal effects of *Holothuria atra* on seawater carbonate chemistry in a sedimentary environment. *Journal of Experimental Marine Biology and Ecology* **474**, 156–163.

Wainwright, P.C., Bellwood, D.R. & Westneat, M.W. 2002. Ecomorphology of locomotion in labrid fishes. *Environmental Biology of Fishes* **65**, 47–62.

Waldie, P.A., Blomberg, S.P., Cheney, K.L., Goldizen, A.W. & Grutter, A.S. 2011. Long-term effects of the cleaner fish *Labroides dimidiatus* on coral reef fish communities. *PLOS ONE* **6**, e21201.

Wall, C.B., Mason, R.A.B., Ellis, W.R., Cunning, R. & Gates, R.D. 2017. Elevated pCO(2) affects tissue biomass composition, but not calcification, in a reef coral under two light regimes. *Royal Society Open Science* **4**, 170683.

Wallace, C.C. 1985. Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora*. *Marine Biology* **88**, 217–233.

Waterhouse, J., Brodie, J., Lewis, S. & Mitchell, A. 2012. Quantifying the sources of pollutants in the Great Barrier Reef catchments and the relative risk to reef ecosystems. *Marine Pollution Bulletin* **65**, 394–406.

Waterhouse, J., Brodie, J. & Maynard, J. 2013. Assessing the relative risk of land based pollutants to the Great Barrier Reef. *20th International Congress on Modelling and Simulation (Modsim) 2013*, 3197–3203.

Watson, S.-A. 2015. Giant clams and rising CO2: Light may ameliorate effects of ocean acidification on a solar-powered animal. *PLOS ONE* **10**, e0128405.

Watson, S.-A., Fields, J.B. & Munday, P.L. 2017. Ocean acidification alters predator behaviour and reduces predation rate. *Biology Letters* **13**, 20160797.

Watson, S.-A., Lefevre, S., McCormick, M.I., Domenici, P., Nilsson, G.E. & Munday, P.L. 2014. Marine mollusc predator-escape behaviour altered by near-future carbon dioxide levels. *Proceedings of the Royal Society B-Biological Sciences* **281**, 20132377.

Watson, S.-A., Southgate, P.C., Miller, G.M., Moorhead, J.A. & Knauer, J. 2012. Ocean acidification and warming reduce juvenile survival of the fluted giant clam, *Tridacna squamosa*. *Molluscan Research* **32**, 177–180.

Wear, S.L. & Thurber, R.V. 2015. Sewage pollution: Mitigation is key for coral reef stewardship. *Year in Ecology and Conservation Biology* 1**355**, 15–30.

Webster, M.S. & Almany, G.R. 2002. Positive indirect effects in a coral reef fish community. *Ecology Letters* **5**, 549–557.

Webster, N.S., Negri, A.P., Botte, E.S., Laffy, P.W., Flores, F., Noonan, S., Schmidt, C. & Uthicke, S. 2016. Host-associated coral reef microbes respond to the cumulative pressures of ocean warming and ocean acidification. *Scientific Reports* 6.

Webster, N.S., Negri, A.P., Flores, F., Humphrey, C., Soo, R., Botte, E.S., Vogel, N. & Uthicke, S. 2013a. Near-future ocean acidification causes differences in microbial associations within diverse coral reef taxa. *Environmental Microbiology Reports* **5**, 243–251.

Webster, N.S. & Reusch, T.B.H. 2017. Microbial contributions to the persistence of coral reefs. *Isme Journal* **11**, 2167–2174.

Webster, N.S., Smith, L.D., Heyward, A.J., Watts, J.E.M., Webb, R.I., Blackall, L.L. & Negri, A.P. 2004. Metamorphosis of a scleractinian coral in response to microbial biofilms. *Applied and Environmental Microbiology* **70**, 1213–1221.

Webster, N.S., Soo, R., Cobb, R. & Negri, A.P. 2011. Elevated seawater temperature causes a microbial shift on crustose coralline algae with implications for the recruitment of coral larvae. *Isme Journal* **5**, 759–770.

Webster, N.S. & Taylor, M.W. 2012. Marine sponges and their microbial symbionts: Love and other relationships. *Environmental Microbiology* **14**, 335–346.

Webster, N.S., Uthicke, S., Botte, E.S., Flores, F. & Negri, A.P. 2013b. Ocean acidification reduces induction of coral settlement by crustose coralline algae. *Global Change Biology* **19**, 303–315.

Wee, H.B., Kurihara, H. & Reimer, J.D. 2019. Reduced Symbiodiniaceae diversity in *Palythoa tuberculosa* at a heavily acidified coral reef. *Coral Reefs* **38**, 311–319.

Weekers, D.P. & Zahnow, R. 2018. Risky facilities: Analysis of illegal recreational fishing in the Great Barrier Reef Marine Park, Australia. *Australian & New Zealand Journal of Criminology*, **52**, 368–389.

Wegley, L., Edwards, R., Rodriguez-Brito, B., Liu, H. & Rohwer, F. 2007. Metagenomic analysis of the microbial community associated with the coral *Porites astreoides*. *Environmental Microbiology* 9, 2707–2719.

Wells, S. 1996a. *Tridacna derasa*. In The IUCN Red List of Threatened Species 1996: e.T22136A9362077.

Wells, S. 1996b. *Tridacna gigas*. In The IUCN Red List of Threatened Species 1996: e.T22137A9362283.

Wen, C.K.C., Bonin, M.C., Harrison, H.B., Williamson, D.H. & Jones, G.P. 2016. Dietary shift in juvenile coral trout (*Plectropomus maculatus*) following coral reef degradation from a flood plume disturbance. *Coral Reefs* **35**, 451–455.

Wenger, A.S., Johansen, J.L. & Jones, G.P. 2011. Suspended sediment impairs habitat choice and chemosensory discrimination in two coral reef fishes. *Coral Reefs* **30**, 879–887.

Wenger, A.S., Johansen, J.L. & Jones, G.P. 2012. Increasing suspended sediment reduces foraging, growth and condition of a planktivorous damselfish. *Journal of Experimental Marine Biology and Ecology* **428**, 43–48.

Wenger, A.S., McCormick, M.I., Endo, G.G.K., McLeod, I.M., Kroon, F.J. & Jones, G.P. 2014. Suspended sediment prolongs larval development in a coral reef fish. *Journal of Experimental Biology* **217**, 1122–1128.

Wenger, A.S., McCormick, M.I., McLeod, I.M. & Jones, G.P. 2013. Suspended sediment alters predator-prey interactions between two coral reef fishes. *Coral Reefs* **32**, 369–374.

Westbrook, C.E., Ringang, R.R., Cantero, S.M.A. & Toonen, R.J. 2015. Survivorship and feeding preferences among size classes of outplanted sea urchins, *Tripneustes gratilla*, and possible use as biocontrol for invasive alien algae. *PeerJ* **3**, e1235.

Westcott, D.A., Fletcher, C.S., Babcock, R. & Plaganyi-Lloyd, E. 2016. A strategy to link research and management of crown-of-thorns starfish on the Great Barrier Reef: An integrated pest management approach. In *Report to the National Environmental Science Programme Reef and Rainforest Research Centre Limited*, Cairns. 80 pp.

Whetton, P., McInnes, K., Jones, R., Hennessy, K., Suppiah, R., Page, C., Bathols, J. & Durack, P. 2005. Australian climate change projections for impact assessment and policy application: A review. *CSIRO Marine and Atmospheric Research Paper No. 1*, CSIRO Marine and Atmospheric Research, Aspendale.

Wild, C., Hoegh-Guldberg, O., Naumann, M.S. et al. 2011. Climate change impedes scleractinian corals as primary reef ecosystem engineers. *Marine and Freshwater Research* **62**, 205–215.

Wild, C., Rasheed, M., Jantzen, C., Cook, P., Struck, U., Huettel, M. & Boetius, A. 2005. Benthic metabolism and degradation of natural particulate organic matter in carbonate and silicate reef sands of the northern Red Sea. *Marine Ecology Progress Series* **298**, 69–78.

Wilkinson, C.R. 1983. Role of sponges in coral reef structural processes. In *Perspectives on Coral Reefs*. D.J. Barnes (ed.). Townsville: Australian Institute of Marine Science, 263–274.

Wilkinson, C.R. 1987. Interocean differences in size and nutrition of coral reef sponge populations. *Science* **236**, 1654–1657.

Wilkinson, C.R. 1999. Global and local threats to coral reef functioning and existence: Review and predictions. *Marine and Freshwater Research* **50**, 867–878.

Wilkinson, C.R. 2006. Status of coral reefs of the world: Summary of threats and remedial action. In *Coral Reef Conservation*. I.M. Cote & J.D. Reynolds (eds). Cambridge University Press, 3–39.

Wilkinson, C.R., Williams, D.M., Sammarco, P.W., Hogg, R.W. & Trott, L.A. 1984. Rates of nitrogen fixation on coral reefs across the continental shelf of the central Great Barrier Reef. *Marine Biology* **80**, 255–262.

Williams, D.M., Dixon, P. & English, S. 1988. Cross-shelf distribution of dopepods and fish larvae across the central Great Barrier Reef. *Marine Biology* **99**, 577–589.

Williams, D.M. & Hatcher, A.I. 1983. Structure of fish communities on outer slopes of inshore, mid-shelf and outer shelf reefs of the Great Barrier Reef. *Marine Ecology Progress Series* **10**, 239–250.

Williams, G.J. & Graham, N.A.J. 2019. Rethinking coral reef functional futures. *Functional Ecology* **33**, 942–947.

Williamson, D.H., Ceccarelli, D.M., Evans, R.D., Hill, J.K. & Russ, G.R. 2014a. Derelict fishing line provides a useful proxy for estimating levels of non-compliance with no-take marine reserves. *PLOS ONE* **9**, e114395.

Williamson, D.H., Ceccarelli, D.M., Evans, R.D., Jones, G.P. & Russ, G.R. 2014b. Habitat dynamics, marine reserve status, and the decline and recovery of coral reef fish communities. *Ecology and Evolution* **4**, 337–354.

Williamson, D.H., Russ, G.R. & Ayling, A.M. 2004. No-take marine reserves increase abundance and biomass of reef fish on inshore fringing reefs of the Great Barrier Reef. *Environmental Conservation* **31**, 149–159.

Willis, B.L., Page, C.A. & Dinsdale, E.A. 2004. Coral disease on the Great Barrier Reef. In *Coral Health and Disease*. E. Rosenberg & Y. Loya (eds). Berlin, Heidelberg: Springer, 69–104.

Wilmes, J.C., Caballes, C.F., Cowan, Z.-L., Hoey, A.S., Lang, B.J., Messmer, V. & Pratchett, M.S. 2018. Contributions of pre- versus post-settlement processes to fluctuating abundance of crown-of-thorns starfishes (*Acanthaster* spp.). *Marine Pollution Bulletin* **135**, 332–345.

Wilmes, J.C., Matthews, S., Schultz, D., Messmer, V., Hoey, A.S. & Pratchett, M.S. 2016. Modelling growth of juvenile crown-of-thorns starfish on the northern Great Barrier Reef. *Diversity* **9**, 1.

Wilmes, J.C., Schultz, D.J., Hoey, A.S., Messmer, V. & Pratchett, M.S. 2020. Habitat associations of settlement-stage crown-of-thorns starfish on Australia's Great Barrier Reef. Coral Reefs doi: 10.1007/s00338-020-01950-6.

Wilson, M.E.J. & Vecsei, A. 2005. The apparent paradox of abundant foramol facies in low latitudes: Their environmental significance and effect on platform development. *Earth-Science Reviews* **69**, 133–168.

Wilson, S.K. 2000. Trophic status and feeding selectivity of blennies (Blenniidae: Salariini). *Marine Biology* **136**, 431–437.

Wilson, S.K. 2001. Multiscale habitat associations of detrivorous blennies (Blenniidae: Salariini). *Coral Reefs* **20**, 245–251.

Wilson, S.K. 2004. Growth, mortality and turnover rates of a small detritivorous fish. *Marine Ecology Progress Series* **284**, 253–259.

Wilson, S.K., Bellwood, D.R., Choat, J.H. & Furnas, M.J. 2003. Detritus in the epilithic algal matrix and its use by coral reef fishes. *Oceanography and Marine Biology* **41**, 279–309.

Wilson, S.K., Burgess, S.C., Cheal, A.J., Emslie, M., Fisher, R., Miller, I., Polunin, N.V.C. & Sweatman, H.P.A. 2008. Habitat utilization by coral reef fish: Implications for specialists vs. generalists in a changing environment. *Journal of Animal Ecology* **77**, 220–228.

Wilson, S.K., Dolman, A.M., Cheal, A.J., Emslie, M.J., Pratchett, M.S. & Sweatman, H.P.A. 2009. Maintenance of fish diversity on disturbed coral reefs. *Coral Reefs* **28**, 3–14.

Wilson, S.K., Graham, N.A.J. & Pratchett, M.S. 2014. Susceptibility of butterflyfish to habitat disturbance: Do 'chaets' ever prosper? In *Biology of Butterflyfishes*. M.S. Pratchett, M.L. Berumen & B.G. Kapoor (eds). Boca Raton, FL, USA: CRC Press, 226–245.

Wilson, S.K., Graham, N.A.J., Pratchett, M.S., Jones, G.P. & Polunin, N.V.C. 2006. Multiple disturbances and the global degradation of coral reefs: Are reef fishes at risk or resilient? *Global Change Biology* **12**, 2220–2234.

Wismer, S., Hoey, A.S. & Bellwood, D.R. 2009. Cross-shelf benthic community structure on the Great Barrier Reef: Relationships between macroalgal cover and herbivore biomass. *Marine Ecology Progress Series* **376**, 45–54.

Wisshak, M., Schonberg, C.H.L., Form, A. & Freiwald, A. 2014. Sponge bioerosion accelerated by ocean acidification across species and latitudes? *Helgoland Marine Research* **68**, 253–262.

Wolfe, K. & Byrne, M. 2017a. Biology and ecology of the vulnerable holothuroid, *Stichopus herrmanni*, on a high-latitude coral reef on the Great Barrier Reef. *Coral Reefs* **36**, 1143–1156.

Wolfe, K. & Byrne, M. 2017b. Population biology and recruitment of a vulnerable sea cucumber, *Stichopus herrmanni*, on a protected reef. *Marine ecology* **38**, e12397.

Wolfe, K., Graba-Landry, A., Dworjanyn, S.A. & Byrne, M. 2015a. Larval phenotypic plasticity in the boom-and-bust crown-of-thorns seastar, *Acanthaster planci*. *Marine Ecology Progress Series* **539**, 179–189.

Wolfe, K., Graba-Landry, A., Dworjanyn, S.A. & Byrne, M. 2015b. Larval starvation to satiation: Influence of nutrient regime on the success of *Acanthaster planci*. *PLOS ONE* **10**, e0122010.

Wolfe, K., Graba-Landry, A., Dworjanyn, S.A. & Byrne, M. 2017. Superstars: Assessing nutrient thresholds for enhanced larval success of *Acanthaster planci*, a review of the evidence. *Marine Pollution Bulletin* **116**, 307–314.

Wolfe, K., Vidal-Ramirez, F., Dove, S., Deaker, D. & Byrne, M. 2018. Altered sediment biota and lagoon habitat carbonate dynamics due to sea cucumber bioturbation in a high-pCO(2) environment. *Global Change Biology* **24**, 465–480.

Wolff, N.H., Mumby, P.J., Devlin, M. & Anthony, K.R.N. 2018. Vulnerability of the Great Barrier Reef to climate change and local pressures. *Global Change Biology* **24**, 1978–1991.

Wolfe, K., Nguyen, H.D., Davey, M. & Byrne, M. 2020. Characterizing biogeochemical fluctuations in a world of extremes: A synthesis for temperate intertidal habitats in the face of global change. Global Change Biology 26, 3858–3879..

Wolff, N.H., Wong, A., Vitolo, R., Stolberg, K., Anthony, K.R.N. & Mumby, P.J. 2016. Temporal clustering of tropical cyclones on the Great Barrier Reef and its ecological importance. *Coral Reefs* **35**, 613–623.

Wolkenhauer, S.M., Uthicke, S., Burridge, C., Skewes, T. & Pitcher, R. 2010. The ecological role of *Holothuria scabra* (Echinodermata: Holothuroidea) within subtropical seagrass beds. *Journal of the Marine Biological Association of the United Kingdom* **90**, 215–223.

Woodley, J.D., Chornesky, E.A., Clifford, P.A. et al. 1981. Hurricane Allens impact on Jamaican coral reefs. *Science* **214**, 749–755.

Woodroffe, C.D., Farrell, J.W., Hall, F.R. & Harris, P.T. 2017. Calcium carbonate production and contribution to coastal sediments. In *The First Global Integrated Marine Assessment*. L. Inniss & A. Simcock (eds). Cambridge: Cambridge University Press, 262–276.

Wooldridge, S., Brodie, J. & Furnas, M. 2006. Exposure of inner-shelf reefs to nutrient enriched runoff entering the Great Barrier Reef Lagoon: Post-European changes and the design of water quality targets. *Marine Pollution Bulletin* **52**, 1467–1479.

Wooldridge, S.A. & Brodie, J.E. 2015. Environmental triggers for primary outbreaks of crown-of-thorns starfish on the Great Barrier Reef, Australia. *Marine Pollution Bulletin* **101**, 805–815.

Wooldridge, S.A. & Done, T.J. 2009. Improved water quality can ameliorate effects of climate change on corals. *Ecological Applications* **19**, 1492–1499.

Wootton, J.T. 1994. Predicting direct and indirect effects: An integrated spproach using experiments and path analysis. *Ecology* **75**, 151–165.

Wootton, J.T. 2002. Indirect effects in complex ecosystems: Recent progress and future challenges. *Journal of Sea Research* **48**, 157–172.

Wulff, J.L. 2006. Ecological interactions of marine sponges. *Canadian Journal of Zoology* **84**, 146–166.

Wulff, J.L. & Buss, L.W. 1979. Do sponges help hold coral reefs together. *Nature* **281**, 474–475.

Xu, Y., Ramanathan, V. & Victor, D.G. 2018. Global warming will happen faster than we think. *Nature* **564**, 30–32.

Yadav, S., Rathod, P., Alcoverro, T. & Arthur, R. 2016. 'Choice' and destiny: The substrate composition and mechanical stability of settlement structures can mediate coral recruit fate in post-bleached reefs. *Coral Reefs* **35**, 211–222.

Yahel, R., Yahel, G. & Genin, A. 2005. Near-bottom depletion of zooplankton over coral reefs: I: Diurnal dynamics and size distribution. *Coral Reefs* **24**, 75–85.

Yamaguchi, M. 1974. Growth of juvenile *Acanthaster planci* (L) in labratory. *Pacific Science* **28**, 123–138.

Yamano, H., Cabioch, G., Pelletier, B., Chevillon, C., Tachikawa, H., Lefevre, J. & Marchesiello, P. 2015. Modern carbonate sedimentary facies on the outer shelf and slope around New Caledonia. *Island Arc* **24**, 4–15.

Yamano, H., Kayanne, H., Matsuda, F. & Tsuji, Y. 2002. Lagoonal facies, ages, and sedimentation in three atolls in the Pacific. *Marine Geology* **185**, 233–247.

Yamano, H., Miyajima, T. & Koike, I. 2000. Importance of foraminifera for the formation and maintenance of a coral sand cay: Green Island, Australia. *Coral Reefs* **19**, 51–58.

Young, M.A.L., Foale, S. & Bellwood, D.R. 2014. Impacts of recreational fishing in Australia: Historical declines, self-regulation and evidence of an early warning system. *Environmental Conservation* **41**, 350–356.

Young, M.A.L., Foale, S. & Bellwood, D.R. 2015. Dynamic catch trends in the history of recreational spearfishing in Australia. *Conservation Biology* **29**, 784–794.

Young, M.A.L., Foale, S. & Bellwood, D.R. 2016. Why do fishers fish? A cross-cultural examination of the motivations for fishing. *Marine Policy* **66**, 114–123.

Young, R.F. & Winn, H.E. 2003. Activity patterns, diet, and shelter site use for two species of moray eels, *Gymnothorax moringa* and *Gymnothorax vicinus*, in Belize. *Copeia* 2**003**, 44–55.

Zambre, A.M. & Arthur, R. 2018. Foraging plasticity in obligate corallivorous Melon butterflyfish across three recently bleached reefs. *Ethology* **124**, 302–310.

Zeppel, H. 2008. Education and conservation benefits of marine wildlife tours: Developing free-choice learning experiences. *Journal of Environmental Education* **39**, 3–17.

Zhang, C.L., Xie, W., Martin-Cuadrado, A.-B. & Rodriguez-Valera, F. 2015. Marine Group II Archaea, potentially important players in the global ocean carbon cycle. *Frontiers in Microbiology* **6**, 1108.

Zhang, Y.S. & Silliman, B.R. 2019. A facilitation cascade enhances local biodiversity in seagrass beds. *Diversity* **11**, 30.

Zhang, Y.Y., McCook, L., Jiang, L., Lian, J.S., Liu, S. & Huang, H. 2018. An outbreak of sea cucumbers hinders coral recruitment. *Coral Reefs* **37**, 321–326.

Zubkov, M.V., Fuchs, B.M., Tarran, G.A., Burkill, P.H. & Amann, R. 2003. High rate of uptake of organic nitrogen compounds by Prochlorococcus cyanobacteria as a key to their dominance in oligotrophic oceanic waters. *Applied and Environmental Microbiology* **69**, 1299–1304.

**Supplementary Tables are provided online at** https://www.routledge.com/9780367367947