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### THE NORTH-EAST ATLANTIC MARGIN: A REVIEW OF THE GEOLOGY, GEOGRAPHY, OCEANOGRAPHY, AND VULNERABLE MEGABENTHIC ECOSYSTEMS OF THE CONTINENTAL SLOPE OF IRELAND AND THE UNITED KINGDOM

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# THE NORTH-EAST ATLANTIC MARGIN: A REVIEW OF THE GEOLOGY, GEOGRAPHY, OCEANOGRAPHY, AND VULNERABLE MEGABENTHIC ECOSYSTEMS OF THE CONTINENTAL SLOPE OF IRELAND AND THE UNITED KINGDOM

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**Abstract** The Irish–Scottish margin is geologically and oceanographically heterogeneous. Source waters of subpolar and subtropical origin interact with banks, seamounts, submarine canyon systems, escarpments, and mound provinces resulting in rich and diverse benthic communities that are influenced by local and regional hydrodynamics (e.g., internal waves, tides, and local turbulence). Reef habitats formed by the cold-water coral *Desmophyllum pertusum* are particularly well studied, such that controls on reef and mound formation are relatively well understood. The distribution of some other Vulnerable Marine Ecosystems (VMEs), such as sponge fields formed by *Pheronema carpeni*, and xenophyophore aggregations, is known due to both field observations and predictive modelling. Some VMEs are poorly known, for example, coral gardens, where in many cases even the characteristic species are not fully identified. The autecology of some component species has been studied, but for others, knowledge is almost completely lacking. The evidence for increased biodiversity associated with all these habitats is clear and all suffer anthropogenic impacts.

**Keywords:** Cold-water Coral Reefs; Sponge Aggregations; Coral Gardens; Deep Sea; Vulnerable Marine Ecosystems

## Introduction

Situated in the North-east Atlantic, the Irish–Scottish Continental Margin has been explored for nearly 150 years making it one of the most intensively researched deep-sea regions. Inspired by the cruises of Norwegian naturalist Michael Sars, Charles Wyville-Thomson, and William Carpenter

led multiple expeditions to the region on HMS LIGHTNING and HMS PORCUPINE between 1868 and 1870, recovering animals from dredges taken at depths of nearly 4500 m; this was a revolutionary finding because, at the time, it was widely believed that animals could not survive at those depths. The Challenger Expedition 1872–1876, a landmark research cruise also led by Charles Wyville-Thomson that traversed the globe, also sampled in Irish deep waters. Ireland and the United Kingdom (UK) have always had a well-developed interest in the deep sea, with the Fisheries Division of the Department of Agriculture in Ireland publishing articles and monographs on the corals and sponges collected offshore during numerous expeditions. Examples include Hickson's account of the Coelenterata from the West of Ireland (Hickson 1905) which included the first account of antipatharian (black coral) species in Irish waters as well as Stephens' monographs on sponges (Stephens 1915, 1921) and corals (Stephens 1909). In 1909, the Liverpool Tidal Institute was established and began its tradition of deep-sea research in the study area. This organisation would eventually become one of the amalgamated institutes that is currently recognised as the National Oceanography Centre (NOC). In more recent times, technological advances have revolutionised deep-sea research. RV CELTIC EXPLORER was commissioned as an Irish national research vessel in 2003, followed by Remotely Operated Vehicle (ROV) HOLLAND I in 2008 and RV TOM CREAN in 2022, providing three platforms with deep-sea capabilities. Research in the region has also been carried out for over a decade by UK vessels RRS JAMES COOK and RRS DISCOVERY supported by ROV ISIS and the Autonomous Underwater Vehicles AUTOSUB6000, AUTOSUB5, and AUTOSUB LONG-RANGE in addition to other equipment from the large Marine Autonomous and Robotic Systems fleet at the NOC. Many other European nations have also worked in the region.

The Irish–Scottish Margin is also geographically extensive: it is estimated that there is more than 175,000 km<sup>2</sup> of seabed at water depths of 800–3000 m in Irish waters alone. It is also geologically heterogeneous, with a wealth of seabed features including volcanic seamounts, submarine canyons, and escarpments. The interaction of this unique topology with various water masses results in an area with complex oceanography. The presence of two large shallow banks, Porcupine and Rockall, above the permanent thermocline leads to high primary productivity along the shelves, which cascades down the slope to benthic communities. Along-shelf and cross-slope currents and internal waves are among the hydrographic features that interact to produce areas of increased current speed that promote the resuspension and transport of organic material. Conditions have combined to produce a high density of cold-water coral carbonate mounds and remarkable bathyal diversity, which is, in part, driven by large areas of '*Lophelia*'<sup>1</sup> reef and other habitat-forming megabenthic species.

Scientific advances in our understanding of the Irish–Scottish margin are extensive, in part due to the very rich history of research which continues to the present, but they tend to be disseminated through disparate specialist journals, although there have been previous efforts to synthesise the relevant literature pertaining to some habitats, particularly with respect to cold-water corals (e.g., Roberts et al. 2009) and submarine canyon systems (e.g., Amaro et al. 2016). Herein, our aim is to provide a synthetic overview of the region that emphasises the importance of geological and oceanographic knowledge in understanding deep-water megabenthic biodiversity and which examines benthic diversity and distribution patterns in the light of that knowledge. We focus on benthic slope habitats within the Exclusive Economic Zones (EEZs) and Extended Continental Shelves (ECSs) of the Republic of Ireland and the UK, but limited to areas where deep bottom water is of Atlantic origin, an area of direct policy relevance for offshore habitats. Geographically, our scope extends from the Wyville-Thomson Ridge and Anton Dohrn Seamount in the north to the southern edge of Whittard Canyon in the south and includes all of the Rockall and Hatton Banks to the west, corresponding to a broadly consistent biogeographical region.

In our review, we first provide a geological framework, introducing major geographic landmarks and seabed features, followed by an overview of basin-scale oceanography, including water mass structure and circulation and dynamics. We examine the biophysical interactions that drive the development of some of the unique biogenic habitats and then provide a more detailed description

of the northern and southern parts of the focal area. For the biology, we focus on megabenthic Vulnerable Marine Ecosystems (VMEs), in each case exploring their distributions, the autecology of component species, the increased biodiversity associated with these habitats, and the anthropogenic impacts upon them, and we summarise the legislation protecting these habitats. We briefly consider megabenthic habitats outside of VMEs and examine megabenthic biodiversity trends where sufficient data exist. Finally, we consider key research gaps and how best these could be resolved.

## Geography and geology

Continental margins are areas with predominantly gentle but consistent slopes extending from the shelf break (the seaward limit of the continental shelf) down to the change in slope marking the continental rise and abyssal plain. They typically occupy water depths of 200–5000 m. They receive sediment from across-shelf sediment transport processes which may be reworked by along-slope contourite currents and can be incised by submarine canyons and be subject to episodic slope failures, and in some places, very significant turbidity currents (e.g., Whittard Canyon system, Heijnen et al. 2022). They host pelagic and benthic fauna throughout their depth range corresponding to intermediate to deep-water mass depths (mesopelagic to abyssopelagic fauna and bathyal to abyssal benthos), with nutrient supply potentially affected by upwelling and downwelling oceanographic processes (Dickson et al. 1980, O'Reilly et al. 2022b).

The North-east Atlantic continental margin of Europe stretches for a geodesic distance of approximately 4000 km from the south of Spain to northern Norway and encompasses the Irish–Scottish margin (south of the Wyville-Thomson Ridge). This underappreciates the true extent of the Irish–Scottish margin, which is much longer as measured by tracing along the margin (~5500 km), as it is heavily embayed and encircles large banks of submerged continental crust and seamounts.

This conjunction of influences leads to high environmental heterogeneity which is a key factor in explaining the rich biodiversity of this margin. The geological and geographical factors controlling, and the features inherent within, this environmentally heterogeneous setting are detailed below.

### *Irish–Scottish margin development*

The geological development of the Irish–Scottish margin has a strong control on benthic environment heterogeneity. At a broad scale, the formation of rifted sedimentary basins, isolated horst-block highs, and volcanic seamounts provides a diverse margin distinct from its southern and northern European counterparts.

The breakup of the Pangaea supercontinent ca. 225 million years ago led to the opening of the Atlantic (Schettino & Turco 2009). Crustal thinning resulted in volcanism during the Carboniferous which may have produced the southern edifices of the Fangorn and Edoras Banks although no dated samples have proven this. Continued crustal extension created the numerous rift basins (including the Porcupine Seabight, Rockall Trough, and Hatton Basin) and intervening horst-block highs (including the Porcupine, Rockall, and Hatton Banks) that dominate the Irish and southern Scottish margins (Shannon et al. 2001). During the Cenozoic, the Iceland Plume volcanic hotspot was situated under Northern Ireland and western Scotland resulting in the formation of a series of seamounts (or submarine volcanic complexes: Rosemary, George Bligh, and Anton Dohrn Banks) as well as the Wyville-Thomson Ridge.

Erosion of the rifted margin possibly started in the Triassic forming subaerial gullies which may then have developed into submarine canyons following marine flooding of the proto-Atlantic rift valley. Continued erosion, through tidal pumping and turbidity current scouring, has resulted in major margin incisions to form submarine canyons. Submarine canyons are better developed in the southern Irish Margin where they are not heavily infilled by glacially derived sediments.



Pleistocene glaciation has had a major impact on the margin, especially in the west and north, but also to the south via across-shelf fluvio-glacial sediment supply into submarine canyons. The limits of the British-Irish Icesheet, which extended on to the Scottish and Irish shelves, have been the focus of several studies (Wilson & Austin 2002, Ó Cofaigh et al. 2012, 2019, Praeg et al. 2015, Peters et al. 2015, 2016, Small et al. 2017, 2018, Callard et al. 2018, 2020, Chiverrell et al. 2018, Wilson et al. 2018, Scourse et al. 2019, Tarlati et al. 2020, Benetti et al. 2021). On the western Irish and UK shelf, the British-Irish Icesheet reached its maximum extent between 29 and 23 ka (Ó Cofaigh et al. 2012, Peters et al. 2015) before finally retreating by 15 ka (Clark et al. 2012) after a complex succession of readvances and retreats (McCabe & Clark 1998, Ó Cofaigh et al. 2012, Peters et al. 2016, Ballantyne & Ó Cofaigh 2017). At approximately 20 ka on the Hebridean and western Irish Margins, the British-Irish Icesheet extended right up to the shelf break (Peters et al. 2016) with the Barra Fan Ice Stream delivering significant sediment on to the Barra-Donegal Fan. After 6 ka, from the Porcupine Bank and northern Porcupine Seabight south and out into the Rockall and Hatton Basins, the margin was ice free although impacted by the significant quantities of icebergs which dropped clay-grade rock flour to boulder sized ice-rafted debris (IRD) over the entire margin as they melted. Icebergs were also grounded on the seabed producing iceberg plough marks down to 580 m water depth (Dorschel et al. 2010).

Sedimentary and postglacial sea-level rise loading of the margins, especially north of the Porcupine Bank (Figure 1), has led to margin collapse leaving slide scarps with steep headwalls and debrite-turbidite sedimentary aprons extending out into the deeper basins, e.g., the Peach Slide (Owen et al. 2018) and Rockall Slide (Georgiopoulou et al. 2013).

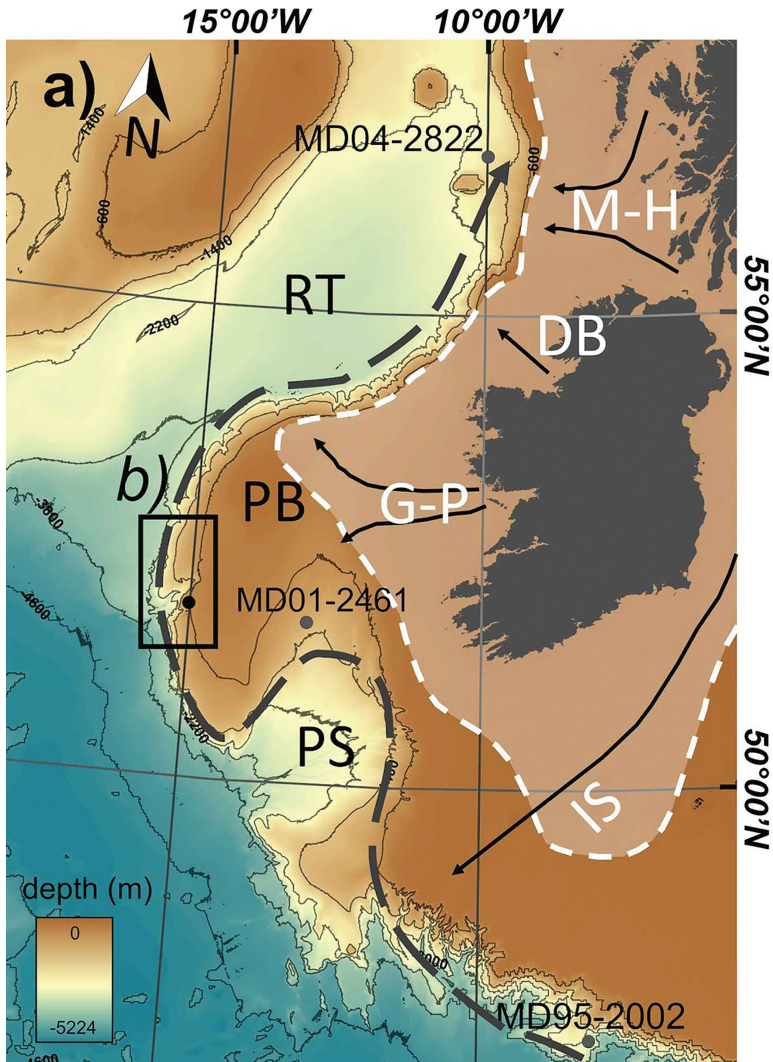
Consequent changes in cross-shelf sediment supply and a rise in sea levels were caused by the retreat of the icesheets; palaeoceanographic changes also included increased current speeds. Today, vigorous currents and a reduced sediment supply across much of the margin have left many IRD dropstones exposed as sites for sessile epifauna colonisation (Wheeler et al. 2005a). Active along-slope contour currents have resulted in sediment wave fields and the continued development of contourites, e.g., on the eastern Porcupine Seabight margin (van Rooij et al. 2009). Erosive sediment regimes persist on the Goban Spur and Porcupine Bank (Dorschel et al. 2009), whereas further north fine-grained hemipelagic sedimentation prevails.

Sediment supply decreases with distance from the shelf, and the Rockall Bank, Hatton Basin and Bank, and seamounts receive considerably less sediment than the shelf-contiguous margin. Strong current on top of the seamounts and the detached margin has resulted in coarse-grained IRD-dominated seafloors with hardgrounds in places (Wheeler et al. 2005a).

### *Geography of the Irish–Scottish margin*

The southern European Atlantic margin is dominated by submarine canyons, several of which connect directly to river systems, e.g., Setúbal Canyons (de Stigter et al. 2007, Arzola et al. 2008, Tyler et al. 2009); others may have connected to river systems during glacial sea-level low stands, e.g., on the Armorican margin (Toucanne et al. 2015). The northern European Atlantic margin morphology is heavily influenced to a much higher degree by sediment delivery from the former Europe icesheets. This has, in places, oversteepened the margin resulting in submarine slides of which the scalloped slide headwalls are a common feature (Taylor et al. 2003). The Irish–Scottish margin occupies a unique setting at the transition between these two domains and exhibits features akin to both glaciated and non-glaciated margins. It is a tectonically passive margin at present although the influence of past tectonics is apparent in some of its configurations.

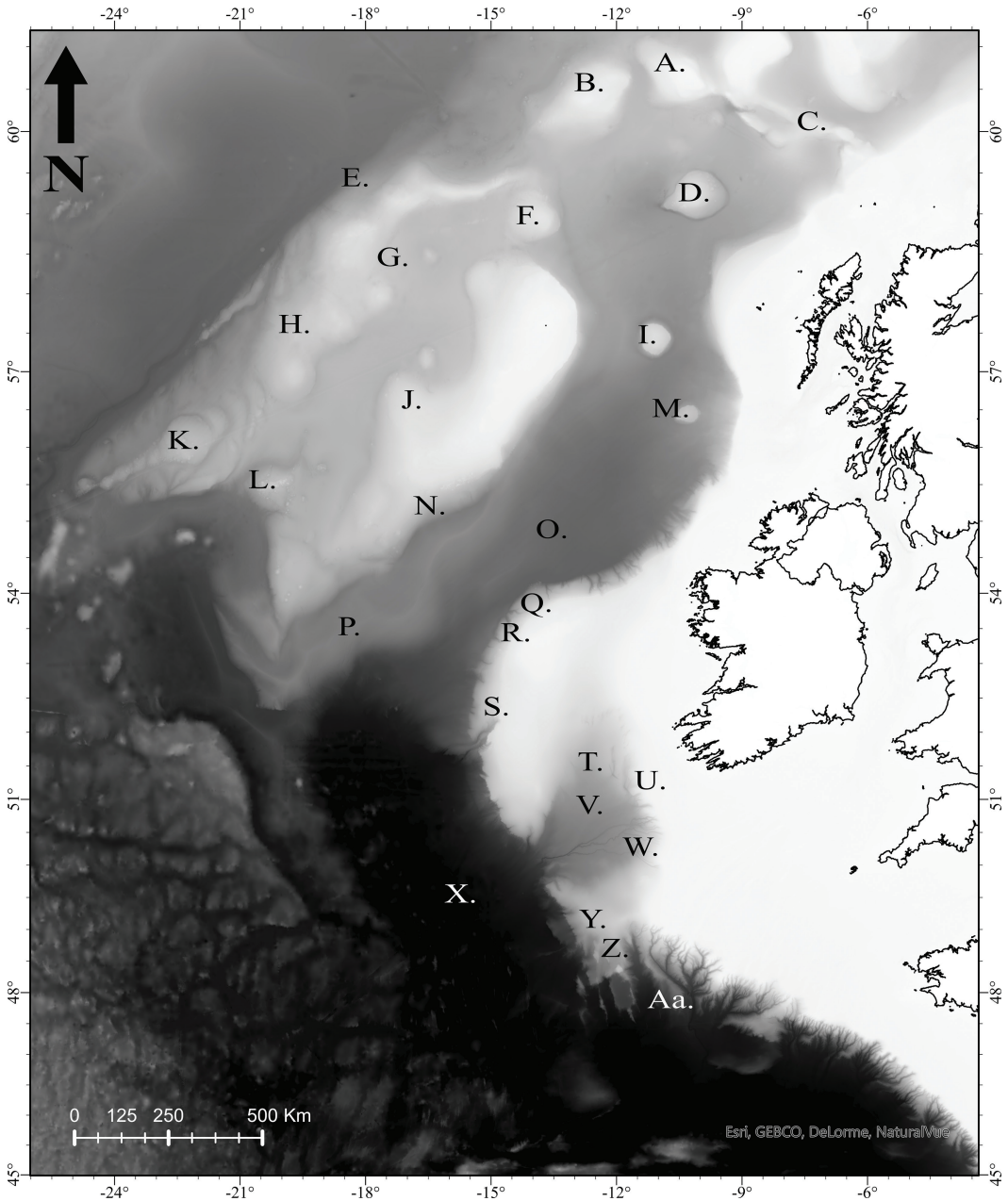
The Irish–Scottish continental margin can be divided into several geographic areas (Figure 2). The northernmost part of the margin is the Hebridean Margin which extends from the Wyville-Thomson Ridge, which forms the northernmost boundary of the Rockall Trough, to the Irish-UK border at the Barra-Donegal Fan. This part of the margin is contiguous with the Hebridean shelf.



**Figure 1** Map of the Irish–Scottish continental margin showing the configuration of the British-Irish Icesheet at the Last Glacial Maximum (white dashed line) based on BRITICE-CHRONO reformulation. (After Roberts et al. 2020, Ó Cofaigh et al. 2021.) Maximum ice extent offshore from western Ireland are likely reached at ~26–24 ka (calibrated thousands of years before present). M-H - Malin-Hebrides, DB - Donegal Bay, G-P - Galway-Porcupine, IS – Irish Sea; PS, Porcupine Seabight; PB, Porcupine Bank; RT, Rockall Trough (visualised using ArcGIS Desktop v10.6) ([www.arcgis.com](http://www.arcgis.com)). (General Bathymetric Charts of the Oceans ([gebco.net](http://gebco.net)) from O’Reilly et al. (2022a).)

Westward of the margin, rising from the floor of the Rockall Trough are a number of seamounts whose flanks fall within the depth zone typically ascribed to the continental margin. From north to south these are Bill Bailey’s Bank, Lousy Bank, Rosemary Bank, George Bligh Bank, Anton Dohrn Seamount, and the Hebrides Terrace Seamount (Figure 2) and are included in this review.

The western Irish Margin extends southwards from the Barra-Donegal Fan and in the south-west broadens where it becomes the Porcupine Bank. Geologically, the Porcupine Bank is a horst block rifted from the island of Ireland with the intervening graben now infilled by shelf sediment (the Slyne Basin, Shannon et al. 2001) to form a continuous margin which extends around the west, south, and east of the Bank and into the Porcupine Seabight. The western Porcupine Bank margin

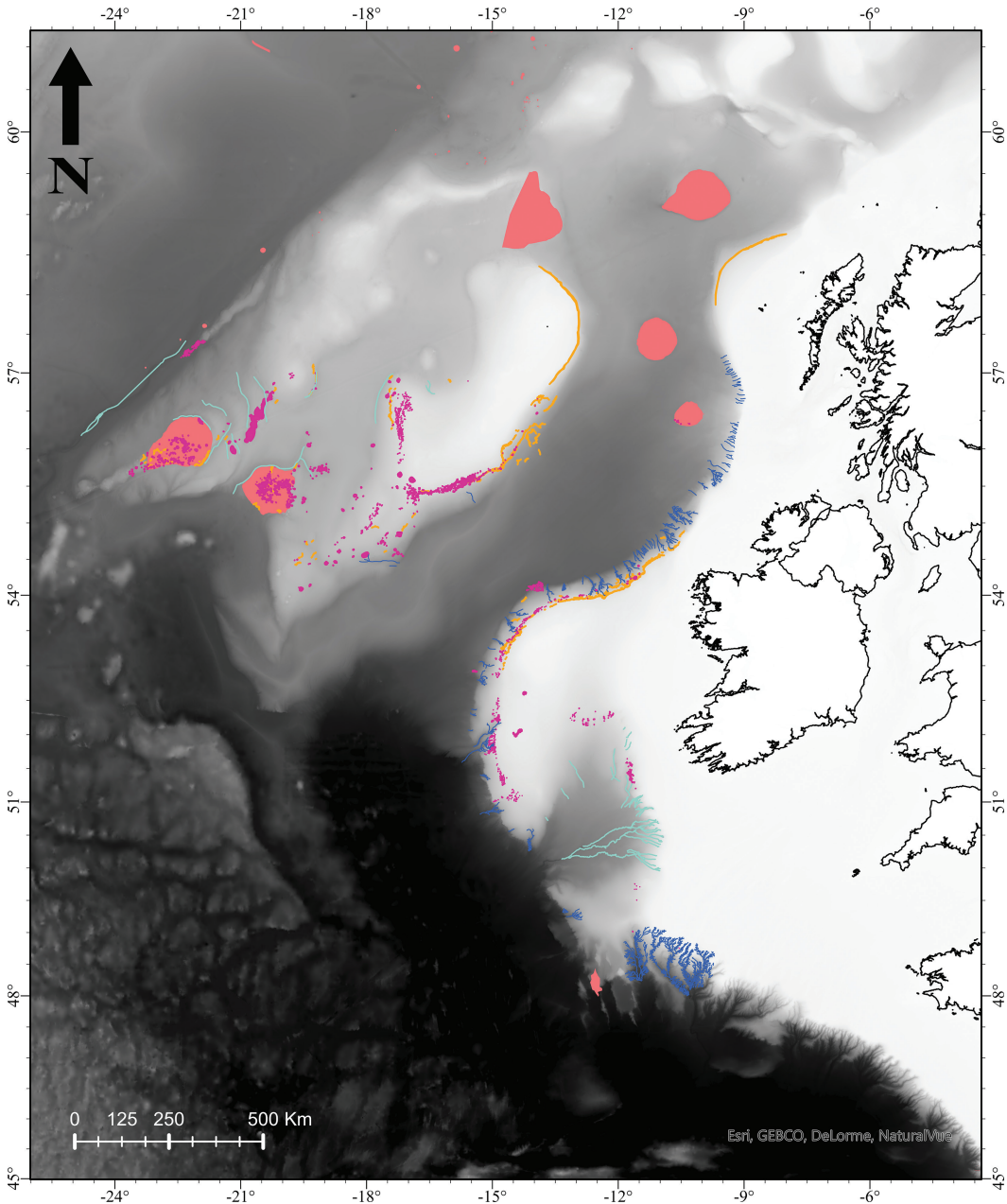


**Figure 2** Extent of the Irish–Scottish margin. A. Bill Bailey Bank; B. Lousy Bank; C. Wyville-Thomson Ridge; D. Rosemary Bank; E. Hatton Bank; F. George Bligh Bank; G. Hatton-Rockall Basin; H. Hatton Bank; I. Anton Dohrn Seamount; J. Rockall Bank; K. Edoras Bank; L. Fangorn Bank; M. Hebrides Terrace Seamount; N. Logachev Mound Province; O. Rockall Trough; P. Feni Ridge; Q. Porcupine Bank; R. Pelagia Mound Province; S. Western Porcupine Bank Mounds; T. Hovland Mound Province; U. Belgica Mound Province; V. Porcupine Seabight; W. Gollum Channel; X. Porcupine Abyssal Plain; Y. Goban Spur; Z. King Arthur Canyon; Aa. Whittard Canyon system. Map visualised using ArcGIS Pro v 2.8 (Esri Inc. 2020).



## THE NORTH-EAST ATLANTIC MARGIN

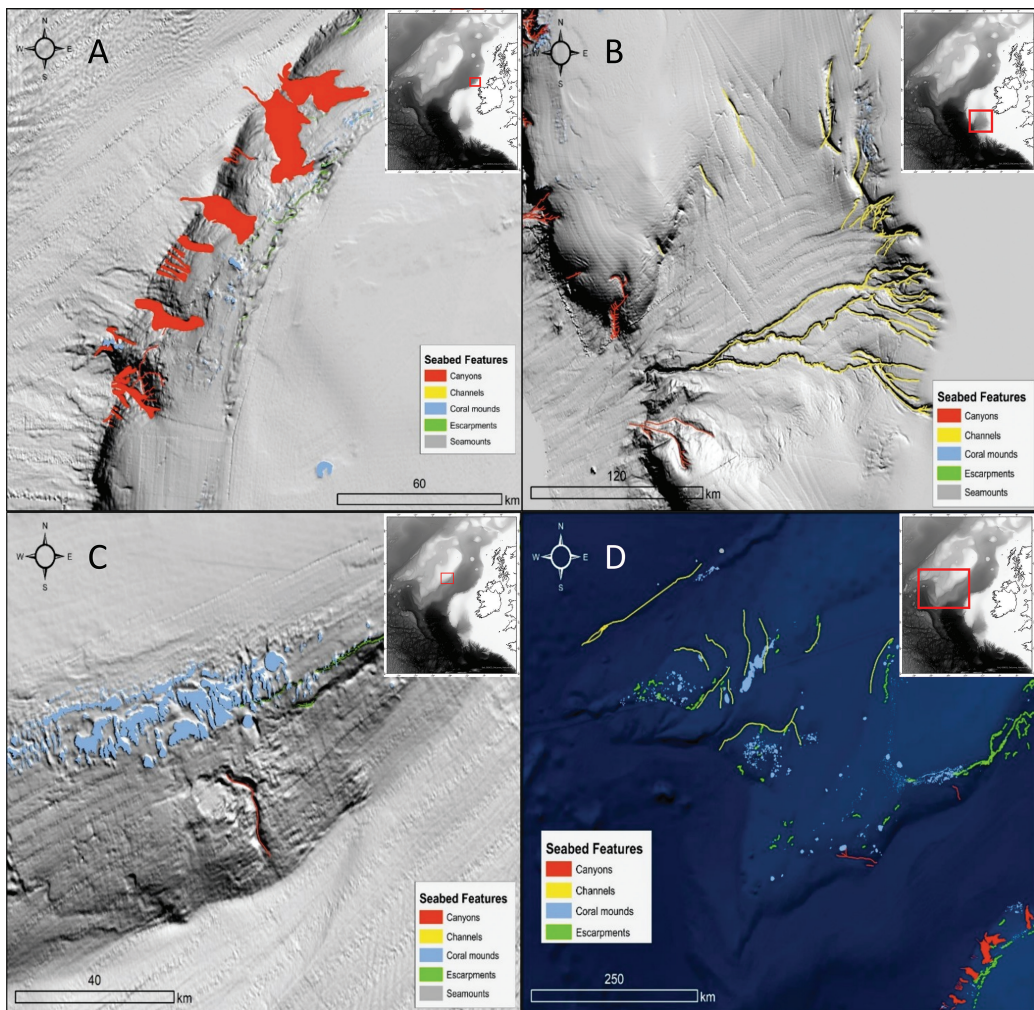
has well-developed submarine canyons (Dorschel et al. 2010, Lim et al. 2020) (Figure 3) with strong contouritic current flows, whereas the eastern margin has a smooth topography due to a thicker sediment cover. Giant cold-water coral carbonate mounds exist on the bank, for example, the Pelagia Mounds (Van Weering et al. 2003) (Figure 2).



**Figure 3** Distribution of canyons (blue), channels (green), escarpments (orange), coral mounds (purple), and seamounts (peach) within the focal area. (ESRI, EMODNET, Dorschel et al. (2010) and the present study. Although classified as a channel system in the EMODNET database, Murphy & Wheeler (2016) found that the Gollum Channel systems fit the definition of a canyon system. Map visualised using ArcGIS Pro v 2.8 (Esri Inc. 2020).)

The Porcupine Seabight is a large embayment cutting into the margin and represents the as yet unfilled remnants of the bigger Porcupine Basin graben. The seabight extends 200 km east to west and 330 km north to south, surrounded by continental margin containing giant cold-water coral carbonate mounds (Figure 4C), including the Hovland Mounds (Huvenne et al. 2005) and Belgica Mounds (Wheeler et al. 2005b), as well as the smaller Moira Mounds (Wheeler et al. 2011). It has an extensive drainage network (Murphy & Wheeler 2016) including the longest Irish submarine canyon, the Gollum Channel (Wheeler et al. 2003). Murphy & Wheeler (2016) found that this channel, which is named as a channel on public databases, has the characteristics of a canyon.

The mouth of the Porcupine Seabight is constrained by the Porcupine Bank to the north-west and the Goban Spur to the south-east. The southern Goban Spur is relatively short (100 km) and runs



**Figure 4** Distribution of canyons, channels, coral mounds, escarpments, and seamounts along (A) the shelf break of the Porcupine Bank; (B) within the Porcupine Seabight and (C) at the Rockall Bank. (D) Large-scale map of the Edoras and Fangorn Volcanic complexes.

into the Southwest Approaches marked by extensive submarine canyon development that continues on to the southern UK and French margins. The continental slope south–south-west of Ireland includes King Arthur Canyon (Hall & McCave 1998) and the multibranching Whittard Canyon system (Amaro et al. 2016) (Figure 2).

West of the shelf-contiguous Irish Margin are two large banks: Rockall Bank, and further west Hatton Bank, which, like the Porcupine Bank, are horst-block continental crust highs separated by graben basins (Stoker et al. 2001). The Rockall Bank also contains the Logachev Mounds, a giant cold-water coral carbonate mound province (Kenyon et al. 2003). South-west of the Hatton Basin is the Fangorn Bank volcanic complex with the Edoras Bank volcanic complex further west again (Figure 2, Figure 4D)

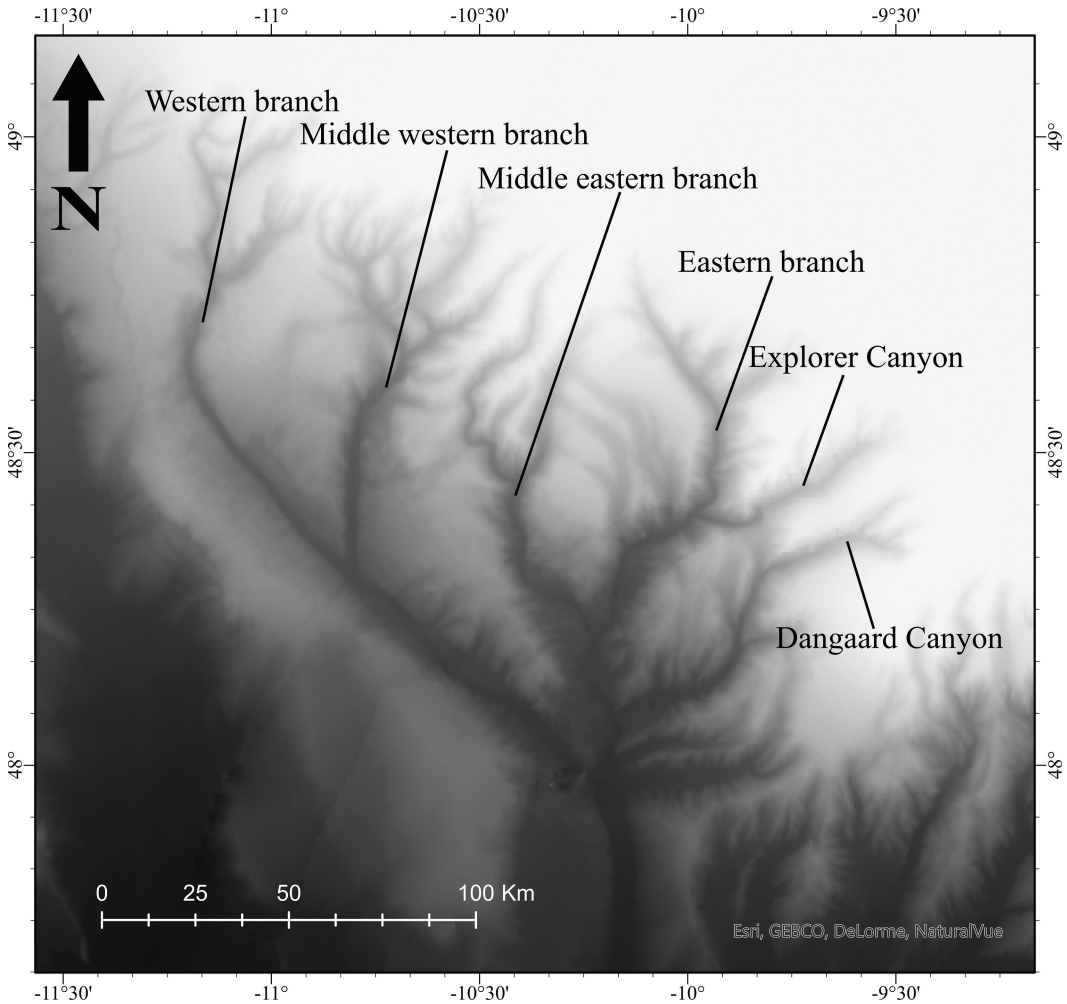
Between the western Scottish and Irish Margins and western Porcupine Bank margin lies the Rockall Trough, another partially infilled graben basin. This contains the Feni Drift (Faugeres et al. 1981), a contourite drift, as well as the previously mentioned northern seamounts. Also in the north are the Darwin Mound cold-water coral mounds (Masson et al. 2003) (Figure 2).

### *Submarine canyons and channels*

Submarine canyons are elongate, steep-sided geomorphic features commonly incised into continental shelves and slopes globally (Shepard 1972), that are the focal point of sediment transport from the continental shelf on to the abyssal plain (Nittrouer & Wright 1994). Submarine canyons are generally oriented perpendicular to the continental slope with canyon type largely controlled by the characteristics of the host continental margin: active margins have a higher density of canyons which are also relatively steep, while passive margins tend to host fewer canyons (Harris & Whiteway 2011). Canyons form as the result of downward erosion cutting into the shelf which can be traced back to tributaries nearshore (Pratson et al. 1994). Submarine canyons can sustain large quantities of biomass and create diverse habitats along continental slopes (de Leo et al. 2010). Like their subaerial equivalents, submarine channels are long, meandering systems that form as a result of both erosional and depositional processes on the seafloor (Deptuck & Sylvester 2018) with channel development directly linked to erosion by turbidity currents (e.g., Maier et al. 2019, Heijnen et al. 2022). These processes form a channel that may eventually confine the flow itself and have both erosional and depositional sections (Hodgson et al. 2022).

Of the 5849 submarine canyons known globally (Harris & Whiteway 2011), 148 or 2.5% are within the study area. On the Irish Margin, canyon limits are interpreted here as occurring at 200–3800m water depth. This relatively wide bathymetric distribution is unsurprising, given that their occurrence is not depth-restricted and that they incise through the full continental slope. There are two submarine canyon systems of note within the study area: the Porcupine Bank Canyon and the Whittard Canyon system. The Porcupine Bank Canyon, found on the western edge of the Porcupine Bank, is a tectonically controlled canyon with two contrasting canyon flanks. The eastern flank is characterised by near-vertical slopes and extensive bedrock, while the western flank is gently sloping and dominated by sediment (Appah et al. 2020, Lim et al. 2020). The canyon overall is a single large canyon system and is oriented north-east to south-west, oblique to the slope, and different from the orientation of neighbouring canyons. By contrast, the Whittard Canyon is a dendritic system with multiple branches converging into a single channel leading on to the abyssal plain. Whittard Canyon is composed of four main steep-sided branches that connect to the shelf at approximately 200m water depth and merge into a main channel named the Whittard Channel at 3500m (Amaro et al. 2016) which exits into the Celtic Sea fan at approximately 4500m water depth. Throughout this review, we will refer to the branches of the Whittard Canyon system by the names used by Amaro et al. (2016); from west to east, the branches are the western, middle western, middle eastern, eastern, Explorer, and Dangaard (Figure 5).





**Figure 5** The dendritic Whittard Canyon system showing the four major branches (western, western middle, eastern middle, eastern) and two smaller canyons (Explorer and Dangaard). Map visualised using ArcGIS Pro v 2.8 (Esri Inc. 2020).

North of the Whittard Canyon system, submarine canyons occur continuously along the Porcupine Bank slope until the Hebrides Terrace Seamount. Here, and further north, no clear and obvious submarine canyons can be observed in the available bathymetric data which could be related to the considerable decrease in slope angle. However, INFOMAR high-resolution bathymetry (25 m gridded resolution, Dorschel et al. 2010) does not extend into this area, and thus, data quality may impact our ability to identify seabed features here. The Gollum Channel system (Figure 4B), one of the most striking features of the Irish Margin and one of the oldest studied submarine channel systems (Berthois & Brenot 1966, Tudhope & Scoffin 1995, Wheeler et al. 2003, Murphy & Wheeler 2016), is located approximately 100 km south-west of Ireland and is spread over 250 km along the Porcupine Seabight (Figure 2). The channel system is made up of many relatively low-sinuosity branches that dendritically merge into a single channel deeper in the Porcupine Seabight that eventually exits on to the Porcupine Abyssal Plain (Murphy & Wheeler 2016). Sediments are largely transported through this area via turbidity currents (van Rooij 2004).

### *Escarpmments*

Submarine escarpments, also referred to as scarps, can form as a result of either erosion by strong benthic currents, such as contour currents, or through the detachment of large blocks of sediment from the edge of the continental shelf. These blocks of sediment flow with gravity down the continental slope and are known as submarine landslides (slumps or slides). The ‘scar’ or steep-sided contour-parallel feature remaining at the top of the slope is named an escarpment. Escarpments have long been known to occur on the Irish Margin (Day 1958), where they exist as pronounced step-like features on the continental slope. Escarpments can be found on the eastern Rockall Bank at 750m and 1400m (Figure 3), while they are found at much shallower depths, 600–650m, on the western Porcupine Bank, where they can extend horizontally for approximately 120km. They are near-vertical and can extend over a depth range of greater than 100m. Images from these areas, taken during ROV surveys, show that escarpments can be suitable substrata for sessile filter- and suspension-feeding organisms due to the strong currents usually associated with these features (Dorschel et al. 2010). Given the processes required to form them, escarpments can act as indicators for slope stability and benthic currents in remote parts of the ocean.

### *Cold-water coral mounds*

The most well-studied cold-water coral mounds globally are found in the North-east Atlantic (Lim et al. 2021). These are mound-shaped features that form as the result of complex interactions between framework-forming cold-water corals, commonly *Desmophyllum pertusum* and *Madrepora oculata*, hydrodynamics, and sediment supply (Roberts et al. 2006). Given their widespread occurrence on the Irish Margin, these have since been divided into coral-mound provinces: the Belgica Mounds, the Hovland Mounds, the Pelagia Mounds, and the Logachev Mounds (de Mol et al. 2002, Wheeler et al. 2007) (Figure 2). Their typical morphology is conical and elongates in the direction of the strongest current (Dorschel et al. 2007b). They range in size from 380m (Mienis et al. 2006) to 3m (Lim et al. 2018a) in height, from base to summit, and can extend lengthways for several kilometres (Dorschel et al. 2009). Cold-water coral mounds exist on the Porcupine Bank, Rockall Bank, Porcupine Seabight, and as far west as the western flanks of the Hatton Bank (Wienberg et al. 2008) and are concentrated in 600–1000m water depth in the focal area. This is unsurprising given the presence of suitable water mass boundaries at these depths which enable enhanced food supply to cold-water corals (White 2007). The depth distribution of coral mounds is similar to that of escarpments, whose formation is also related to enhanced benthic currents. However, the sediment baffling ability of dense coral frameworks allows for the deposition of sediments rather than erosion (Wheeler et al. 2008).

The Belgica Mound Province occurs on the eastern flank of the Porcupine Seabight and hosts some of the largest known coral mounds, including the Challenger Mound (Kano et al. 2007, Thierens et al. 2013), the Galway Mound (Dorschel et al. 2007a), and the Therese Mound (de Mol et al. 2007), as well as the smallest mounds, known as the Moira Mounds (Wheeler et al. 2005b). These smaller mounds are quite dynamic, and despite being over 11 thousand years old, showed changes in sediment facies and species abundance over a 4-year period in repeat photogrammetric mapping (Lim et al. 2018b, Boolukos et al. 2019).

On the Rockall Bank, cold-water coral mounds have distinctly different morphologies. On the south-east margin (Porcupine Bank), mounds occur as single isolated mounds, while on the south-west margin (Rockall Bank), mounds occur as extensive clusters (de Haas et al. 2009). While the Whittard Canyon hosts cold-water coral, it is not known for extensive and large coral mounds, but there are some mini-mounds (Stewart et al. 2014, Price 2021).

On the north-west Porcupine Bank, many complex and unusual forms of coral mounds exist where they have formed under erosive conditions: an environmental gradient of increasing current speed. It is thought that beyond an unspecified current-speed threshold, coral framework can no longer baffle sediment to form mound features. This is evidenced by the presence of escarpments and scours (Dorschel et al. 2009). Furthermore, *in situ* current-speed measurements of almost 100 cm s<sup>-1</sup> show that this framework is subject to physical erosion (Lim et al. 2020).

### *Seamounts*

When large quantities of typically basaltic magma ascend through the overlying lithosphere and erupt on the seabed, prolonged volcanism may eventually form large edifices called seamounts. They are large dome-like topographic features on the seabed (Staudigel & Clague 2010) and can be well over 1000 m in height, several kilometres in diameter, and often equidimensional (Hillier & Watts 2007). They often arise from abyssal plains where the surrounding seabed is relatively featureless and, given their topography, can accelerate passing currents or possess circulatory Taylor Columns that trap and concentrate nutrients on their summits (White et al. 2008). This, coupled with their increased elevation, can create suitable habitat for benthic and near-bottom dwelling organisms in otherwise relatively sparse parts of the ocean (Rogers 2018). Seamounts in the North-east Atlantic have been studied for a long time, in particular at the Rockall-Hatton Basin (Roberts 1971) where gravity and magnetic data were used to infer their size and composition. It is thought that the Lousy Bank, Bill Bailey Bank, George Bligh Bank, Rosemary Bank, Anton Dohrn Seamount, and Hebrides Terrace Seamount (Figure 2) are all seamounts formed as volcanic edifices during the late Cretaceous–early Palaeogene (Stoker & Hitchen 2003) as a result of the migration of the Iceland Plume, which is also responsible for the formation of the Antrim Basalts and Faeroe Islands. These volcanic seamounts occur in the northern Rockall Trough (UK margin); there are no volcanic seamounts in Irish waters. Although the Edoras and Fangorn Banks are volcanic in origin, they are not technically classed as seamounts based on their geomorphological attributes. Ireland, however, does possess one small topographic rise on the southern tip of the Goban Spur (as yet unnamed) that is of sufficient elevation and steepness to be classified morphologically as a seamount. It is a tectonic detached sliver of continental crust at the foot of the continental rise. In the focal area, seamounts are most common in the Rockall Trough with summits at water depths of 500–1200 m (Figure 2), diameters of approximately 70–230 km, and although broadly dome-shaped, can be elongated, likely in the direction of tectonic plate movement over the hotspot.

## **Oceanography and hydrology**

### *Regional overview*

#### *Water mass structure*

The continental margin of the focal area lies at the eastern fringe of the main North Atlantic gyre systems, with the northern portion lying in the subpolar realm and the southern area being between the subpolar and subtropical gyres. It is an important pathway for warm, saline waters to polar regions and there is significant influence of the basin-scale ocean climate dynamics on both water properties and regional circulation across a vast range of timescales (e.g., Kuyppers et al. 1998, Johnson & Gruber 2007). For clarity, we have adopted a uniform broad description of the water masses in the region (Table 1).

The water masses and water column properties in the region are determined by the advection, transformation, and competition of source waters with both a subpolar and subtropical origin (Brambilla & Talley 2008), which undergo both seasonal and interannual variability (Holliday et al. 2008, Sherwin et al. 2012). Upper layer waters at depths <700 m above the permanent thermocline (700–1200 m) are sourced from two regions. These are the more saline Eastern North Atlantic Water (ENAW) from the south, formed at the eastern margin of the subtropical gyre (Pollard et al. 1996) and cooler, fresher Western North Atlantic Water (WNAW) associated with transport from the west via the North Atlantic Current (Pérez et al. 1995, Holliday 2003). To the north of the Porcupine Bank, mixing processes result in a more homogenous water mass (Modified North Atlantic Water, MNAW), which provides a pathway for warm, saline water to Nordic Seas via the northern Rockall Trough (e.g., Holliday et al. 2000, 2008). At the permanent thermocline depth range, fresher, shallower Sub-Arctic Intermediate Water (SAIW) subducts under the North Atlantic Current from the subpolar gyre to the west, while from the southern subtropical Atlantic, warm,

**Table 1** Water masses present within the focal area of the North-east Atlantic Margin

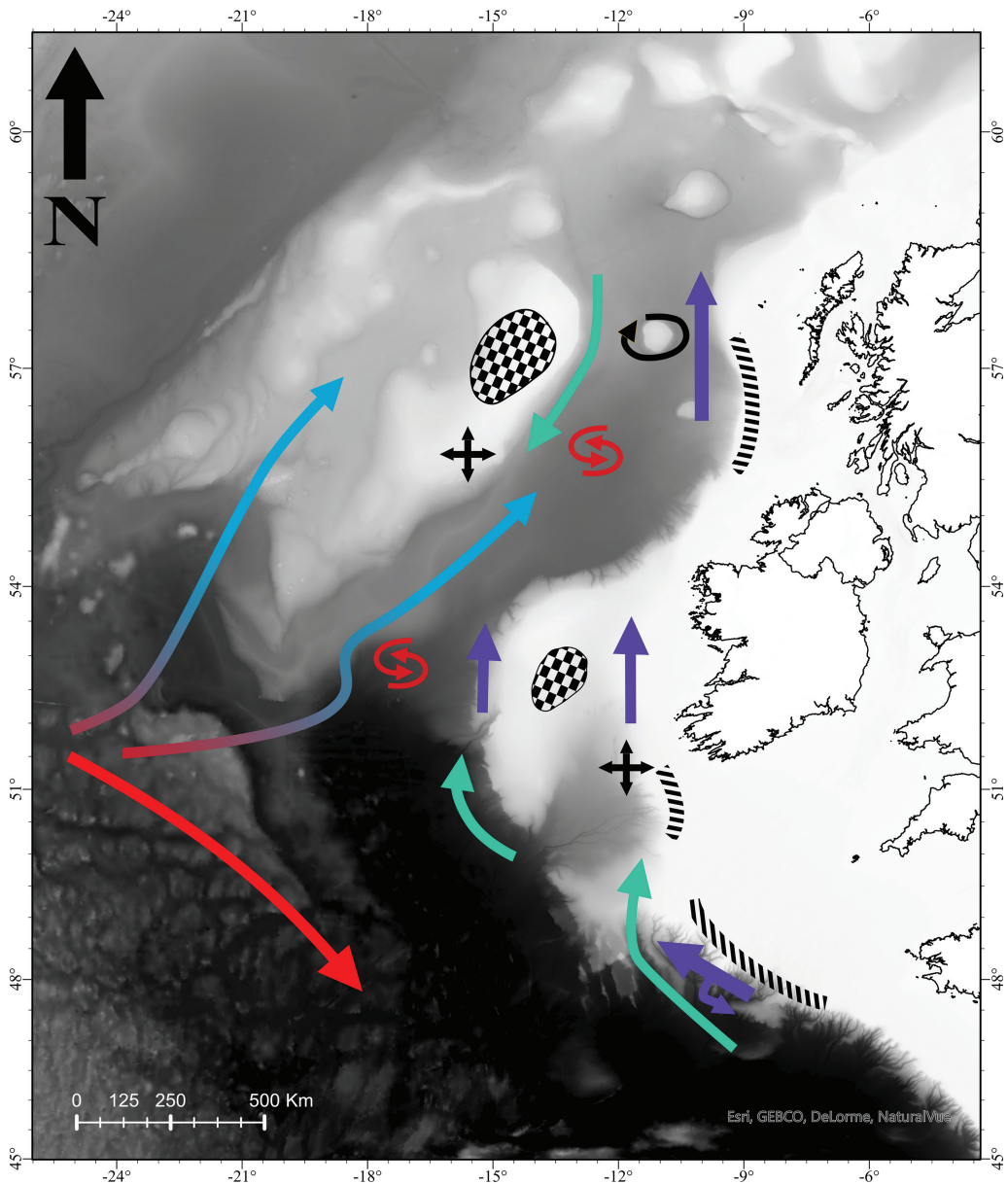
	Water Mass	Acronym	Approximate Depth (m)	Notes
Upper layers	Eastern North Atlantic Water	ENAW	100–600 throughout southern region	Temperature/Salinity maximum associated with European Slope Current at margin.
	Western North Atlantic Water	WNAW	Western periphery	Colder/fresher than ENAW and associated with the North Atlantic Current.
	Modified North Atlantic Water	MNAW	100–600 in the northern region	Dilution of ENAW with other surface and upper thermocline waters through mesoscale and winter mixing.
Thermocline Waters	Sub-Arctic Intermediate Water	SAIW	600–1000	Mostly west of 18°W and Rockall Bank. Salinity minimum.
	Mediterranean Outflow Water	MOW	800–1300	Influence north of Porcupine Bank uncertain but likely diminished. Salinity maximum, reduced oxygen.
	Wyville-Thomson Overflow Water	WTOW	600 – 1200 Also, an intermittent deeper core 1200 – 1500 (WTOWL)	If present, it will be evidenced as a mid-depth inflection point on the mixing line in a TS plot.
Deeper waters	Labrador Seawater	LSW	1500 – 2200	Salinity minimum, high oxygen.
	North Atlantic Deep Water	NADW	Greater than 2400	Weak presence between LSW and deepest waters with increased salinity from LSW minimum.

saline Mediterranean Outflow Water (MOW) enters the southern region and circulates north-westwards into the subpolar gyre. Both SAIW and MOW compete and interleave, generating significant variability in the southern Rockall Trough water mass properties. The extension of MOW into the northern Rockall Trough has not been fully established (McCartney & Mauritzen 2001, New et al. 2001, Smilenova et al. 2020). In the northern Rockall Trough, Wyville-Thomson Overflow Water (WTOW) has recently been appreciated as a significant source of intermediate/deep water flowing directly into the region (Johnson et al. 2010, 2017, Schulz et al. 2020), along with a more intermittent lower intermediate depth branch (WTOW<sub>L</sub>) at depths exceeding 1500 m. Labrador Sea Water (LSW) is the major component of lower intermediate depth (1600–2200 m) water and is associated with a salinity minimum. LSW enters from the subpolar west and recirculates in the northern Rockall Trough. It flows south-west into the Porcupine Seabight and Biscay regions with a degradation of the salinity minimum at its core (van Aken 2000, Kieke et al. 2009, Liu & Tanhua 2021). Below 2200 m, overflow waters from the Nordic Seas occupy the region, referred to as North Atlantic Deep Water (NADW) or generally Lower Deep Water (LDW), and there is some evidence for a weak influence of Antarctic Bottom Water (AABW, e.g., Van Aken 2000, McGrath et al. 2012).

The North-east Atlantic is also a region of both significant deep winter convection (McCartney & Talley 1982, Brambilla et al. 2008) and mesoscale variability (Ullgren & White 2012, Sherwin et al. 2015, Smilenova et al. 2020), which both redistribute ocean properties (e.g., nutrients) and mix water masses entering the region. The winter mixed layer depth is typically 350–400 m in the southern area of interest, increasing to 450–600 m or more in the northern Rockall Trough (Brambilla et al. 2008). Winter mixing replenishes surface layer nutrients (Dumousseaud et al. 2010, Mathis et al. 2019) and sets the depth of the permanent thermocline: the deepest level of direct atmospheric influence in altering upper



layer properties. Typical depths of the winter mixed layer are greater than the depths of the adjacent continental shelf and the relatively shallow Rockall and Porcupine Banks. This results in enhanced heat loss and densification of the water above the shelf and banks, which may result in cascading from the continental shelf (e.g., Hill et al. 1998) and/or formation of long-lived dense (nutrient-rich) domes over the larger Rockall and Porcupine Banks (White et al. 2005, Mohn & White 2007) (Figure 6).



**Figure 6** Schematic diagram of main dynamic processes of importance to continental margin ecosystems: red/blue arrows – deep ocean (gyre) influence; green/purple arrows – Upper and Lower Boundary currents (the black loop arrow signifies a likely Taylor Column over Anton Dohrn Seamount); black and white stripes – enhanced shelf edge internal wave activity; black cross – bottom intensified baroclinic diurnal tides; black and white checks – dense cold nutrient domes over submarine banks; red loops – mesoscale variability. Map visualised using ArcGIS Pro v 2.8 (Esri Inc. 2020).

*Circulation and dynamics*

The dynamics at the Irish Continental Margin are dominated by three main processes (Figure 6):

1. Deep North Atlantic circulation and general basin-scale air–sea interaction and dynamical processes.
2. Boundary Currents, such as contourite currents, and the European Slope Current (ESC).
3. Tidal dynamics and baroclinic (see the later definition) wave generation and propagation.

Surface and intermediate depth circulation both transports source water masses and induces significant mesoscale variability, helping to mix these water masses and setting the water properties at the margin. While the main branches of the North Atlantic Current recirculate some distance away from the eastern boundary, filaments of the North Atlantic Current advect into the Rockall Trough and between Hatton and Rockall Banks (e.g., Xu et al. 2015). At the thermocline level, most currents recirculate within the Atlantic gyres (e.g., Bower et al. 2002). From the south, surface flows are predominantly poleward with a concentrated boundary flow at the margin – the Shelf Edge Current (SEC) or European Slope Current (e.g., Pingree & Le Cann 1990, Xu et al. 2015). Further north along the northern Rockall margin, the slope current is generally stronger and more persistent (e.g., Marsh et al. 2017), whereas south of 53°N, seasonality in the upper layer slope current is recognised (e.g., Pingree et al. 1999).

At the permanent thermocline depth, MOW flows poleward (Bozec et al. 2011), and where cores of the MOW outflow are present at the margin, they create contourite currents (e.g., Van Rooij et al. 2007, Liu et al. 2020). At lower intermediate depths, LSW enters the region from the west and recirculates cyclonically in the northern Rockall Trough (Fischer et al. 2018). The confluence of both upper and intermediate waters from west/southern sources along the Rockall Trough induces significant mesoscale variability and mixing (e.g., Ullgren & White 2012, Sherwin et al. 2015, Smilenova et al. 2020). As a result, there is a net poleward transport of typically 3.5–4.5 Sv of more homogenous MNAW through the northern Rockall Trough region (Holliday et al. 2000, Houpert et al. 2020), comprising a poleward transport of order 6 Sv, predominantly in the slope current at the margin, and a southward transport of about 2 Sv mostly found on the western side of the Rockall Trough, and including that associated with WTOW transport.

The North-east Atlantic margin is a region of significant tidal energy dissipation and conversion of barotropic to baroclinic tidal energy (Baines 1982). [Here, barotropic means a vertically homogenous horizontal current in a frictionless flow (e.g., the ideal tide), whereas baroclinic flow has vertical structure caused by the changes in temperature and salinity (and hence density) within the water column, e.g., internal waves.] An estimated ~50% of the global barotropic to baroclinic energy (~1.7 TW) converted in the principal semi-diurnal (M2) tidal component is dissipated in depths less than 2000m (Müller 2013). The Celtic Sea Shelf edge is a particular hotspot of tidal conversion (e.g., Vlasenko et al. 2014), creating both high-frequency non-linear solitons (Holt & Thorpe 1997) and beams of internal tidal energy propagating downward off slope to the lower continental margin (Pingree & New 1989, Vlasenko & Stashchuk 2015). The rough and corrugated nature of the Celtic Shelf Edge is important in the generation of a 3-dimensional spatial structure in the internal wave field with waves generated in all directions (Vlasenko et al. 2014). Additionally, steep-sided canyons at this part of the North-east Atlantic margin can generate and focus significant baroclinic tidal energy (Vlasenko et al. 2016), particularly the dendritic Whittard Canyon system (e.g., Hall et al. 2017, Aslam et al. 2018).

*Biophysical interactions*

The key environmental conditions that control any ecosystem distribution are the basic geochemical properties and tolerances, substratum, and an adequate supply of nutrients/food. In addition, the local dynamics in terms of the range of current strength experienced are required to be in a tolerable



range for appropriate ecosystem function (e.g., to not damage organisms or to keep substratum swept). The background physio-chemical environment (e.g., temperature, oxygen, calcite/aragonite saturation, and overlying primary productivity) will likely be important over large, but multiscale, spatial scales (e.g., Guinotte et al. 2006). Often habitat suitability models are utilised to assess the importance of physical (and geological) variables for many benthic species (e.g., Davies & Guinotte 2011, Yesson et al. 2012, Ross & Howell 2013).

The supply of food to benthic systems found in the region is dependent on both a source, ultimately related to pelagic primary productivity, and the regional dynamics that transport food/energy to the ecosystem – whether primarily filter/suspension-feeding or deposit-feeding in character.

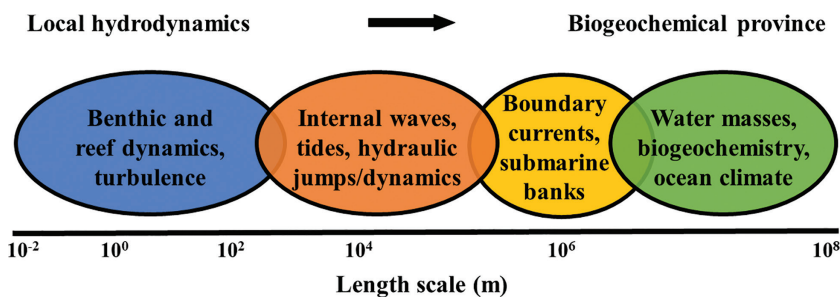
In simple terms, therefore, the (food) energy density flux could be thought of as a basic relationship that can be written as follows:

$$\text{Energy Flux} = \text{Concentration} \times \text{Transport magnitude} \quad (1)$$

Here, we may think of organic carbon as the energy and the advective fluxes can be both vertical and horizontal. Vertical fluxes to deeper water will result from the export of surface primary production at the continental margin (Walsh 1991, Lutz et al. 2002) or net vertical movement related to cross-margin fluxes (e.g., Wollast & Chou 2001, Painter et al. 2016). A myriad of dynamical processes result in complex variation of vertical and horizontal exchange fluxes both at the shelf edge (e.g., Huthnance 1995, Graham et al. 2018, Huthnance et al. 2022) or near the seabed (e.g., White & Dorschel 2010).

Flow magnitude will principally determine the sediment depositional environment, and hence, a broad division between a deposit- or a suspension-feeding dominance within a benthic community. Based on an assessment of the forces created by seabed boundary friction retarding the flow approaching the seabed, Thomsen & Gust (2000) estimated that a current magnitude ~1 m above the seabed of about ~15 cm s<sup>-1</sup> was required to resuspend fresh detrital material in the region of the Goban Spur. Together with measurements to estimate a percent of time currents exceed that threshold (e.g., White 2007), this can provide a good first-order estimate for the suspended sediment environment in the benthic layer at a given locality.

One may expect Eqn. 1 to be scale dependent (Figure 7). At the larger scale, it is likely that the overlying productivity which provides the basic necessary (likely bottom-up) supply of nutrients/food will, in part, determine the regional biogeographic provinces (e.g., Sathyendranath et al. 1995, Proud et al. 2017). As length scales diminish, the influence of the region/local dynamics will increase with respect to delivering the (background concentration of) food to the ecosystems, hence shaping spatial distribution. Within the focal region, these dynamic processes will, at scales of the order of 100 km, include the role of the slope current in driving benthic cross-slope sediment fluxes



**Figure 7** The relative influence of productivity/ocean environment properties versus physical dynamics in controlling the flux of energy to continental margin benthic ecosystems of the North-east Atlantic.

(White et al. 2005) and the enhancement of tidal period baroclinic waves (White 2007, White & Dorschel 2010). At further reduced length scales, internal waves, or hydraulic processes associated with flow over topographic features, such as banks or carbonate mound provinces, can pulse food to the benthic communities (e.g., Mohn et al. 2014, Van Haren et al. 2014, Soetaert et al. 2016, Cyr et al. 2016). At smaller length scales, flow-topography interactions may shape development of benthic structures (van der Kaaden et al. 2021), for example, at carbonate mounds (1–10 km scale, Cyr et al. 2016), local near-seabed flow acceleration (scales of the order of 1 km, Genin et al. 1986), and turbulence within reef-building structures (scales of the order of 100 m, Guihen et al. 2013). Such biophysical interactions at a range of scales can generate feedbacks between hydrodynamics and ecosystem development, as has been suggested for the cold-water coral carbonate mounds at the margin of the Rockall Bank (van der Kaaden et al. 2020, 2021).

### *Regional description*

#### *North Irish–Scottish margin*

The Rockall Trough dynamics are associated with a net poleward flow, concentrated at the continental margin, and deeper flows with significant mesoscale variability, including a southward directed component of overflow waters from the Wyville-Thomson Ridge. In addition, topographically steered residual flows and tidally associated dynamics are significant at Rockall Bank.

There is a relatively strong ( $\sim 10\text{--}20\text{ cm s}^{-1}$ ) and persistent residual flow along the continental margin west of Scotland – the ESC (e.g., Souza et al. 2001, Marsh et al. 2017) – with some seasonality measured. Currents are somewhat uniform with depth in winter months (barotropic character), whereas in the summer months, there is significant structure in the vertical distribution of currents; maximum currents typically found associated with a core of warm, saline ENAW (Souza et al. 2001) – a baroclinic character. A small cross-slope residual flow has also been measured in the lower frictional (Ekman) layer. This is important because it provides a cross-margin transport mechanism for sinking organic sediments sourced at the shelf edge (e.g., Holt et al. 2009, Painter et al. 2016). Thiem et al. (2006) have shown that variations in modelled cross-slope transport (proportional to the square of the residual flow magnitude) can produce regions of input and output to the benthic layer and have correlated enhanced particle encounter rate with the highest abundance of the cold-water coral *Desmophyllum pertusum*, as an example of a suspension-feeder, at the Norwegian margin. At the western edge of the northern Rockall Trough, southward residual flows along the Rockall Bank margin are associated with the rectification of diurnal tides (see below) in water depths 600–900 m, and also, at a similar depth range, with the main core of WTOW (Johnson et al. 2010). The occurrence of this water mass also coincides with the depth range of the presence of the carbonate mounds and a relationship between the two has been suggested (Schulz et al. 2020), although other processes make a correlation of the mound depth range with any particular biophysical interaction process difficult. In part, this is due to the significant tidal-related dynamics at Rockall Bank. There, the diurnal tide is enhanced, which results in strong along-margin rectified currents with strong conversion to baroclinic diurnal tides (e.g., Huthnance 1974, Cyr et al. 2016). Related to these dynamics, hydraulic control of flow over the topography of the carbonate mounds has been suggested (e.g., Mohn et al. 2014, Soetaert et al. 2016), associated with rapid vertical (downwelling) movement of chlorophyll-rich and other detrital particles from the upper pelagic layer (Soetaert et al. 2016). A similar process was suggested at the Mingulay reef (Davies et al. 2009) found on the Scottish shelf, and while studies have concentrated on the influence for specific cold-water coral species, the mechanism of food supply would have importance to the whole ecosystem in these regions.

The winter mixed layer depth in the north Rockall region far exceeds the depths of the adjacent continental shelf and shallow Rockall Bank, which has two implications for resident ecosystems as shelf/bank water is densified through enhanced loss of heat content. Hill et al. (1998) have

observed cascading of such dense water off the Malin slope down to depths of 700–800 m. The cascaded water carried a high chlorophyll signal in transported shelf sediments, thus providing a potential food delivery mechanism to margin ecosystems. In a similar way, water over the Rockall Bank – and indeed over the Porcupine Bank further south – is densified in winter, and in addition, will also be resupplied with deep-water nutrients. The dense water does not immediately cascade off the banks; instead, it slowly drains through Ekman or bottom friction layer dynamics in the benthic layer. As a result, these domes may last several months supplying nutrients for enhanced and prolonged productivity over the banks (Figure 7), as well as a mechanism to advect exported pelagic material to lower continental slopes (e.g., White et al. 2005, Mohn & White 2007). At the local scale of the Anton Dohrn Seamount, the general flow pattern in the Trough likely promotes a Taylor Column system and cyclonic eddy shedding from the seamount (e.g., Booth 1988). A Taylor Column is an enclosed, recirculating flow feature that may be generated over a seamount or similar feature under certain conditions of impinging flow speed, seamount length scale, and water column stratification (e.g., White et al. 2008). A Taylor Column generated at a seamount with a shallow (pelagic) summit depth has been suggested to promote bottom-up primary productivity and act as a retention system for organic material to support biomass at these features (e.g., Dower et al. 1992, White et al. 2008), although the temporal stability of such features to allow transfer to higher trophic levels is not always certain (e.g., Genin & Dower 2007).

#### *Southern Irish margin – Celtic Shelf Edge including Whittard Canyon, Goban Spur and Porcupine Seabight*

The southern Celtic/Biscay region is associated with a seasonally varying slope current and strong influence of tidal dynamics and energy conversion. Seasonality in the ESC here has been termed a SOMA (Sept-Oct-Mar-Apr) response as the changes in flow character are evident in those months (Huthnance 1995, Pingree et al. 1999). In particular, there is a weakening or reversal in the ESC in spring months, which can manifest as a detachment of the slope flow from the margin around the Goban Spur region (Pingree et al. 1999). At the margin of the Porcupine Bank and inner Irish Shelf, the ESC is also not as strong or as well established, perhaps in part due to the large topographic variability in the region as well as the location between the subpolar/tropical realms. The springtime seasonality in the slope current may have an (unquantified to date) influence on along- and cross-slope advection of (post) bloom exported organic material, relative to the more persistent along-slope current flows further north in the Rockall Trough.

Significant tidal energy is converted to baroclinic (internal) tides and waves at the Celtic Shelf Edge (Green et al. 2008, Vlasenko et al. 2014), with beams of internal (semi-diurnal period) tides propagating off shelf into the lower continental margin (e.g., Pingree et al. 1986, Pingree & New 1989), as well as producing shorter, non-linear internal waves (solitons) at the shelf edge from the breakup of the internal tide (New & Da Silva 2002, Green et al. 2008). These processes are fundamental to both pelagic biogeochemical processes and benthic ecosystems at the deeper margin. The internal tidal energy propagating offshore, concentrated in beams, may interact with the sloping bottom of the continental slope and this may lead to conditions of enhanced benthic currents where resonant conditions of bottom slope and the internal wave energy propagation characteristics (beam angle, controlled by the vertical stratification) match (e.g., Cacchione & Wunsch 1974, White 2007, Puig et al. 2014). This results in localised elevated turbulent conditions and vertical mixing confined to certain depth zones that likely extend on horizontal length scales of ten to hundreds of kilometres.

Associated with these regions may be the generation of an Intermediate Nepheloid Layer (INL) from resuspended sediment clouds that can detach from the benthic boundary layer. Examples have been documented at the upper depths of the north-west Porcupine Bank (Dickson & McCave 1986, Mienis et al. 2007). These INLs were found at a depth relating to the resonance conditions

for the internal tide (internal waves of M2 tidal period), and they were also found adjacent to the cold-water coral carbonate mounds. A relationship between warmer water and more turbid conditions in benthic layer waters suggested the large vertical displacement associated with the resonant internal waves advected suspended material over the mounds (Mienis et al. 2007). This highlights the role of internal waves in creating an increased particle flux in the benthic layer and possible depth control for both carbonate mounds and other suspension-feeding dominated systems. These INLs may also occur at deeper depths, e.g., on the south-west Porcupine Bank at approximately 1750 m depth (Thorpe & White 1988). In addition, the generation of baroclinic diurnal tides, trapped within 100 m of the seabed topography with associated enhanced currents, observed at parts of Rockall Bank, is also found at the eastern margin of the Porcupine Seabight, specifically the northern portion of the Belgica Mound Province (White 2007) (Figure 2). Here, currents are variable within the province, but strong bottom currents have been measured near the summit of the mounds and in some gullies (e.g., Dorschel et al. 2007a). Such small-scale topographic control on the dynamics will influence sedimentary structures and benthic habitats (e.g., Van Rooij et al. 2003, Lim et al. 2017), as has been observed elsewhere, such as the small mounds of the west Porcupine Bank (Lim et al. 2020).

It is highly likely, therefore, that a zonation of dynamical conditions (and hence hydrographic control on benthic fauna) occurs across the range of continental and deep ocean depths in the region and at varying spatial scales. In particular, the depth range of the permanent thermocline (typically 600–1000 m), which is associated with strong vertical density stratification and where continental margin slopes are also greatest, is one of particularly high baroclinic energy resulting in strong tidal and residual currents (White & Dorschel 2010).

In the upper layer at the shelf edge, internal waves increase turbulent vertical mixing via soliton decay creating a large vertical nutrient flux to enhance primary production (e.g., Rees et al. 1999, Sharples et al. 2007, Tweddle et al. 2013). Mixing at the shelf edge also creates a varying cross-slope distribution in the phytoplankton community with larger (energy-rich) phytoplankton occupying the more vertically mixed shelf edge region where the nutrient fluxes are largest. Consequently, Sharples et al. (2009) have suggested a fundamental role of internal wave generation/interaction at the shelf edge on continental margin ecosystems by providing a favourable food source (large phytoplankton) and removing the need to time their spawning to the spring bloom for early-stage fish (and other mesozooplankton).

The Celtic Shelf Edge is incised by numerous canyons, including the dendritic Whittard system, and the rough ‘corrugated’ nature of the slope likely enhances tidal energy conversion to the internal wave spectrum (e.g., Holt & Thorpe 1997). Within the Whittard Canyon system, Wilson et al. (2015b) documented depth ranges where nepheloid layers were common and related to permanent thermocline depth range, as well as also where internal wave resonance was expected to be generated. Aslam et al. (2018) showed a varying magnitude of baroclinic energy within the various branches, but most energy was sourced from the shelf edge adjacent to the system, and Hall et al. (2017) observed partly standing internal waves in one channel, thus indicating strong heterogeneity in the internal wave field and dynamic conditions in the different branches. This process overlies the sediment transport process typically associated in canyons, i.e., via gravity flows. In Whittard Canyon, episodic sediment transport events have been recorded in a number of the individual branches (e.g., Duineveld et al. 2001, Amaro et al. 2015, Haalboom et al. 2021, Heijnen et al. 2022). The sediment transport is further complicated by the anthropogenic process of bottom trawling-induced sediment dynamics and plume generation, as highlighted by Wilson et al. (2015a). Here, the dendritic nature of the system, together with non-uniform trawling activity and slopes of the interflaves, results in likely (but unquantified) variation of plume strength and activity in the separate branches and variation in the quality of organic matter transport (Daly et al. 2018).

## Deep-sea vulnerable marine ecosystems

The unique environmental conditions on the region's margin have led to an abundance of rich and biodiverse deep-sea habitats, dominated by suspension- and filter-feeding megabenthic species. Many of these habitats can be classified as VMEs which are sensitive benthic communities, vulnerable to fishing pressure, as identified by United Nations General Assembly Resolutions 61/25 and 61/105. They are defined by five criteria: uniqueness and rarity, functional significance, fragility, life-history traits of component species (which make them slow to recover from fishing pressure), and structural complexity (FAO 2009). Species groups and habitat-forming communities that may indicate the presence of a VME in the deep sea include certain groups of cold-water corals (Scleractinia, Antipatharia, Octocorallia, and Stylasteridae), sponge-dominated communities, bryozoan and hydroid communities, xenophyophore-dominated communities, and chemosynthetic communities (FAO 2009, Table 2). Ireland has recently added substantial records of VMEs to the ICES VME database due to the extensive mapping of the SeaROVER (Sensitive Ecosystem Assessment

**Table 2** List of OSPAR threatened and declining habitats along with their ICES Vulnerable Marine Ecosystem category and subcategory equivalent

OSPAR threatened and declining habitats	ICES Vulnerable Marine Ecosystems	ICES Vulnerable Marine Ecosystems subcategory
<i>Lophelia pertusa</i> reefs	Cold-water coral reef	<i>Lophelia pertusa</i> / <i>Madrepora oculata</i> reef <i>Solenosmilia variabilis</i> reef
Coral gardens	Coral gardens	Hard-bottom coral garden Hard-bottom gorgonian and black coral gardens Hard-bottom colonial scleractinians on rocky outcrops Hard-bottom non-reef scleractinian aggregations Hard-bottom stylasterid corals on hard substrata Soft-bottom coral garden Soft-bottom gorgonian and black coral gardens Soft-bottom cup-coral fields Soft-bottom cauliflower coral fields Sea pen fields
Deep-sea sponge aggregations	Deep-sea sponge aggregations Xenophyophore aggregations Tube-dwelling anemone aggregations Stalked crinoid aggregations Mud and sand emergent fauna Bryozoan patches Hydrothermal vents/fields Cold seeps	Soft-bottom sponge aggregations Hard-bottom sponge aggregations Soft-bottom anemone aggregations Hard-bottom anemone aggregations
Oceanic ridges with hydrothermal vents		

Source: Adapted from Picton et al. (2021).



and ROV Exploration of Reef Habitat) project (Picton et al. 2021) and the annual International Groundfish Surveys and Underwater TV surveys (ICES 2020). The structural and functional aspects in the definition of VMEs mean that they are also Marine Animal Forests (Rossi et al. 2017, 2022, Orejas et al. 2022). Marine Animal Forests alter the environment by creating complex biogenic structures that provide additional ecological niches and consequently increase biodiversity. Examples from the region include scleractinian reefs, coral gardens, sponge aggregations, bivalve reefs, as well as aggregations of stalked crinoids, tube worms, anemones, and xenophyophores.

### *Scleractinian reefs*

Deep-water reefs were discovered growing in the North-east Atlantic in the eighteenth century (Gunnerus 1768). All deep-water corals are azooxanthellate, meaning that, in contrast to their shallow and mesophotic counterparts, they do not possess symbiotic algae. Bathyal scleractinian reefs are often found in areas where complex topology interacts with the overlying hydrography such that there may be increases in current flow or downslope particle transport leading to higher inputs of particulate matter (Roberts 2009, Roberts & Cairns 2014). Reef-building corals are important ecosystem engineers, adding complexity to the environment and altering the oceanographic conditions around them (Roberts et al. 2009, Corbera et al. 2022). Biogenic reefs may form in areas with little available hard substrata by corals forming their initial attachment to shells before growing and breaking off providing more hard substrata for future growth (Wilson 1979). Along the North-western European Margin, there are three reef-building scleractinian corals: *Desmophyllum pertusum*, *Solenosmilia variabilis*, and *Madrepora oculata*. Reef-building scleractinians are capable of drastically altering the topology of the environment forming mound clusters that can extend for several kilometres in length and between 3 m (Lim et al. 2018a) and 380 m high (Mienis et al. 2006). There is a clear research bias in the literature towards *D. pertusum* due to its recognised importance in forming reefs and mounds. There are few empirical studies focusing on the ecological contribution of *M. oculata* to reef structure and function. *Madrepora oculata* does not form extensive reef systems, instead, it is shown to nearly always occur in association with *D. pertusum* from the individual colony to reef scale (Arnaud-Haond et al. 2017). Both species are found growing in association with one another from the Bay of Biscay to Iceland (Arnaud-Haond et al. 2017). The occurrence of *M. oculata* decreases further north towards Iceland, while *D. pertusum* is less abundant further south towards the Mediterranean (Wienberg et al. 2009, Arnaud-Haond et al. 2017). It is unclear whether this distribution is driven by temperature (but see Howell et al. 2022).

### *Known distribution of reef-building scleractinians*

*Desmophyllum pertusum* was recorded in the region in the nineteenth century, appearing on biogeographic maps (as *Oculina prolifera*, Forbes, 1856). It was known at that time that deep-sea corals were capable of forming large reefs and aggregations (Forbes & Godwin-Austen 1859). *Desmophyllum pertusum* was dredged off the North-western European Margin during the HMS Porcupine expedition of 1869–1870 (Duncan 1870). Since then, our understanding and knowledge of deep-sea scleractinian distributions have drastically increased, especially with the intensification of fossil fuel exploration offshore (Rogers 1999). In the majority of settings, *D. pertusum* and *M. oculata* co-occur in both patches and reef habitats with the more fragile *M. oculata* forming a secondary reef framework (Freiwald 2002). *Desmophyllum pertusum* is widespread along the North-east Atlantic, spanning from the extensive reefs off Norway and south of the Greenland–Scotland Ridge (an undersea ridge that extends from east Greenland, south of Iceland, to Scotland, Buhl-Mortensen et al. 2015), along the Scottish and Irish Continental Margin (Table 3), including the Faroe and Rockall Plateau and Porcupine Bank (Wheeler et al. 2007), and continues down the Iberian Margin (Somoza et al. 2014), and into the Mediterranean Sea (Rogers 1999).



**Table 3** Reports of living *Desmophyllum pertusum* reef habitat, including thickets at the summit of carbonate mounds, in the Irish and UK Exclusive Economic Zone

Location	Depth (m)	Selected references	Potential biophysical control	Notes
Darwin Mounds	920–1070	Bett (2001), Wheeler et al. (2008), Huvenne et al. (2016)	Likely topographically steered near-seabed current	Live coral thickets on small coral mounds.
Logachev Mounds	500–740	Kenyon et al. (2003), Van Weering et al. (2003), de Haas et al. (2009), de Clippele et al. (2019), Maier et al. (2021)	Bottom-trapped baroclinic diurnal waves, hydraulic control, WTOW flow	Living coral on the summit and flanks of large mounds. However, the percentage of living reef is variable between individual mounds.
North-east Rockall Bank	103–1004	Howell et al. (2009, 2014b)	Winter mixing generated, dense/cold-water nutrient domes; Ekman drainage	Live coral thickets on bank summit, extensive reef areas on the slope.
George Bligh Bank	~800	Howell et al. (2016b)	Internal wave interaction on/above bank	Large coral mound with extensive live coral.
Anton Dohrn Seamount	747–791	Davies et al. (2015)	Likely relation to Taylor Column and local topographic effects/Internal waves	Living coral found on the summit
Porcupine Bank Canyon Mounds	800	Howell et al. (2015), Lim et al. (2020)	Winter mixing generated dense water nutrient domes, Ekman drainage, local dynamics?	Large extensive coral mounds: live coral found along mounds near canyon head and canyon flank ranging from 16% to 78% coverage
Hovland Mound Province: Propeller Mound	650–900	Heindel et al. (2010)	Local dynamics at mounds likely, but not fully assessed	Live coral on the summit
Belgica Mound Province: Piddington Mound	980	Lim et al. (2017)	Bottom-trapped baroclinic diurnal waves, local topographic influenced currents	Dense live coral on the northern flank
Belgica Mound Province: Galway Mound	600–900	Dorschel et al. (2007a)	Bottom-trapped baroclinic diurnal waves, local topographic influenced currents	Dense coral coverage on the summit and western flank
Whittard Canyon system: Explorer Canyon	795–940	Davies et al. (2014), Price et al. (2019)	Bottom-trapped baroclinic diurnal waves, local topographic influenced currents	Live cold-water coral reef

Note that depths relate to the depths of video transects from which the species was recorded, not the actual depth of the species as video transects may encompass broad depth ranges.

Carbonate mounds are formed when *Desmophyllum* reef framework is infilled with sediments and the live coral continues growing, eventually forming a mound where living reef is still found at the summit and flanks of the mound. The largest known concentration of carbonate mounds in the world is located off the west coast of Ireland (Hall-Spencer et al. 2009), with the first mounds described in the 1990s (Hovland et al. 1994). Coral mounds are found along the

North-west European slope in a relatively narrow belt between 500–1000 m depth, with a peak in density at 650 m (White & Dorschel 2010). The relatively narrow depth distribution is thought to be heavily influenced by the presence of the permanent thermocline. Residual current speeds at depths of 500–1000 m at the near seabed are 3-fold stronger compared to current speeds at both shallower and deeper depths (White & Dorschel 2010). The permanent thermocline favours the formation and maintenance of an along-slope current that interacts with both internal waves and other baroclinic tidal currents that introduce more organic material to the area (Mohn et al. 2014, van Haren et al. 2014, Soetaert et al. 2016). In favourable areas, these mounds can form clusters referred to as ‘provinces’. Either side of the Rockall Trough are the Logachev Mounds and the Pelagia Mounds (de Haas et al. 2009). Along the Irish Margin, notable coral-mound provinces include the Hovland Mounds and Belgica Mounds (de Mol et al. 2002). Living *D. pertusum* reef, sometimes referred to as thickets, is found at the summit and flanks of mounds where there is usually increased organic matter input, e.g., depths of 500–740 m on the Logachev Mounds (Kenyon et al. 2003, Van Weering et al. 2003, de Haas et al. 2009, de Clippele et al. 2019, Maier et al. 2021).

*Solenosmilia variabilis* occurs in deeper waters than *D. pertusum* and *M. oculata* and its distribution is hypothesised to be linked to LSW which is richer in oxygen, cooler, less saline, and less saturated in aragonite (Henry & Roberts 2014b). In the North-east Atlantic region, *S. variabilis* is distributed in water depths of 888–2803 m (mean ~1500 m, Howell et al. 2014a). *Solenosmilia variabilis* reef has been found across the Irish and UK EEZs on video transects taken at water depths of 1160–1763 m. On Anton Dohrn Seamount, *S. variabilis* reef is a component of two separate biotopes in water depths of 1267–1763 m, *S. variabilis* reef with the ophiuroid *Ophiactis* sp. on the north-west of the seamount (1318–1351 m), and *S. variabilis* with encrusting sponges on both the north-west and south-east of the seamount (1267–1763 m and 1496–1573 m, respectively) (Davies et al. 2015). On the Rockall Bank, just north of the Logachev Mound Province, *S. variabilis* reef occurred in water depths of 1150–1750 m (O’Sullivan et al. 2018, La Bianca et al. 2019). While most of the Rockall Bank reef comprised living *S. variabilis*, one dive at 1500–1700 m water depth found hugely degraded reef, which transitioned to a reef with a maximum of 50% live coral (O’Sullivan et al. 2018). On the North Porcupine Bank, *S. variabilis* reef has been reported at 1253–1650 m on the upper slopes and at canyon mouths, with reef at 1253 m primarily comprising dead coral framework (O’Sullivan et al. 2017, Ross et al. 2018). Reef habitat with only 50% live reef was found in the Gollum Channel System at 1100–1600 m (O’Sullivan et al. 2019, La Bianca et al. 2020). *Solenosmilia* reef is also present on George Bligh Bank and the Hebrides Terrace Seamount (Howell et al. 2016b).

Other reports of *S. variabilis* throughout the Irish and UK EEZs specify the presence of the species but do not specifically confirm the presence of reef habitat (Table 4). Colonies originally identified as *D. pertusum* (Huvenne et al. 2011) but tentatively reassigned as *S. variabilis* (Amaro et al. 2016) have also been reported from the eastern part of Whittard Canyon at 1650 m. Deeper *Desmophyllum* occurrences reported by Morris et al. (2013) may also be *S. variabilis*, suggesting its presence as deep as 2448 m in Whittard Canyon.

Video-derived imagery is the primary resource for non-destructive deep-sea investigations. The lack of taxonomic characters present in standard definition imagery can lead to taxonomic confusion between *D. pertusum* and *S. variabilis* reefs. Branching pattern is the primary character used to distinguish the two corals. The different branching patterns are in fact a result of the contrasting budding patterns of new polyps. *Solenosmilia variabilis* has distomodeal budding, whereby two polyps emerge at the same time from the same tentacular ring leading to the classical bifurcating polyps. *Desmophyllum pertusum* exhibits monostomaeous budding where just a single polyp emerges at a time, which results in sharper angles (less than 45°) between polyps and the main skeleton. While these features are readily seen in high-definition video, they are not easy to see in lower quality images and this has resulted in misidentifications between the two species (Huvenne et al. 2011, Morris et al. 2013, Howell et al. 2014a).

**Table 4** Reports of both *Solenosmilia variabilis* reef and non-VME *Solenosmilia* occurrences throughout the Irish and UK Exclusive Economic Zones

Location	Depth (m)	Reference	Notes
<b><i>Solenosmilia variabilis</i> reef habitat</b>			
George Bligh Bank	1096–1200	Howell et al. (2016b)	
Anton Dohrn	1267–1763	Davies et al. (2015)	
Flanks of the Hebrides Terrace Seamount	1004–1695	Cross et al. (2014), Henry et al. (2014)	More abundant at depths below 1500 m
Rockall Bank	1150–1750	O’Sullivan et al. (2018), La Bianca et al. (2019)	
North Porcupine Bank	1253–1650	O’Sullivan et al. (2017), Ross et al. (2018)	
Gollum Channel System	1100–1600	O’Sullivan et al. (2019), La Bianca et al. (2020)	
<b>Non-VME records of <i>S. variabilis</i></b>			
Hatton Bank outcrop	600–1600	Sayago-Gil et al. (2012)	
Rockall Bank	800–1900	O’Sullivan et al. (2018), La Bianca et al. (2019)	
North Porcupine Bank	1350–2100	O’Sullivan et al. (2018), La Bianca et al. (2019)	
Porcupine Seabight including the Goban Spur and Gollum Channel	1230–1793	O’Sullivan et al. (2019), La Bianca et al. (2020)	
Small canyons west of the Belgica Mound Province	1230–1600	O’Sullivan et al. (2019), La Bianca et al. (2020)	

Note that depths relate to the depths of video transects from which the species was recorded, not the actual depth of the species as video transects may encompass broad depth ranges.

#### Autecology of reef-building scleractinians

Similar to other deep-water species, basic biological aspects of reef-building scleractinians are lacking. *Desmophyllum pertusum* is gonochoric and is mostly found inhabiting waters with temperatures of 4–12°C (Rogers 1999, Roberts et al. 2003). *In situ* growth rates of *D. pertusum*, estimated by measuring the same 15 colonies from ROV imagery taken over 9 years, were 26 mm yr<sup>-1</sup> on northern North Sea oil rigs where the water temperature was 7–11°C (Gass & Roberts, 2006). Growth studies of *D. pertusum* in aquaria estimated linear extension rate of 9.4 mm yr<sup>-1</sup> for Norwegian samples incubated at 8–11°C for 12 months (Buhl-Mortensen 2001) and 8.8 mm yr<sup>-1</sup> for Mediterranean individuals incubated at 12°C in the dark (Orejas et al. 2011). *Madrepora oculata* collected from the Mediterranean and incubated in an aquarium at 12°C grew at a rate of 5.1 mm yr<sup>-1</sup> (Orejas et al. 2011).

In the North-east Atlantic, *D. pertusum* has a seasonal reproductive cycle, spawning in January/February and producing around 3300 small (maximum observed diameter 140 µm) oocytes per cm<sup>2</sup> of skeleton in a single cohort each year (Waller & Tyler 2005). This reproductive strategy of a larger number of smaller oocytes contrasts with the reproductive biology of *M. oculata* found in the same area. *Madrepora oculata* produced an average of 256 larger (maximum observed diameter 405 µm) oocytes per cm<sup>2</sup> (Waller & Tyler 2005). Multiple cohorts of *M. oculata* oocytes at different development stages were observed, suggesting that spawning occurs periodically when physical and environmental conditions are favourable rather than seasonally (Waller & Tyler 2005). The cues that initiate spawning in deep-water species are poorly understood, however, in UK and Irish waters, detritus from phytoplanktonic blooms reaches the seafloor in April and May (Billett et al. 1983, Rice et al. 1994, Bett 2001), although observations from the Rockall Bank indicate that phytodetritus reaches the seafloor as early as February (Duineveld et al. 2007), which may prompt the observed onset of gametogenesis in July/August

(Waller & Tyler 2005). It has previously been hypothesised that *D. pertusum* larvae are lecithotrophic (Waller & Tyler 2005), but the formation of an oral pore suggests the larvae may be feeding and hence planktotrophic (Larsson et al. 2014).

Pelagic larval duration is an important indicator of species population connectivity; the longer the larvae can spend in the water column, the greater the dispersal potential and the possibility for populations to be more connected over long distances (but see Morrissey et al. 2022a). While no robust *in situ* estimates exist, aquarium observations imply that *D. pertusum* larvae can survive up to 10 months in the absence of predators (Strömberg & Larsson 2017). *Desmophyllum pertusum* larvae have a precompetency stage (defined as the time before a larva is capable of settling) of 3–5 weeks (Strömberg & Larsson 2017). Larvae swam upwards when introduced to the bottom of the tank and crossed salinity gradients, which suggests they may be able to move vertically between water masses, overcoming a recognised barrier to dispersal in many deep-sea species. This could suggest an ontogenetic migration, which could allow them to find favourable currents to disperse further away from the natal range (Strömberg & Larsson 2017).

A recent study that modelled *D. pertusum* larval dispersal among the UK and Irish Marine Protected Area networks (Ross et al. 2017) found that the majority of MPAs in the network released larvae spreading to an average of seven other MPAs, including an average of three strong (upper quartile) connections. Larval flow appeared to be predominantly northwards. Anton Dohrn Seamount had the best average ranking of all MPAs, being both the joint best-performing supplier MPA and the best retainer. Four MPAs acted as net larval sinks (*sensu* Pulliam 1988): the Barra Fan and Hebrides Terrace Seamount, Hatton Basin, NW Rockall Bank, and the Darwin Mounds. The Darwin Mounds retained 61 times more larvae than it supplied (Ross et al. 2017).

While not panmictic, *D. pertusum* maintains high levels of gene flow in populations along the North-western European Margin (Le Goff-Vitry et al. 2004). The proportion of clones of *D. pertusum* varies by location. In the Darwin Mounds, where reefs have been extensively damaged by trawling, there is a high proportion (49%) of clones present (Le Goff-Vitry et al. 2004). Trawling, compounded by low habitat suitability in the area, may prevent recruitment of sexually reproduced individuals allowing clones, perhaps formed through breakage, to colonise. On the Darwin Mounds, no reproductively active polyps were found (Waller & Tyler 2005) consistent with the high level of clonality reported. Clones have been found in the Porcupine Seabight but were not as abundant as at the Darwin Mounds (Le Goff-Vitry et al. 2004, Le Goff-Vitry & Rogers 2005).

Analysis of nuclear internal transcribed spacer (ITS) sequences and nine microsatellite markers showed that the genetic structure of *D. pertusum* was very homogenous in the North-east Atlantic, with pairwise  $F_{ST}$  comparisons only indicating significant structure in comparisons involving the distinct population at the Logachev Mounds (Boavida et al. 2019). A single ITS haplotype was largely dominant from the Bay of Biscay to Iceland. Other populations were found in the eastern and western Mediterranean basin.

Using ITS and six microsatellites, four distinct populations of *M. oculata* were identified, one in the Mediterranean Sea, one largely confined to the Bay of Biscay, one shared between the Azores and Logachev Mounds, and one largely restricted to Iceland (Boavida et al. 2019). Pairwise  $F_{ST}$  comparisons of *M. oculata* sampling locations using ITS sequences only distinguished the Logachev Mounds, whereas microsatellites showed much more structure within the North-east Atlantic with nearly all sampled locations significantly different from each other.

No study has investigated the larval ecology of *M. oculata* and so no robust inferences can be made about how larval behaviour may influence the dispersal potential of the species. The fact that *M. oculata* produces larger oocytes, is less fecund, and has a seemingly opportunistic reproductive output (see above, Waller & Tyler 2005) may partly explain the observed differences in genetic structure of *D. pertusum* and *M. oculata*.

### *Modelled distributions of scleractinian reef*

The inaccessibility and high cost of deep-sea research has led to incomplete knowledge on the distribution of deep-sea scleractinian reef habitat in the wider North-east Atlantic. To fill distribution knowledge gaps, there is a growing body of research that has focused on using modelling approaches to determine a probability of occurrence for scleractinian species, and more importantly, for scleractinian reef habitat. An early species distribution model using genetic algorithms (GARP) and Ecological-niche Factor Analysis indicated that *Desmophyllum pertusum* occurs at a mean depth of 480m in the North-east Atlantic and is highly likely to occur on mound summits (Davies et al. 2008, Guinan et al. 2009). More recent studies have modelled the occurrences of *Desmophyllum* reef habitat rather than just species occurrences, which may give more realistic predicted reef distributions (Howell et al. 2011, 2022, Ross & Howell 2013, Ross et al. 2015).

Maximum entropy models in Maxent (a technique for modelling species distributions, Phillips & Dudík 2008), with environmental data gridded at 200 m resolution and based on presence records of *D. pertusum* in 102 grid cells and nine grid-cell occurrences of *D. pertusum* reef, predicted 10 times less reef habitat than species occurrence (0.56% vs. 7.17%) on the Hatton and George Bligh Banks (Howell et al. 2011). This huge reduction in predicted reef habitat versus predicted species occurrence is important for mapping VMEs. The better performance of the reef model as compared with the species occurrence model may be due to the reef habitat being found in a narrower niche than the species (Howell et al. 2011). Substratum type was the most important variable in both models.

Since then, more extensive models covering the Irish and/or parts of the UK Extended Continental Shelves have been produced and they have demonstrated that temperature (or depth as a correlated proxy) is the most important variable in driving distributions (Ross & Howell 2013; Howell et al. 2022); inclusion of oceanographic variables can improve model performance (Rengstorf et al. 2014, Pearman et al. 2020); and high-resolution environmental data produces better performing models and a lower predicted extent of reef habitat (Howell et al., 2022).

Recently, and for the first time, previously published *D. pertusum* reef habitat models were ground-truthed using newly collected data from transects conducted during five research cruises in the Irish and UK EEZs (Howell et al. 2022). This truly independent model validation demonstrated that all models performed worse than expected based on earlier cross-validation results but were still considered good. A new data-rich model of *D. pertusum* reef habitat in UK and Irish waters, built incorporating the *Desmophyllum* reef records from previous studies and the new data, predicts a similar distribution to the earlier 200m resolution models (Ross et al. 2015) with *D. pertusum* reef habitat predicted along banks, seamounts, and continental slope but with a more contracted distribution (Howell et al. 2022). Temperature was an important predictor in this new model with predicted reef habitat occurring in waters of 8°C (Howell et al. 2022). Approximately 40% of *D. pertusum* habitat predicted by this new model is currently within an MPA (84% in UK and 4% in Irish waters), which is an increase from previous estimates (Ross et al. 2015), with 42% below 800 m water depth and thus protected by the EU ban on deep-water demersal trawling (Howell et al. 2022).

### *Biodiversity associated with scleractinian reefs*

Coral reefs provide both hard substratum and numerous microhabitats for the wider faunal community with species found living within, on, and around both living and dead framework (Buhl-Mortensen et al. 2010, Price et al. 2019). In areas where dead coral framework is present, other suspension-feeders (e.g., octocorals and black corals) are often found in high abundances (Roberts et al. 2008, de Clippele et al. 2019) as well as filter-feeding sponges (Van Soest & Lavaleye 2005).

Approximately 1300 species of animals are associated with scleractinian reefs, with the estimated number ever increasing (OSPAR Commission 2009), while 191 species of encrusting sponge have been reported growing on dead coral matrix in the Porcupine and Rockall Banks (Van Soest



& Lavaleye 2005, Van Soest et al. 2007, Van Soest & De Voogd 2015). An initial study based on 20 box cores taken at two sites, 10 each from the 'HAAS' and 'CLAN' mounds at water depths of 557–1407 m within the Logachev Mound Province in the South-east Rockall Bank, found no clear correlation between abundance and diversity of encrusting sponges and live or dead coral cover, as assessed through photographs (Van Soest & Lavaleye 2005). There was huge variability in species composition between box cores with 39 of the 95 identified species reported from a single box core. A more extensive study found a clear correlation between sponge diversity and coral cover, with the highest number of species found in cores containing high levels of dead framework (Van Soest et al. 2007). It is hypothesised that there is lower species richness in areas with live coral cover due to the potential competition between the two groups. Where there is a higher amount of dead coral cover, there is less competition, but more space to colonise (Van Soest et al. 2007). *Hexadella dedritifera*, *Lissodendoryx diversichela*, and *Hymeraphia verticillata* were species that were strongly associated with live coral cover, while *Cyamon spinispinosum*, *Desmoxya pelagiae*, and *Acanthella erecta* were associated with no living coral cover. *Desmophyllum pertusum* can prevent colonisation by other organisms, such as encrusting sponges. It secretes large amounts of mucus which can smother any larva or animal that has initially settled and then selectively secretes calcium carbonate over the invader (Freiwald & Wilson 1998). A Bray-Curtis dissimilarity cluster analysis separated communities found in areas with live coral cover and without live coral cover, which also split live coral into shallow (632 m) and deep (728 m) communities (Van Soest et al. 2007). HAAS and CLAN sponge communities were more similar to each other than to communities found on the Porcupine Bank (Van Soest et al. 2007). Comparisons of the encrusting sponge community composition among Porcupine Bank, Logachev Mounds, Mingulay Reef, and Skagerrak cold-water coral reefs revealed that geographic proximity was not a robust predictor of sponge community similarity (van Soest & De Voogd 2015). While Rockall and Porcupine Bank sponge communities were similar, Mingulay Reef was most similar to the more geographically distant reefs in the Skagerrak (van Soest & De Voogd 2015). Similarity of sample depths in the Skagerrak (78–112 m) and at Mingulay reef (82–214 m) indicates that depth is an important factor, but it could be a proxy for other factors such as oceanic barriers to larval transport, temperature, or anthropogenic influences (sediment, eutrophication) at shallow locations.

Areas of live *D. pertusum* often have reduced diversity and abundance of other coral species. In the Whittard Canyon, both *D. pertusum* reef habitat and rocks where *D. pertusum* patches were observed had a much lower diversity and abundance of associated corals, with some families, such as Primnoidae and Stylasteridae, completely absent; octocorals were more abundant and diverse in mixed rock and sediment environments (Morris et al. 2013). On the summits of the Logachev Mounds, which are densely populated with live *D. pertusum* thickets, there was a low density and diversity of other corals; only five of 1707 non-scleractinian coral observations were made here (de Clippele et al. 2019). Dead coral framework does tend to be richer in megabenthic species than other hard substrata (Roberts et al. 2008).

Coral reef habitat can act as a nursery for sharks and other invertebrates. At least two species of elasmobranch egg cases were observed attached to *S. variabilis* colonies in water depths of 1523–1652 m at 16 stations along the Hebrides Terrace Seamount (Henry et al. 2014). A field of egg cases belonging to *Galeus melastomus*, along with a dense aggregation of this catshark, was observed on dead *Desmophyllum* framework at 750 m in the Hovland Mound Province SAC (O'Sullivan et al. 2018). *Galeus melastomus* spawning grounds have also been found in *D. pertusum* reefs in the Mingulay Reef Complex, located 120–190 m off western Scotland (Henry et al. 2013). It is hypothesised that there is a correlation between the catch rates of *G. melastomus* using longlines and the density of small cold-water coral mounds in Norway because the catshark uses the coral framework to protect their young and uses scleractinian reef generally as a nursery ground (Kutti et al. 2014). Swollen, presumably pregnant female, *Sebastes* have been observed at reefs at Sula Ridge (Fosså



et al. 2002, Husebø et al. 2002, Costello et al. 2005) although there were no juveniles of *Sebastes* or other fish species living specifically in association with *Desmophyllum* reefs; however, it is possible that juveniles are hiding within the framework and are not easily observed (Costello et al. 2005).

Polychaetes appear to use reef habitat to protect their young, since only juveniles of certain species (*Eulalia* sp., *Eumida* sp., *Nereis* sp.) were found on a *Desmophyllum* reef on the Faroe Shelf (Jensen & Frederiksen 1992), while adults live off reef (Rogers 1999).

### *Coral gardens*

There is difficulty in providing a robust and widely accepted definition of a ‘coral garden’. For example, OSPAR defines a coral garden as a dense aggregation of single or multiple species of corals that occurs on either soft or hard substratum. Coral in this definition refers to soft corals and sea pens (Orders Malacalcyonacea and Scleralcyonacea, the latter includes the sea pen Superfamily Pennatuloidae), black corals (Order Antipatharia), solitary cup corals (Family Caryophyllidae), patches of reef-forming scleractinians (*Desmophyllum pertusum*, *Madrepora oculata*, and *Solenosmilia variabilis*), and stylasterids (Class Hydrozoa, Family Stylasteridae, OSPAR Commission 2010). ICES includes all the above corals in its definition of a coral garden except deep-sea sea pens, which are designated as a separate VME: ‘sea pen fields’. The ICES definition of coral garden is subdivided into nine subcategories based on hard versus soft substrata and the dominant coral type. Neither definition refers to a density threshold that would need to be reached for a patch to be considered a coral garden and instead relies on judgement from experts in identifying when coral garden habitat is found among other habitats. An interim definition was provided for coral gardens in the UK that applied density thresholds to account for the large variation in sizes and natural occurrences of certain coral garden species (Henry & Roberts 2014a), e.g., soft-bottom bamboo coral gardens dominated by *Acanella arbuscula* or smaller soft coral dominated gardens, with species such as *Anthomastus grandiflorus*, must occur at densities of 1–9 corals per 10 m<sup>2</sup>, while gorgonian coral gardens dominated by large arboreal species such as *Callogorgia verticillata* require densities of 1–9 corals per 100 m<sup>2</sup> (Henry & Roberts 2014a). Other classification systems have tried to integrate deep-sea specific biotopes into widely used systems, for example, a deep-sea section for the Marine Habitat Classification for Britain and Ireland was produced by Parry et al. (2015), based in part on Howell et al. (2010) and Howell (2010). Several coral garden subtypes are defined under this heading, including discrete coral (*D. pertusum*) colonies on hard substratum; discrete coral (*S. variabilis*) colonies on hard substratum; *Corymorpha*, *Gersemia*, and *Zoantharia*. Soft-bottom coral gardens are recognised separately as ‘sea pens and burrowing megafauna’, ‘solitary scleractinian fields’, and ‘erect coral fields’, the latter of which includes *Acanella arbuscula* assemblages. The European Nature Information System (EUNIS) marine section is based on the UK’s system. Deep-sea biotopes fall under the Marine Category ME and MF for upper and lower bathyal (Shelf edge to 2000 m, no depth limit is made between upper and lower bathyal as it is suggested this changes regionally) and MG for abyssal habitats (greater than 2000 m). However, there are gaps within the EUNIS system for certain deep-sea habitats; for example, while there exists a classification for ‘sea pens and burrowing megafauna on Atlantic upper bathyal mud’ (ME622), there is no lower bathyal equivalent. Currently, EUNIS does not have any stylasterid-dominated coral garden classification. The only currently defined classification to include stylasterids is ME1222 ‘lobose sponge and stylasterid assemblage on Atlantic upper bathyal rock’. A hierarchical classification of cold-water coral habitats was proposed as suitable for incorporation into the EUNIS system (Davies et al. 2017), but this was based on visual classification of types only with no quantitative analysis. Within the reviewed literature, we attempt to match the coral gardens observed with a relevant classification using both the most up-to-date official EUNIS classifications as well as the system proposed by Davies et al. (2017) (Table 5).

THE NORTH-EAST ATLANTIC MARGIN

**Table 5** Reports of coral gardens throughout the focal region

Location	Coral Garden Type	Depth (m)	Reference	Davies et al. (2017)	EUNIS 2022	Notes
Hatton Bank	HBCG: stylasterid corals	491–562	Narayanaswamy et al. (2006)	3.4		<i>Pliobothrus</i> sp.
	HBCG: black corals and gorgonians	616–665	Bullimore et al. (2013)	6.1	ME2212	<i>Stichopathes</i> cf. <i>gravieri</i> dominated
George Bligh Bank	HBCG: black corals and gorgonians	>1000	Narayanaswamy et al. (2006)	6.1 or 6.2	ME123/MF121	<i>Leiopathes</i> sp., antipatharian corals, bamboo whip corals
Logachev Mound Province	HBCG: black corals and gorgonians	547–874	de Clippele et al. (2019)	6.1	ME123/MF121, ME2212, ME322/MF321	Most likely monospecific gardens or at least dominated by <i>Leiopathes</i> sp.
Rockall Bank	SBCG: cup-coral fields	196–285	Howell et al. (2014b)	10.1	ME3212	‘Shallow Cup-Coral Garden’ – <i>Caryophyllia smithii</i>
	SBCG: cup-coral fields	387–685	Howell et al. (2014b)	10.1	ME321/MF322	‘Deep Cup-Coral Garden’ – <i>Caryophyllia</i> sp.
North Feni Ridge	SBCG: gorgonian and black coral gardens	1920	Hughes & Gage (2004)	11.1.3	ME6241/MF6231	<i>Acanella arbuscula</i>
Anthon Dohrn Seamount	HBCG: stylasterid corals	810	Davies et al. (2015)	3.4		
	HBCG: black corals and gorgonians	1724–1740	Davies et al. (2015)	7.1	ME123/MF121	<i>Lepidisis</i> sp. and <i>Parantipathes</i> sp.
	HBCG: black corals and gorgonians	1542–1565	Davies et al. (2015)	6.1	ME123/MF121	<i>Keratoisis</i> sp. and <i>Solenosmilia variabilis</i>
	HBCG	1076–1544, 1714–1770	Davies et al. (2015)	6.1	ME123/MF121	Patches of live <i>S. variabilis</i> , <i>Anthomastus grandiflorus</i> , Keratoisididae, and zoanthids
	SBCG: cup-coral fields	1367–1768	Long et al. (2010)	10.1		
	SPF	1367–1768	Long et al. (2010)	14.1	ME622	

(Continued)

**Table 5 (Continued)** Reports of coral gardens throughout the focal region

Location	Coral Garden Type	Depth (m)	Reference	Davies et al. (2017)	EUNIS 2022	Notes
Hebrides slope	SBCG: black corals and gorgonians	2500	Gage (1986)	11.1.3	ME6241/MF6231	<i>A. arbuscula</i>
	SBCG: black corals and gorgonians	1295	Roberts et al. (2000)	11.1.3	ME6241/MF6231	<i>A. arbuscula</i>
Irish Continental Slope	SBCG: black corals and gorgonians	956–1907	Ross et al. (2018), La Bianca et al. (2019, 2020)	11.1.3	ME6241/MF6231	<i>A. arbuscula</i>
	SPF	612–2275	Ross et al. (2018), La Bianca et al. (2019, 2020)	14.1	ME622	
Porcupine Seabight	SPF	1114–1184	ICES VME habitats records	14.1	ME622	
Goban Spur	SBCG: black corals and gorgonians	2200	Duineveld et al. (1997), Lavaleye et al. (2002)	11.1.3		<i>A. arbuscula</i>
Whittard Canyon	HBCG: black corals and gorgonians	~1550 <sup>a</sup>	Robert et al. (2015)	7.3	ME123/MF121	<i>Primnoa</i> sp. Identified from Robert et al. (2015), Fig. 3f.
	HBCG: black corals and gorgonians	a	Robert et al. (2015)	5.1.1		<i>Anthomastus</i> sp. Identified from Robert et al. (2015), Fig. 3K
	HBCG: non-reef scleractinian aggregations	1350	Huvenne et al. (2011)	3.1.1	ME1231	<i>Desmophyllum pertusum</i> on steep walls.
	HBCG: non-reef scleractinian aggregations	1515–1690	Huvenne et al. (2011)	3.1	MF1211	<i>S. variabilis</i> – reassigned from <i>D. pertusum</i> by Amaro et al. (2016)
	HBCG: non-reef scleractinian aggregations	633–762	Johnson et al. (2013)	3.1		<i>Acesta excavata</i> with <i>Desmophyllum dianthus</i> and <i>Madrepora oculata</i>
	SBCG: black corals and gorgonians	520–4073	Morris et al. (2013)	11.1.3	MF6231	Unspecified depth. Study was 520–4073 m
						<i>Acanella</i> sp.

(Continued)

**Table 5 (Continued)** Reports of coral gardens throughout the focal region

Location	Coral Garden Type	Depth (m)	Reference	Davies et al. (2017)	EUNIS 2022	Notes
	SBCG: black corals and gorgonians	a	Robert et al. (2015)	11.1.3	MF6231	<i>A. arbuscula</i> , identified from Robert et al. (2015), Fig. 3G.
	SPF	800–900	Robert et al. (2015)	14.1	ME6221	<i>Kophobelemnion</i> sp. (800–900 m)
	SPF	900–1000	Robert et al. (2015)	14.1	ME622	<i>Pennatula</i> sp. (900–1000 m)
	SPF	674–1039	ICES VME habitats records	14.1	ME622	
	SPF	463–1059	Davies et al. (2014)	14.1	ME622	Explorer, Dangaard, and East Whittard canyons

EUNIS habitat classification according to Davies et al. (2017), and the official 2022 classification (EUNIS 2022).

HBCG, hard-bottom coral garden; SBCG, soft-bottom coral garden; SPF, sea pen field.

<sup>a</sup> Depth unspecified.

When determining which studies reported on coral gardens, we exercised caution and only included studies that explicitly used the term ‘garden’ or another descriptive term that implied there were multiple colonies or individuals that could be considered a garden (e.g., dense aggregations, large patches, and increased abundance) or if there was an image of a coral garden included in the manuscript. It was sometimes difficult to distinguish between references to *D. pertusum* and *S. variabilis* reef habitat and coral gardens comprising non-reef scleractinian aggregations, as studies often focus on the habitat-forming properties of *D. pertusum* and *S. variabilis* and how that may influence the wider community diversity (Huvenne et al. 2011, Morris et al. 2013, Henry et al. 2014, Robert et al. 2015, de Clippele et al. 2019) rather than on the specific structure and density of the hermatypic scleractinian itself.

### Distribution of coral gardens

While coral gardens are widespread, only a limited number of studies provide insight into the types of coral assemblages present in UK and Irish waters. The species that comprise coral gardens are rarely reported because octocorals are rarely identified to species due to a lack of taxonomic expertise, poorly understood species boundaries, and a low-resolution species barcode (France & Hoover 2002, McFadden et al. 2011). However, recent progress has been made in identifying the octocorals present along the Irish Continental Slope (Morrissey et al. 2022b, Hogan et al. 2023).

On the Hatton Bank, multiple hard-bottom coral gardens have been observed (Howell et al. 2010). Stylasterid coral gardens have been found in areas of boulders, cobbles, and hard bedrock at 491–562 m water depth (Narayanaswamy et al. 2006). *Stichopathes* cf. *gravieri* dominated coral gardens, also containing octocorals such as *Anthomastus grandiflorus*, occur on the Hatton Bank on coral rubble habitats at depths of 616–665 m (Bullimore et al. 2013).

Species potentially indicative of coral gardens (VME indicator species) have been taken as by-catch in longlines on the Hatton Bank (Muñoz et al. 2011). Soft corals and cup corals were frequently caught in water depths of ~700–900 m and 900–1000 m, respectively, just outside the Hatton

Bank NEAFC closure zone. Large structural corals such as plexaurid sea fans, *Acanthogorgia* sp., *Acanella* sp., and other bamboo corals, the primnoids *Callogorgia verticillata* and *Primnoa resedaeformis* are present along the Western Hatton Bank (Muñoz et al. 2011) at depths of 950–2200 m. Along the south-east, east, and summit of Hatton Bank, *Paragorgia*, *Anthothela*, and *Paramuricea* have been recorded as by-catch. Further investigation using video transects could confirm whether any of these records are indicative of actual coral gardens, which would complement the known gardens of systerids and black corals on Hatton Bank.

The deep-sea biotope ‘Discrete coral (*Desmophyllum pertusum*) colonies on hard substratum’ and ‘Discrete coral (*Solenosmilia variabilis*) colonies on hard substratum’, have been observed on the south-east flank of Rockall Bank (Ross et al. 2018, La Bianca et al. 2019, 2020). Cup-coral fields are found on Rockall Bank with contrasting characterising species that vary with depth. The shallow summit biotope, 218–286 m water depth, consists of *Caryophyllia smithii* cup corals on gravelly sand in association with the anemone *Actinauge richardi* (Howell et al. 2014b). Deeper examples consisting of *Caryophyllia* corals and xenophyophores have been recorded at 1068–1651 m (Bullimore et al. 2013). Stylasterid gardens occur just below the shallow cup-coral field at 387–685 m, and their distribution has been modelled by Piechaud et al. (2015). Coral garden assemblages have been reported from the Franken Mound region on the Rockall Bank comprising discrete colonies of octocorals, antipatharians, and few *Desmophyllum*, along with sponges, hydroids, actinians, crustaceans, echinoderms, and fish, specifically associated with hard ground ridges (Wienberg et al. 2008).

Black coral dominated gardens have been observed on ROV transects at 547–874 m in the Logachev Mound Province (de Clippele et al. 2019). Densities of *Leiopathes* sp. in the eastern Logachev Mounds were 9.9–14.5 ind. m<sup>-2</sup>. Of the 1707 individuals, 1583 were *Leiopathes* sp. and 60 were *Parantipathes* sp. suggesting that even though eight species of black coral and two octocorals (*Acanella* sp. and *Paramuricea* sp.) were observed, coral gardens in that area are dominated by *Leiopathes* sp. The overall density of all observed corals increased from west to east, 0.03 ind. m<sup>-2</sup> to 0.14 ind. m<sup>-2</sup>, suggesting that more coral gardens are likely to occur closer to the summit of Rockall Bank and that conditions for coral growth are therefore more optimal in this area (de Clippele et al. 2019).

Anton Dohrn Seamount has multiple types of hard-bottom coral gardens on its flanks. Stylasterid-dominated coral gardens occur at 810 m depth on cobbled substrata (Stewart et al. 2009, Long et al. 2010, Henry & Roberts 2014a), while octocoral-dominated coral gardens are present at 1318–1740 m on the north-west and south-east flanks. On the north-west flanks at 1724–1740 m, there are gardens comprising bamboo corals (*Lepidisis* sp.) and black corals (*Parantipathes* sp.) on bedrock (Davies et al. 2015). Along the south-east flanks, coral gardens comprising bamboo corals (*Keratoisis* sp.) and *S. variabilis* on bedrock are found at 1542–1565 m associated with radial ridges (Davies et al. 2015). A mixed coral garden was observed at 1311–1598 m growing on *S. variabilis* framework. This garden comprised patches of live *S. variabilis*, *Anthomastus grandiflorus*, an unidentified species of bamboo coral, and zoanthids growing in abundance on dead octocoral skeletons (Davies et al. 2015). Cup-coral gardens comprising *Caryophyllia* sp. were found in association with xenophyophores and sea pens at 1367–1768 m water depth on cobble and softer substrata (Davies et al. 2015). Sea pen fields have also been found in association with cup corals on cobble and softer substrata (Long et al. 2010).

There is also evidence of coral gardens on George Bligh Bank. Narayanaswamy et al. (2006) described bedrock slopes and terraces deeper than 1000 m, which have characteristic fauna associated with them such as *Leiopathes* sp., other antipatharian corals, bamboo whip corals (*Lepidisis* sp.), large numbers of unidentified orange anemones, and small patches of *D. pertusum*.

Many distinct coral gardens are found in Whittard Canyon. Dense aggregations of *Primnoa* sp. and aggregations of *Anthomastus* sp. with brisingids have been observed on vertical walls (Robert et al. 2015 Figure 3F and 3K), although the depth of these observations was unspecified. Dense





**Figure 8** *Primnoa* sp. and *Solenosmilia variabilis* coral garden on a wall at ~1550 m in the western branch of the Whittard Canyon. Image is copyright of the Marine Institute and taken by ROV HOLLAND I aboard RV CELTIC EXPLORER during cruise CE16006.

aggregations of *Primnoa* sp. with patches of *S. variabilis* have also been observed at ~1550 m in the western branch of the Whittard Canyon (Figure 8). *Desmophyllum pertusum* dominated coral gardens have been reported growing under overhangs on steep walls in the eastern branch of Whittard Canyon at 1350 m water depth and associated with ‘gorgonians’ (most likely *Primnoa* sp.), *Acesta* sp. bivalves, and crinoids (Huvenne et al. 2011). A potential *S. variabilis* dominated garden was observed in the western canyon in depths of 1515–1690 m, initially identified as *D. pertusum* in Huvenne et al. (2011), but subsequently reclassified as possibly *S. variabilis* by Amaro et al. (2016). Large aggregations of *Kophobelemnon* sp. (800–900 m) and *Pennatula* sp. (900–1000 m) have been observed on soft sediments in Whittard Canyon (Robert et al. 2015) and at ~710 m in the middle eastern canyon (A.L. Allcock, pers. obs). In the eastern branch of the canyon, a soft-bottom aggregation comprising *Kophobelemnon stelliferum* with cerianthids on mud/muddy sand was found at 463–1059 m water depth, with the same biotope found in the neighbouring Explorer and Dangaard Canyons (Howell 2010, Davies et al. 2014). Further sea pen fields have been observed along the Irish Continental Margin (Ross et al. 2018, La Bianca et al. 2019, 2020) (Table 5, Figure 9) and records from the public ICES VME habitats database (ICES, 2020) list sea pen aggregations in the Porcupine Seabight at 1114–1184 m and in Whittard Canyon at 674–1039 m.

*Acanella arbuscula* coral gardens are another common habitat found on soft substrata. *Acanella* is an easily recognisable coral due to its distinctive gross morphology (alternating proteinaceous black nodes with white calcium carbonate internodes and a distinctive orange bush shape), and thus, it is widely reported in the literature. When records of *A. arbuscula* coral gardens were reviewed (Howell 2010), it was found that these gardens were widespread throughout the study area: Rockall Trough at 2500 m on pelagic ooze (Gage 1986), the North Feni Ridge at 1920 m (Hughes & Gage 2004), and at 1295 m along the Hebrides slope (Roberts et al. 2000), 2200 m from the Pendragon Escarpment at the Goban Spur (Duineveld et al. 1997, Lavaleye et al. 2002). ‘Large patches’ of *Acanella* were reported and photographed from unspecified locations on soft sediment in Whittard Canyon (Morris et al. 2013, Robert et al. 2015 Figure 3G), and further *A. arbuscula* gardens have been identified at locations spanning the entire Irish Continental Slope (Ross et al. 2018, La Bianca et al. 2019, 2020).

#### *Autecology of coral garden forming species*

The growth rates (both axial and radial) and longevity ( $^{14}\text{C}$  and  $^{210}\text{Pb}$ ) of colonies of the bamboo corals *Acanella arbuscula* and *Keratoisis grayi* as well as the primnoid *Primnoa resedaeformis* off



**Figure 9** Sea pen field from the north Porcupine Bank at ~940 m. Image taken by ROV HOLLAND I aboard RV CELTIC EXPLORER during cruise CE18012 and is copyright of the Marine Institute.

the coast of Newfoundland have been measured. The growth rates of the two bamboo corals were  $20\text{--}75\ \mu\text{m yr}^{-1}$  for radial growth and  $0.3\text{--}1\ \text{cm yr}^{-1}$  for axial growth, while the primnoid had a radial growth of  $83\text{--}215\ \mu\text{m yr}^{-1}$  and an axial growth rate of  $1\text{--}2.6\ \text{cm yr}^{-1}$  (Sherwood & Edinger 2009). By counting growth rings, similar to the logic of counting rings on a tree, the age of the 16 measured primnoids ranged from 23 to 100 years old, while the age of three *K. grayi* specimens estimated by  $^{14}\text{C}$  and  $^{210}\text{Pb}$  dating was 94–200 years (Sherwood & Edinger 2009). In the Gulf of Mexico, the radial growth rates of *Chrysogorgia* sp. and *Paramuricea* species were  $\sim 5.2\ \mu\text{m yr}^{-1}$  and  $0.4\text{--}14.3\ \mu\text{m yr}^{-1}$ , while the axial growth rates were  $0.02\text{--}0.16\ \text{cm yr}^{-1}$  and  $0.03\text{--}0.23\ \text{cm yr}^{-1}$ , respectively (Prouty et al. 2016). One individual of *Paramuricea biscaya* was dated at 660 years, while *Chrysogorgia* sp. was 525 years (Prouty et al. 2016). In eastern Canada, maximum ages of *Anthoptilum grandiflorum* and *Pennatula aculeata* colonies, estimated by counting growth rings in the axial rod, were 28 and 21 years, respectively (Murillo et al. 2018), while one *Umbellula encrinus* from Baffin Bay was estimated to be 68–75 years old with a linear growth rate of approximately  $4.5\ \text{cm yr}^{-1}$  and an axial growth rate of  $0.07\ \text{mm yr}^{-1}$  (de Moura Neves et al. 2018). Off Newfoundland, *Balticina finmarchia* colonies were a maximum of 22 years old with an average of  $4.9\ \text{cm yr}^{-1}$  linear growth (de Moura Neves et al. 2015). Sea pens seemingly grow faster and have shorter lifespans than other octocorals with an axial skeleton. Growth rates and longevity of octocoral species are summarised in Table 2.6 of Watling et al. (2011).

Off eastern Canada, the large arboreal species *P. resedaeformis* has overlapping size classes of oocyte cohorts and shows no clear signal of annual periodicity to gametogenesis (Mercier & Hamel 2011); in contrast, *K. grayi* has a clear annual cycle (Mercier & Hamel 2011). The spawning period of *A. grandiflorum* off eastern Canada closely follows the onset on the spring bloom, which varies from late April in southern Newfoundland to July in Labrador (Baillon et al. 2014). Along the Irish Margin, the remnants of phytodetritus from the spring bloom reach the bathyal seafloor between February and April (Billett et al. 1983, Bett 2001, Mienis et al. 2007) and this deposition has been shown to have an effect on bathyal meio- and macrobenthos communities (Gooday & Lamshead 1989, Lamshead & Gooday 1990, Flach & Heip 1996, Soltwedel 2000, Hughes & Gage 2004) and could influence reproduction of some megabenthic species in the North-east Atlantic (Baillon et al. 2014).

Black coral species exhibit vastly different estimates of longevity and growth (summarised in Table 2.4 of Wagner et al. 2012), but most data are from shallow species. The longest-lived species

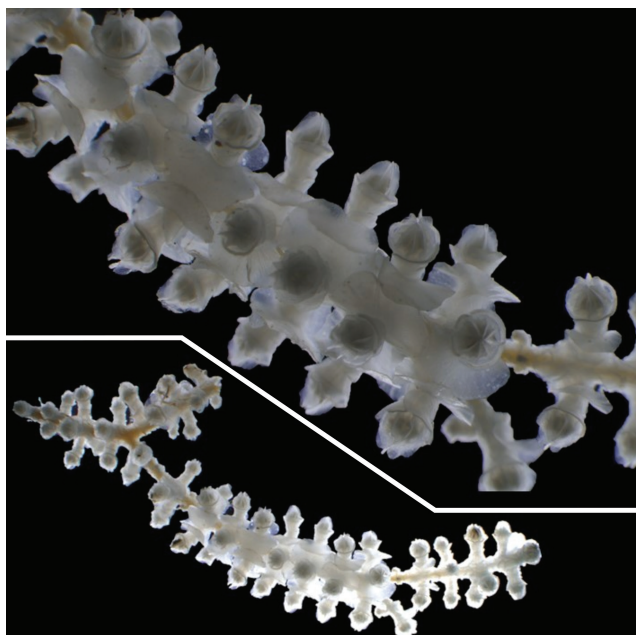
of black corals are members of the genus *Leiopathes* which have lifespans estimated to be of the order of centuries to millennia; the oldest individual had an estimated longevity of ~4250 years (Roark et al. 2009) and was collected from 400–500 m water depth in the waters off Hawaii. Most information about black corals comes from studies on individuals gathered from waters shallower than 100 m; however, off eastern Canada, *Stauropathes arctica* specimens collected in water depths of 812–876 m were estimated to be 55–88 years, with axial growth rates of 1.22–1.36 cm yr<sup>-1</sup> and radial growth rates of 33–66 µm yr<sup>-1</sup> (Sherwood & Edinger 2009), while in the Gulf of Mexico, *Leiopathes* sp. were found to be 530–2100 years old (Prouty et al. 2011). It seems that deep-sea black corals, while the focus of fewer studies, are longer lived than their shallow-water counterparts (Wagner et al. 2012); however, this could be due to greater fishing pressure or other human-mediated influences that are more prevalent in shallower waters.

With the exception of a few studies in shallow water, most knowledge on black coral reproductive strategies is gleaned from the limited information on reproductive tissues found within species descriptions (summarised in Table 1 of Wagner et al. 2011, Wagner et al. 2012). All black corals studied to date have gonochoric polyps, that is they either have oocytes or spermatocytes (Wagner et al. 2012). In the Azores, *Antipathella wollastoni* sampled from ~30 m was found to be a seasonal spawner: gametogenesis began in June/July triggered by the increase in sea-surface temperature and was completed by October (Rakka et al. 2017). *Antipathella wollastoni* occurs to a depth of 1425 m; however, it is unknown if spawning in deep-sea representatives of this species is also triggered by changes in temperature or when gametogenesis is triggered.

#### *Biodiversity associated with coral garden forming species*

Octocoral and black coral colonies can add 3-dimensional complexity to an environment and in turn act as a habitat for other invertebrate species. Large colonies and diverse morphologies add different microhabitats for a wide range of commensal fauna to inhabit. Most associations reported in the literature are transient where no facultative requirements between host and commensal exist, e.g., squat lobsters walking on a coral or crinoids perched on an exposed dead branch (Wagner et al. 2012, Parimbelli 2020). Obligate, or presumed obligate, associates are rare, possibly due to a lack of sampling in the deep sea (see Table 2.4 in Watling et al. 2011, and Table 2.5 in Wagner et al. 2012).

Many associations between octocorals and other invertebrate species have been reported. The scale worm *Gorgoniapolynoe caeciliae* (and more recently, *G. pseudocaeciliae*, Maxwell et al. 2022) is found living on octocorals of the families Paramuriceidae, Corallidae, and Primnoidae. *Gorgoniapolynoe* species modify the sclerites of their host, e.g., *Candidella imbricata*, to form a gallery that they inhabit (see Figure 9C of Britayev et al. 2014). Modifications to *C. imbricata* sclerites similar to those shown in Britayev et al. (2014) have been observed in *C. imbricata* colonies collected from the Irish Margin suggesting the relationship is also present there (Figure 10). *Asteroschema* sp. serpent stars are commonly reported on species of *Paragorgia*, *Paramuricea*, and *Metallogorgia* and have been reported on colonies of *Paramuricea* on the Irish Margin (Parimbelli 2020). Data following the Gulf of Mexico oil spill suggests *Asteroschema clavigerum* physically removes particles that could smother its host and it is thought to prevent the settlement of other invertebrates (Girard et al. 2016). Along the Irish Margin, 8.3% of all observed octocorals had a visible invertebrate association from the phyla Cnidaria, Arthropoda, and Echinodermata. Only two pennatuloidaeans from the Irish Margin have been reported with associates, and only one of these was identified: *Balticina finmarchica* hosted an ophiuroid (Parimbelli 2020). In Norway, ROV video data shows that the fauna associated with more arborescent corals, e.g., *Paragorgia arborea*, *Paramuricea placomus*, and *Primnoa resedaeformis*, is more biodiverse than that associated with sea pens (de Clippele et al. 2015) and that crustaceans are the dominant commensal organism (Buhl-Mortensen & Mortensen 2004, de Clippele et al. 2015).

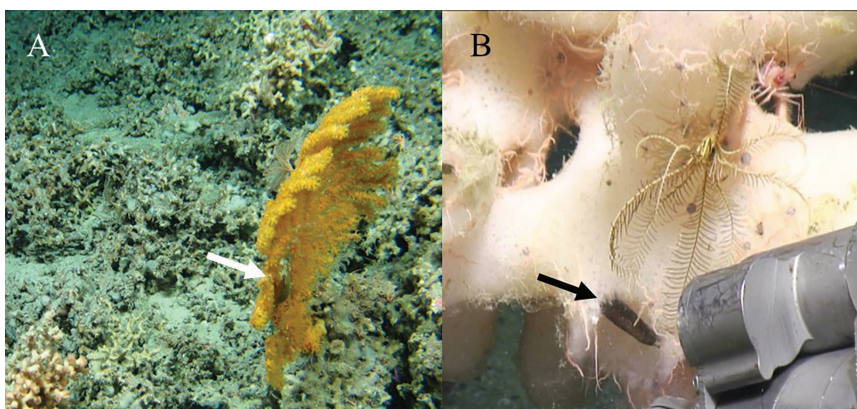


**Figure 10** Close-up of a branch from a *Candidella imbricata* colony with a gallery created by the scale worm *Gorgoniapolynoe* sp. modifying the coenenchyme sclerites. Image taken by D. Morrissey.

Within black corals, four microhabitats have been identified, surfaces of living branches, surfaces of dead branches, cavities inside tissues, and the free space between branches (Wagner et al. 2012). Many of the known faunal associations of black corals have been reported from shallow waters (less than 200m, see Wagner et al. 2012 Table 2.5), with most associations involving eumalacostracans (crustaceans), which have also been found on pennatuloidaeans and other octocorals. The most reported associations with deep-sea black corals are barnacles (Crustacea, Cirrpedia) on living branches, sometimes embedded in live tissue (Wagner et al. 2012). Other deep-sea faunal associations with black corals include polychaetes, copepods, gastropods, and other anthozoans. Along the Irish Margin, 5.6% of observed black corals had visible invertebrate associations – from the phyla Arthropoda, Brachiopoda and Bryozoa, subphylum Crustacea (including family Chirostylidae), class Asterozoa and Ophiurozoa, and the family Comatulidae (crinoids, Parimbelli 2020).

Octocorals, including sea pens, and black corals, have all been found to act as nursery grounds for commercially important fish, cephalopods, and elasmobranchs. Seapens, including *Anthoptilum grandiflorum*, *Halipterus finmarchica*, *Funiculina quadrangularis*, *Pennatula aculeata*, and *P. grandis* harbour redfish larvae (*Sebastes fasciatus* and *S. mentella*, Baillon et al. 2012), and *Acanella* sp. harbour snailfish eggs (*Paraliparis* sp., A.L. Allcock, pers. obs.). Elasmobranch eggs have been found on large black corals on Fangorn Bank (A.L. Allcock, pers. obs.), on *Paramuricea* sp. (Figure 11A), and within large sponges (Figure 11B). Catshark (*Scyliorhinus canicula*) eggs were found exclusively on *Leiopathes glaberrima* in a black coral garden in the SW of Sardinia (Cau et al. 2017), which suggests that elasmobranchs frequently attach their eggs to black corals. Cirrate octopus eggs have been observed on bubblegum corals (most likely *Paragorgia* sp.) and a *Chrysogorgia* sp. from the Pacific Ocean (Vecchione 2019), as well as on *Chrysogorgia artospira* from the New England and Corner Rise Seamounts in the North-west Atlantic (Shea et al. 2018). While not observed, this relationship between cirrate octopuses and octocorals likely exists off the Irish Margin, where several cirrate species co-exist (e.g., Collins et al. 2001).





**Figure 11** Shark eggs found on a (A) *Paramuricea* sp. and within a (B) sponge. Images are copyright of the Marine Institute and taken by ROV HOLLAND I aboard RV CELTIC EXPLORER during cruise CE18012.

### *Deep-sea sponge aggregations*

Sponges are important components of deep-sea benthic ecosystems. They are capable of creating complex habitats, and particularly on soft sediments, they can alter the composition of the local substratum they occupy through the production of large spicule mats (Bett & Rice 1992, Meyer et al. 2019). Sponge aggregations, such as those formed by *Geodia barretti*, can filter  $250 \times 10^6 \text{m}^3$  per day over a  $300 \text{km}^2$  area, consuming 60 t of carbon (Kutti et al. 2013), making these habitats important compartments of benthic–pelagic coupling by turning dissolved organic matter (DOM) into particulate organic matter (POM) (de Goeij et al. 2013, Bart et al. 2021). Off the west coast of Canada glass sponge reefs comprising *Heterochone calyx*, *Farrea occa*, and *Aphrocallistes vastus* are known from Queen Charlotte Basin (Conway et al. 2006). There are relatively few reports of glass sponge reefs on hard bottoms in the North Atlantic with known occurrences including the *Poliopogon amadou* reef at ~2700 m on the Great Meteor Seamount south of the Azores (Xavier et al. 2015), *Asconema setubalense* aggregations on seamounts off Portugal and the Canary Islands (Maldonado et al. 2015), the *Vazella pourtalesi* sponge reef at 75–275 m water depth along the Scotian Shelf (Beazley et al. 2018), and a mixed sponge reef with *Phakellia*, *Axinella*, and other sponge species off Norway (Buhl-Mortensen et al. 2019). Recently, examples of hard-bottom glass reefs, including mixed sponge reef dominated by *Phakellia* and encrusting sponges, areas dominated by stalked crinoids, sponges, and corals, and examples dominated by lobose sponges and stylasterids have been reported in the Irish and UK EEZs (Ross et al. 2018, La Bianca et al. 2019, 2020). Most notably, a dense aggregation of the glass sponge *Aphrocallistes* sp. was reported at 1125 m on the South Rockall Bank (O’Sullivan et al. 2018, La Bianca et al. 2019). The aggregation was recorded from a single dive, during a survey which aimed for wide spatial coverage rather than detailed community analysis, so little information on this habitat is yet available (but see La Bianca et al. 2019).

Three well-defined habitats are formed by aggregations of sponges on soft sediment (Howell 2010). The first two, boreal ostur and cold-water ostur, are formed by dense aggregations of astroporhiid demosponges (Klitgaard & Tendal 2004). Boreal ostur are found around the Faroe Islands, Norway, Sweden, the western Barents Sea, and south of Iceland, and are characterised by *Geodia barretti*, *G. macandrewi*, *G. atlantica*, *Isops phlegraei*, *Stryphnus ponderosus*, and *Stelletta normani* (Klitgaard & Tendal 2004). Cold-water ostur are found North of Iceland, in the Denmark Strait, off eastern Greenland, and north of Spitzbergen (Svalbard archipelago), and are composed of *Geodia hentscheli*, *Isops phlegraei pyriformis*, and *Stelletta raphidiophora* (Klitgaard & Tendal



2004). *Geodia* species are thought to be constrained and shaped by water masses, with boreal species associated with Upper and Intermediate Atlantic Water and Atlantic-derived water in the Nordic Seas, while cold-water species are associated with Arctic intermediate and deep-water masses in the Nordic Seas (Roberts et al. 2021). *Geodia* species are known to occur along the North-western European Margin; however, there are no reported occurrences of dense aggregations along the Irish Margin.

The other recognised habitat-forming sponge on soft sediment is the spherical glass sponge *Pheronema carpenteri* (Rice et al. 1990). Along the Irish Margin, huge aggregations have been reported on soft sediments, at densities up to 1.53 ind. m<sup>-2</sup> (Rice et al. 1990, Hughes & Gage 2004, Vieira et al. 2020) and 2.4 ind. m<sup>-2</sup> at the North-east Rockall Bank (Piechaud & Howell 2022). *Pheronema carpenteri* individuals anchor themselves with tufts of long spicules projecting into soft substrata. The Rockall-Hatton Basin Nature Conservation MPA is the only MPA designated for the protection of *P. carpenteri* aggregations (<https://jncc.gov.uk/our-work/hatton-rockall-basin-mpa/>). Due to their important ecological functions and the potential impacts of fishing activities on them, *P. carpenteri* aggregations have been listed as VMEs.

#### *Pheronema carpenteri* known distributions and density

Within the study area, *P. carpenteri* has been reported at high abundances in a narrow bathyal depth band, 930–1450 m, from the Goban Spur (1450 m: Duineveld et al. 1997, Flach et al. 1998, Lavaleye et al. 2002), the Porcupine Seabight (1000–1300 m: Rice et al. 1990, Vieira et al. 2020), from Ireland to Spain in 1000–2000 m water depth (Le Danois 1948) and the Rockall-Hatton Basin (1100 m, Hughes and Gage 2004, Howell et al. 2007, Muñoz et al. 2012). It also occurs in Whittard Canyon (950–1317 m, A.L. Allcock, pers. obs.) (Table 6). The dense aggregation in the narrow band at the Porcupine Seabight has been attributed to the complex hydrodynamics of the region. Rice et al. (1990) hypothesised that areas of *P. carpenteri* aggregations lie downslope of regions of amplified near-bottom currents as a result of tidally generated internal waves, favouring downslope transport of suspended materials to the *P. carpenteri* aggregations. However, increased near-bottom currents are likely primarily caused by bottom-trapped baroclinic diurnal tides, although internal wave reflection could act as an additional component (White 2003). A recent study suggests that *P. carpenteri* density in this area is related to regions of intermediate variability in temperature and salinity, used as a proxy for internal waves (Graves et al. 2022). Other sponge aggregations have been found in areas of complex hydrography. Along the Scotian Shelf, *Vazella pourtalesii* aggregations are found in areas where semi-diurnal tides promote constant resuspension of particulate matter in the benthic boundary layer (Hanz et al. 2021a), and along the Schulz Bank, a sponge aggregation is found at the boundary of two water masses where semi-diurnal tides promote turbulent mixing

**Table 6** Reports of sponge aggregations throughout the Irish and UK Exclusive Economic Zones

Location	Depth (m)	References	Notes
<b><i>Pheronema carpenteri</i> reefs</b>			
Rockall-Hatton Basin	1100	Hughes & Gage (2004), Howell et al. (2007), Muñoz et al. (2012)	
Porcupine Seabight	1000–1300	Rice et al. (1990), Vieira et al. (2020)	
Goban Spur	~1450	Duineveld et al. (1997), Flach et al. (1998), Lavaleye et al. (2002)	
Whittard Canyon	950–1317	A.L. Allcock, pers. obs.	
<b>Glass sponge reefs</b>			
South Rockall Bank	1125 m	O'Sullivan et al. (2018), La Bianca et al. (2019)	<i>Aphrocallistes</i> sp.

Note that depths relate to the depths of video transects from which the species was recorded, not the actual depth of the species as video transects may encompass broad depth ranges.

(Hanz et al. 2021b). There is also evidence for complex interactions between sponge diversity and internal waves; in the Faroe-Shetland channel where demosponges (*Geodia* spp.) are found in the highest abundance at 400–600 m, the depth range associated with the critical slope angle for internal semi-diurnal tidal waves, which increase the suspended particulate matter in the area (Davison et al. 2019).

A combination of trawl and photographic data collected in 1986 showed high spatial variability in the distribution of *P. carpenteri* in the Porcupine Seabight, with dense sponge aggregations encountered in a narrow bathymetric zone, 1000–1300 m (Rice et al. 1990). Re-examination of the same study area in 2011, using comparable methods, found that in the ~25 years between the two surveys, the mean densities of *P. carpenteri* had dropped 20-fold from 0.39 ind. m<sup>-2</sup> to 0.02 ind. m<sup>-2</sup> (Vieira et al. 2020). Maximum densities fell from 1.6 ind. m<sup>-2</sup> at 1200 m (Rice et al. 1990) to 0.03 ind. m<sup>-2</sup> (Vieira et al. 2020). Additionally, barrel diameter and wet biomass estimates were significantly lower in the later study. Vieira et al. (2020) provided images of trawl marks in the sediment and suggested decreases could be due to increased fishing pressures in the area, noting that OSPAR fishing pressure data from 2009–2017 indicate that bottom trawling occurred in the vicinity of the study site. However, due to a lack of data between the 1986 and 2011 surveys, it is difficult to assign definitive cause and effect to bottom trawling and the reduced densities of *P. carpenteri* (Vieira et al. 2020). Densities of *P. carpenteri* in 2011 in the Porcupine Seabight are two orders of magnitude lower than those reported from the Rockall-Hatton Basin (1.53 ind m<sup>-2</sup>, Hughes & Gage 2004). The Rockall-Hatton Basin was surveyed between April and July 1998 using both imagery from a mounted camera and catch data from an epibenthic sled, and densities were similar to those originally observed in the Porcupine Seabight. In 1998, there were no protection measures in place in the Rockall-Hatton Basin. Following a resurvey of the area in 2006 and 2012 (Howell et al. 2007, 2014b), the Rockall-Hatton Basin was designated an MPA in July 2014 and NEAFC fishery closures were brought into effect in 2017. A deep-sea fishery started on the Hatton Bank in 1996, with fishing pressure concentrated in the south, north, and west Bank. There was little pressure in the east where the highest abundance of *P. carpenteri* was reported, and a more recent survey did not note any evidence of fishing impacts. As with all VMEs, fishing pressure is likely the greatest threat, as exemplified in the Faroe-Shetland Sponge Belt MPA, where fishing pressure has been shown to be the main driver of differences in sponge biodiversity inside and outside the protected area (Kazanidis et al. 2019).

#### *Physiology and autecology of Pheronema carpenteri*

Despite the importance of *P. carpenteri* as a habitat-forming species, there is little empirical information about its autecology. For example, there are no direct experimental studies of the temperature tolerance of *P. carpenteri* and no studies of growth rate. Habitat models suggest that it inhabits a narrow temperature range of 6–8°C (Howell et al. 2022). The closest comparable species where growth was recorded is *Asconema setubalense*, another deep-sea hexactinellid. Growth rates of 2.2 cm yr<sup>-1</sup> (sponge diameter) were calculated for *A. setubalense* in the Cantabrian Sea using Structure-from-Motion to obtain morphometric measurements from 3-dimensional photogrammetry (Prado et al. 2021). Height, diameter, cup perimeter, and cup surface area were measured from 3-dimensional models constructed from image transects in 2014, 2017, and 2019 to derive this growth rate. In comparison, a shallow-water hexactinellid, *Rhabdocalyptus dawsoni* from British Columbia, was estimated to grow at 2.0 cm yr<sup>-1</sup> based on length measurements from 2-dimensional photographs taken twice yearly for 3 years (Leys & Lauzon 1998). While these growth estimates of hexactinellids are similar, it is unknown whether the optimal oceanic conditions that allow the dense sponge aggregations of *P. carpenteri* along the narrow bathymetric range on the Porcupine Seabight and Rockall Banks are optimal for growth of individual sponges within the aggregation or whether growth rates are density dependent.

Nothing is known about the reproductive strategies of *P. carpenteri*, except for presumptions based on observations of other hexactinellid species. For example, as all hexactinellid sponges examined to date are viviparous (Leys & Ereskovsky 2006), it is presumed that *P. carpenteri* is the same. It has also been suggested that deep-water hexactinellids may experience seasonality in growth rates and life-history strategies (Leys and Lauzon 1998). In the Porcupine Seabight, where large densities of sponges have been reported (Rice et al. 1990), there is known seasonal phytodetrital input into the deep-water benthos between April and May (Billett et al. 1983, Rice et al. 1994). It may not be unreasonable to think that *P. carpenteri* sponges may exploit the increase in phytodetrital input, as other benthic organisms do (Gooday & Lamshead 1989, Lamshead & Gooday 1990). However, sponges can uptake a large range of food sources including DOM and microorganisms of varying sizes, and they vary considerably in both their assimilation efficiency and food preferences (Bart et al. 2020). While sponges are also capable of assimilating both DOM and bacteria, hexactinellids are more efficient than demosponges at assimilating bacteria (Bart et al. 2020). Furthermore, sponges with a high microbial abundance have a DOM uptake that is up to five times lower, yet is more efficient, than low microbial abundance sponges (Bart et al. 2020).

### *Modelling the distribution of Pheronema carpenteri*

Maxent habitat suitability models have been used to predict the occurrence of *P. carpenteri* aggregations on a large scale in the North Atlantic (Howell et al. 2016a), as well as on finer scales in UK and Irish waters (Ross & Howell 2013, Ross et al. 2015). The North Atlantic model (Howell et al. 2016a), constructed with environmental layers gridded at 1 km and 117 presence records, predicted a distribution broadly following the known distribution for the habitat, including the Darwin Mounds, Rockall-Hatton Basin, Porcupine Seabight, and Goban Spur. Depth was the most important single variable predictor of the species. While temperature was not strongly correlated with depth, both variables are known proxies of many other parameters, and variables not considered, such as current speed and substratum, might also be important. When just the Irish and UK EEZ were modelled at a slightly finer scale (750 m grids, 53 occurrence records, Ross & Howell 2013), the predicted distribution of *P. carpenteri* aggregations was patchier along the continental slope and Porcupine Seabight than predicted at the coarser scale. Only 2.3% of the predicted distribution of *P. carpenteri* aggregations within the Irish and UK EEZs fell within an MPA (3.2% in the UK and 1.1% in Irish waters). Again, bathymetry was identified as the most important predictor in both the 1 km and 750 m resolution models. When variables were gridded at a higher resolution (200 m grids, 74 occurrence records, Ross et al. 2015) and combined with more occurrences of *P. carpenteri*, the predicted extent of *P. carpenteri* was 53% greater than the extent predicted by the 750 m low-resolution model. The high-resolution model predicted increased habitat suitability along the slopes of the Rockall Trough and Porcupine Seabight, with 2.9% occurring in an MPA. While bathymetry was again identified as the most important variable, slope was also important in this high-resolution model. This could be due to the finer cell size detecting the potential relationship between slope and internal waves (Ross et al. 2015), which was the original hypothesis proposed to explain the distribution of *Pheronema* aggregations in the Porcupine Seabight (Rice et al. 1990, although see White 2003).

Independent validation of model outputs using biological data from transects of five research cruises from the Irish and UK EEZs suggested poor model performance (Howell et al. 2022). New models constructed from 139 occurrences (merging previous data with the new occurrences from the independent validation dataset) and high-resolution environmental layers gridded at 200 m were not dissimilar to previous models (e.g., Ross et al. 2015), but there were notable differences, particularly at Hatton Bank (Howell et al. 2022). While the predicted extent of *P. carpenteri* aggregations is reduced significantly from 218,726 km<sup>2</sup> (Ross & Howell 2013) to 54,289 km<sup>2</sup> (Howell et al. 2022), the amount of habitat predicted to occur in MPAs had risen to 11% (Howell et al. 2022). The amount of habitat protected varies nationally, with 49% in the UK and only 4% for Ireland. The addition of

multiple MPAs in the UK between 2015 and 2020 and the exclusion of part of the UK continental shelf from the model due to a lack of high-resolution bathymetry data suggest that the proportion of predicted habitat within an MPA is likely an over estimation (Howell et al. 2022).

Two unconnected metapopulations of *P. carpenteri*, separated by the Rockall Trough, were found in the UK and Ireland when dispersal scenarios were incorporated into the 750m resolution model (Ross et al. 2019). The northern population included Hatton Bank and Hatton Basin, while the southern included the Gollum Channel, Porcupine Seabight, and Porcupine Bank. Within each population, up to 53.1% of predicted habitat could be reached in a single dispersal event implying a high level of within-population connectivity. The latest 200m resolution model (Howell et al. 2022) predicts a 4-fold decrease in predicted *P. carpenteri* extent compared with the 750m resolution model, potentially making the reported connectivity an overestimate due to the substantially reduced extent of predicted habitat. Combining dispersal and distribution models clearly showed that both metapopulations need to be conserved to ensure long-term survival of this VME.

#### *Macrofaunal diversity associated with sponges*

Sponge reefs are biodiversity hotspots, on par with tropical coral reefs (Maldonado et al. 2015). *Pheronema carpenteri* and other sponges can alter the surrounding environment by forming large dense aggregations. The spicule mats which form around them modify and stabilise the sediment and can affect faunal associations by providing hard substrata for attachment of diverse species (Bett & Rice 1992, Barthel 1992, Beazley et al. 2015, McIntyre et al. 2016). For example, in Antarctica, areas with high hexactinellid biomass and dense spicule mats have been shown to be species rich, whereas areas with very fine sediment were species poor (Barthel 1992). Furthermore, there were only small, presumed young, individuals of the hexactinellid *Rosella racovitzae* where spicule mats were absent, whereas *R. racovitzae* grew much larger (Barthel 1992) in densely spiculed areas. Dense aggregations of *P. carpenteri* at 1000–1300m water depth in the Porcupine Seabight have produced large dense spicule mats which have altered the composition of fauna present when compared with nearby areas directly below (>1500m) and above (<900m) the sponge aggregation (Bett & Rice 1992). Gastropods were more common on the dense spicule mats, while sipunculids were more common at shallower depths. Overall, the total abundance of fauna between densely spiculed areas and less densely spiculed areas did not differ significantly, although community composition did. Spicule density was found to be a driver of faunal community structure, as was depth.

When Vieira et al. (2020) revisited the known sponge belt in the Porcupine Seabight, they found two peaks of increased megabenthic biomass in the associated invertebrate community. The first peak was at 1190m and was associated with a diverse invertebrate community with living *P. carpenteri* sponges. The second peak corresponded to the most dense area of *P. carpenteri* found by Rice et al. (1990), now presumed lost to trawling activity (see above). Vieira et al. (2020) suggested that the dense spicule mat left behind by the former aggregation provides hard substrata for the now large population of ascidians present. Spicule mats may provide further substratum for other sponges to settle (Barthel 1992, Leys et al. 2004). Therefore, even when sponge grounds are altered due to fishing pressures, or naturally ‘wander’ over time (Barthel et al. 1996), hexactinellids have the potential, as with corals, to cause a succession of macrofaunal communities and can promote the growth of more sponges.

#### *Xenophyophore aggregations*

Xenophyophores are single-celled protists that are confined to water depths greater than 400m (Tendal 1972) ranging in size from a couple of millimetres to 25cm in diameter (Levin 1994). They have a global distribution and are commonly found in both Atlantic and Pacific basins. They are abundant in the North-east Atlantic, where their aggregations form VME habitats. Similar to sponges and corals, they are found in areas with increased organic matter availability adjacent to areas of increased currents. They are important structural habitats for other organisms and function

as fish nurseries (Levin & Rouse 2019). *Syringammina fragilissima* is a common xenophyophore in the Irish and UK EEZs. Xenophyophores are large and have a unique agglutinated test that makes them easily identifiable and thus quantifiable in photographic surveys.

### *Xenophyophore aggregation distribution*

Xenophyophore aggregations have been found across Irish and UK waters in water depths of 798–2270 m (Table 7). In a review of the known distribution of xenophyophore aggregations in the North Atlantic (Howell 2010), it was found that these aggregations are widespread in the study area: in the ‘tails’ of the Darwin Mounds at 950 m at densities of up to 7 m<sup>-2</sup> (Bett 2001); the northern Feni Ridge, Rockall Trough at 1920 m, BENBO site C (Gooday & Hughes 2002); and in mud habitats along the northern Hatton Bank at water depths of 798–855 m (Narayanaswamy et al. 2006, Roberts et al. 2008). More aggregations have been recently observed on video transects at 900–1500 m in and around the South-east Rockall Bank SAC (O’Sullivan et al. 2018, La Bianca et al. 2019), at ~1200 m at the North-east Rockall Bank (Piechaud & Howell 2022), further west on the Fangorn Bank at 1357–1536 m (A.L. Allcock, pers. obs.), on Anton Dohrn Seamount (Davies et al. 2015, see below), and the Hebrides slope (Roberts et al. 2000, Hughes 2014).

*Syringammina fragilissima* dominates two different biotopes on the Anton Dohrn Seamount, which both occur proximal to topological features that induce higher current speeds (Davies et al. 2015). The first occurs on both the north-west and south-east of the seamount at 1076–1544 m and includes ophiuroids and sponges on a mixed pebble dominated substratum. The second is on the north-west of the seamount at 1714–1770 m, where *S. fragilissima* is associated with solitary stony corals (Caryophylliidae) and occurs on gravelly sand and mixed substratum (Davies et al. 2015).

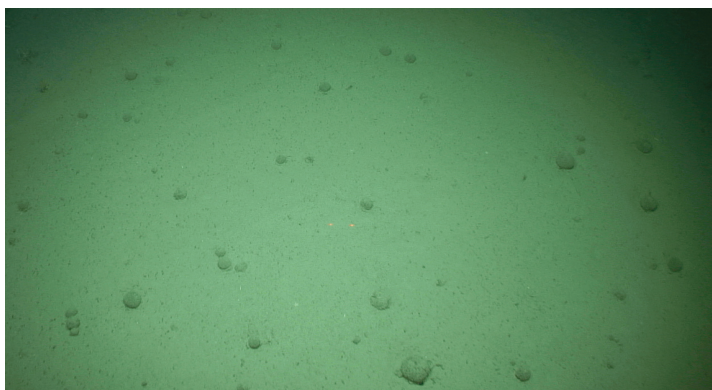
In the northern part of the Hebrides slope, located just below the Wyville-Thomson Ridge, xenophyophores were found in dense aggregations at water depths of 992–1300 m (Roberts et al. 2000, Hughes 2014) with mean densities of 2–10 ind. m<sup>-2</sup> (Roberts et al. 2000), but highest densities of 10 ind. m<sup>-2</sup> (Roberts et al. 2000) and 8.3 ind. m<sup>-2</sup> (Hughes 2014) at 1000–1100 m. These xenophyophores were typically ~5 cm in diameter, but individuals up to ~15 cm were recorded (Roberts et al. 2000). Xenophyophores have been observed on ROV video transects taken at 679–2270 m along the North

**Table 7** Reports of xenophyophore aggregations throughout the Irish and UK Exclusive Economic Zones

Location	Depth (m)	Reference
Wyville-Thomson Ridge	888–1238	ICES VME habitat records, Howell et al. (2014b)
North Rockall Bank	861–1443	Howell et al. (2014b)
North-east Rockall Bank	~1200	Piechaud & Howell (2022)
South-east Rockall Bank	900–1500	O’Sullivan et al. (2018), La Bianca et al. (2019)
Northern Hatton Bank	798–855	Narayanaswamy et al. (2006), Roberts et al. (2008)
Fangorn Bank	1357–1536	A.L. Allcock, pers. obs.
Anton Dohrn Seamount	1076–1544, 1714–1770	Davies et al. (2015)
Northern Hebrides slope	992–1300	Roberts et al. (2000), Hughes (2014)
	1367–1608	ICES VME habitat records
North Porcupine Bank and Goban Spur	679–2270	O’Sullivan et al. (2017), Ross et al. (2018)
Whittard Canyon system: Eastern and Western branches	1200	Robert et al. (2015), La Bianca et al. (2020)
Whittard Canyon system: Middle western branch	1104–1058, 2820	A.L. Allcock, pers. obs.
Whittard Canyon system: Middle eastern branch	1065–1337	A.L. Allcock, pers. obs.

Note that depths relate to the depths of video transects from which the species was recorded, not the actual depth of the species. Video transects may encompass broad depth ranges.





**Figure 12** Xenophyophore aggregation located at 2820m in the middle western branch of the Whittard Canyon system. Image is copyright of the Marine Institute and taken by ROV HOLLAND I aboard RV CELTIC EXPLORER during cruise CE14009.

Porcupine Bank, in the Porcupine Seabight, and Whittard Canyon (O’Sullivan et al. 2017, Ross et al. 2018, La Bianca et al. 2019, 2020). In fact, xenophyophore aggregations are reported from all four main branches of the Whittard Canyon, 1200m in the eastern and western branches (Robert et al. 2015), observed during ROV transects in the middle western branch at 1104–1058 m and at 2820 m (Figure 12), and during transects in the middle eastern canyon at 1065–1337 m (A.L. Allcock, pers. obs.).

#### *Modelling the distribution of xenophyophores and xenophyophore aggregations*

A low-resolution Maxent global habitat suitability model, constructed from 40 grid squares (30 arcseconds in extent), containing *Syringammina fragilissima* occurrences, predicted that *S. fragilissima* is largely restricted to the North Atlantic (Iceland’s continental slope, the Iceland-Faroe Rise, the Reykjanes Ridge, the Mid-Atlantic Ridge near the Azores, Rockall Bank, Hebrides Terrace, Anton Dohrn, Rosemary Bank, Wyville-Thomson Ridge), isolated regions of the Madagascar Plateau, and the Campbell Plateau in New Zealand (Ashford et al. 2014). The model is potentially spatially biased as most input occurrences are from Rockall Bank and the Irish EEZ. Although it may be less reliable globally, it is a valuable tool to inform conservation management in Irish and UK waters. Depth was isolated as the single most important predictor of *S. fragilissima* in this model. A regional Maxent habitat suitability model of *S. fragilissima* aggregations using environmental data gridded at 750m predicted *S. fragilissima* aggregations to be widespread across the Irish and UK EEZs, along the Irish and Scottish continental slope, Rockall Bank and Hatton Bank, and Anton Dohrn Seamount with 6.1% of the distribution located inside an MPA (Ross & Howell 2013). Known habitat located on geomorphic features less than 750m in extent, such as carbonate mounds, would not be properly represented in a model of this resolution leading to an overestimation of the predicted extent (Ross & Howell 2013). When modelled using high-resolution (200m grid) environmental data, the predicted extent of *S. fragilissima* aggregations was only 83% of that predicted by low-resolution models (Ross et al. 2015). The predicted extent of the high-resolution (200m) model is broadly in agreement with the model of Ashford et al. (2014), but the former identifies a higher occurrence for *S. fragilissima* aggregations on the Western Rockall Plateau near Edoras and Fangorn Banks, as well as along the Porcupine Seabight and Goban Spur. Depth was identified as the most important predictor of *S. fragilissima* aggregations in low-resolution global (Ashford et al. 2014) and regional models (Ross & Howell 2013) and high-resolution regional models (Ross et al. 2015).

#### *Biodiversity associated with xenophyophores*

Xenophyophores can modify the surrounding metazoan communities (Levin & Thomas 1988). In the North-east Pacific, macrofaunal and meiofaunal abundances were significantly elevated in the sediment directly below xenophyophores at water depths of 1239–3353 m when compared to

communities examined from sediments taken 1 m away (Levin & Thomas 1988). Both meiofaunal and macrofaunal abundances were greater in the sediments beneath xenophyophore tests with ophiuroids, isopods, and tanaids increasing most in the macrofauna, and nematodes and harpacticoid copepods in the meiofauna (Levin & Thomas 1988). The presence of xenophyophores did not affect the vertical distribution of either macrofauna or meiofauna in the sediment (Levin & Thomas 1988). Xenophyophores in the North-east Atlantic may play a similar role in altering the meiofaunal and macrofaunal assemblages in their habitats.

Xenophyophore tests can act as a habitat with polychaetes, ophiuroids, peracarid crustaceans, nematodes, and harpacticoid copepods all found living on the tests (Levin & Thomas 1988). Some metazoans, especially polychaetes and isopods, have been found exclusively on tests (Levin 1991). Density, but not species richness or diversity, of Foraminifera is significantly greater on *S. fragilissima* tests (160–664 ind. per 10 cm<sup>3</sup>) compared with the surrounding sediment (55–110 ind. per 10 cm<sup>3</sup>, Hughes & Gooday 2004) and many of the abundant species are common to both habitats (e.g., *Nonionella iridea* and *Epoindes pusillus*).

In the North-west Atlantic, a high density of juvenile ophiuroids lives on and under the tests of xenophyophores (Levin et al. 1986), which may act as a nursery by providing shelter from predators (Levin 1991). In the North-east Atlantic, xenophyophore aggregations located in water depths of 600–1000 m on the Hebrides slope were associated with high densities of the ophiuroid *Ophiocten gracilis* (Hughes & Gage 2004), and a xenophyophore and ophiuroid biotope was found at 1076–1544 m on Anton Dohrn Seamount (Davies et al. 2015). However, there is no indication of the size of the ophiuroids associated with these xenophyophore aggregations, and the association may simply be explained by both groups having an overlapping habitat preference.

### *Less well-studied VMEs*

#### *Bivalve reef*

In the middle western branch of the Whittard Canyon, at 633–762 m water depth, an *Acesta excavata* dominated biotope with the deep-water oyster *Neopycnodonte zibrowii*, *Desmophyllum dianthus*, and *Madropora oculata* has been reported on vertical walls at the canyon heads where there is increased organic matter due to the presence of internal waves (Johnson et al. 2013). This habitat is present elsewhere in the Whittard Canyon system where the heads of canyon branches have similar topology (A.L. Allcock, pers. obs.). The mean size of *A. excavata* in this habitat in Whittard Canyon is >10 cm (Johnson et al. 2013). This size is thought to be reached by around 20 years of age with the typical lifespan of *A. excavata* estimated at 50–80 years (Correa et al. 2005). The maximum lifespan of *Neopycnodonte zibrowii* individuals from approximately 500 m depth in the Azores was estimated by radiocarbon dating at 523 years (Wisshak et al. 2009).

#### *Serpulid habitat*

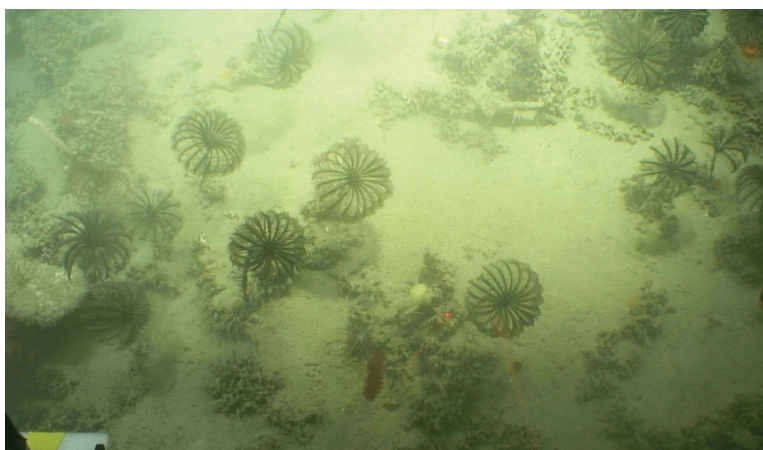
Within the Irish and UK EEZs, serpulid habitats have been found on the summit of Anton Dohrn at 813–1016 m water depth in association with encrusting sponges and holothurians on a mixed substratum (Davies et al. 2015), and along the flanks of upper Dangaard Canyon between 691 m and 764 m in association with brachiopods in soft sediment (Davies et al. 2014).

#### *Tube-dwelling or burying anemone aggregations*

Aggregations of anemones have been described across the study area including Hatton Bank, Rosemary Bank Seamount, Dangaard and Explorer Canyons, and the Wyville-Thomson Ridge at 321–1006 m water depth (Howell 2010, Table 8), which include communities dominated by hexacorallians, for example, halcampoidid anemones anchored into soft sediments (Howell 2010) as well as those dominated by cerianthids. The VME designation is typically only associated with ceriantharian aggregations, although hexacorallian aggregations dominated by burrowing anemones may

**Table 8** Locations of less well-studied VMEs within the focal area

Location	Depth (m)	References	Notes
<b>Anemone aggregations</b>			
Wyville-Thomson Ridge (north)	518–809	Howell (2010)	Halcampoididae in sand
Hatton Bank	321–1006	Howell (2010)	Halcampoididae on coarse sediment
Rosemary Bank Seamount		Howell (2010)	Halcampoididae
Whittard Canyon system: Main branches	413–1019	ICES VME habitats records	
Whittard Canyon system: Dangaard and Explorer Canyons		Howell (2010)	
Irish Continental Margin	310–1100	Ross et al. (2018), La Bianca et al. (2019, 2020)	
<b>Stalked crinoid fields</b>			
Irish Continental Margin	1866–2318	Ross et al. (2018), La Bianca et al. (2019, 2020)	<i>Anchalypsicrinus nefertiti</i> or <i>Democrinus</i>
Whittard Canyon system: Middle eastern branch	~1500	A.L. Allcock, pers. obs.	<i>Endoxocrinus wyvillethomsoni</i>
	2164–2292	A.L. Allcock, pers. obs.	Mixed assemblage
Whittard Canyon system: Middle western branch	2496–2546	A.L. Allcock, pers. obs.	Mixed assemblage on canyon walls



**Figure 13** Stalked crinoid field comprising *Endoxocrinus wyvillethomsoni* located at ~1500 m in the middle eastern branch of the Whittard Canyon system. Image is copyright of the Marine Institute and taken by ROV HOLLAND I aboard RV CELTIC EXPLORER during cruise CE14009.

also meet the criteria for definition as a VME. Further aggregations have been reported from the wider Irish Continental Slope over a similar depth range and also on soft sediment (Ross et al. 2018, La Bianca et al. 2019, 2020).

#### *Stalked crinoid aggregations*

Stalked crinoid fields have been observed in the Whittard Canyon system: a monospecific *Endoxocrinus wyvillethomsoni* field at ~1500 m in the middle eastern canyon (Table 8, Figure 13); a mixed species assemblage found at water depths of 2164–2292 m in the same canyon branch and on canyon walls at 2496–2546 m in the middle western branch (Table 8, Figure 14). Other stalked



**Figure 14** Multispecies crinoid field located between 2496 m and 2546 m in the middle western branch of the Whittard Canyon system. Image is copyright of the Marine Institute and taken by ROV HOLLAND I aboard RV CELTIC EXPLORER during cruise CE13008.

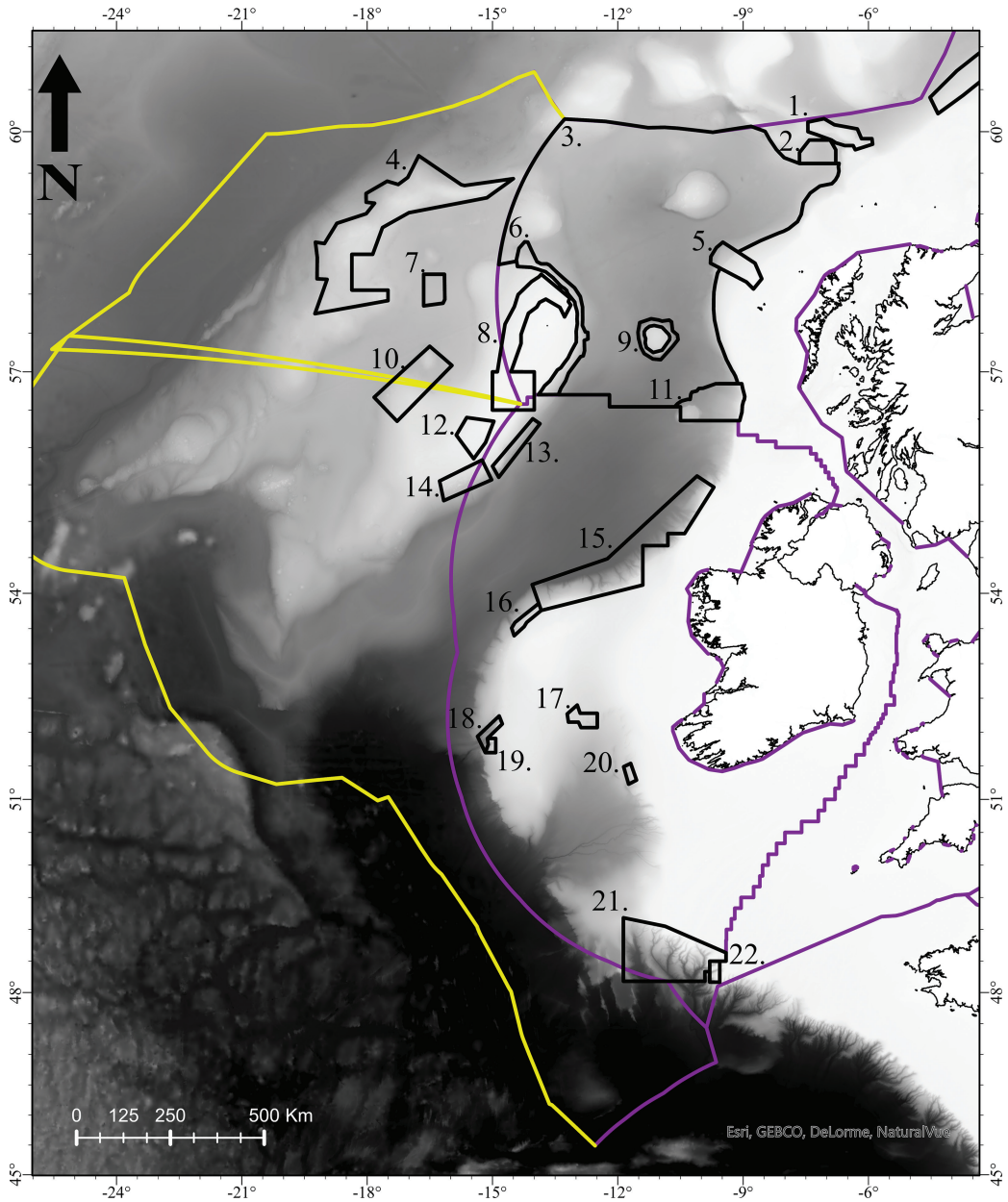
crinoid fields have been found throughout the Irish Continental Margin at water depths of 1866–2318 m dominated by *Anchalypsicrinus nefertiti* in rocky areas or *Democrinus* in soft sediment areas (Ross et al. 2018, La Bianca et al. 2019, 2020). Absolute longevity of stalked crinoids has not been established, but studies have reported individuals more than 20 years old both in relatively shallow waters around Grand Cayman (*Cenocrinus asterius* in 215 m, Messing et al. 2007) and deep waters of the North-east Atlantic (*Endoxocrinus wyvillethomsoni*, Roux 1976). This, and their fragile nature, reinforces stalked crinoids as characteristic taxa of VMEs.

### Legislation protecting VMEs

The European Union (EU) has passed two regulations for the protection of sensitive habitats by managing fishing within its waters. EU regulation 2016/2336 restricts bottom trawling to the 2009–2011 footprint at depths greater than 400 m in areas where VMEs are known or likely to occur, and a blanket ban on bottom trawling at depths greater than 800 m to protect VME species. These regulations are currently still in effect in the UK, transposed into UK law as part of The Common Fisheries Policy and Aquaculture (Amendment etc.) (EU Exit) Statutory Instrument (S.I) 2019 No. 753, and The Common Fisheries Policy and Animals (Amendment etc.) (EU Exit) Regulations 2019 S.I. 2019, No. 1312. The ban on trawling below 800 m is estimated to protect 42% of predicted *Desmophyllum pertusum* reef habitat (Howell et al. 2022). Many Marine Protected Areas (MPAs) and Special Areas of Conservation (SACs) already exist in both Irish and UK waters which protect VME habitats. EU regulation 2019/1241 closes the North-western Porcupine Bank Special Area of Conservation (SAC), South-western Porcupine Bank SAC, Hovland Mound Province SAC, and the Belgica Mound Province SAC for the protection of VME habitats. In 2023, two candidate new SACs were created in Irish waters for the protection of deep reef habitat: Porcupine Shelf SAC and the Southern Canyons SAC. In UK waters, SACs receive protection from fishing activities via the aforementioned statutory instruments; this includes the Wyville-Thomson Ridge SAC, North-west Rockall SAC, East Rockall Bank SAC, Anton Dohrn SAC, and the Darwin Mounds SAC (Figure 15). This is also the case for the West of Scotland MPA, Geike Slide and Hebrides Slope MPA, and The Barra Fan and Hebrides Terrace Seamount MPA. Within the Canyons MCZ, a new bye-law prohibits the use of bottom towed fishing gear, demersal seines, and anchored nets and lines.



THE NORTH-EAST ATLANTIC MARGIN



**Figure 15** Location of Marine Protected Areas (MPAs), North-East Atlantic Fisheries Commission (NEAFC) closures and Special Areas of Conservation (SACs) within the focal area. 1. Wyville-Thomson Ridge SAC; 2. Darwin Mounds SAC; 3. West of Scotland MPA. 4. Hatton Bank SAC; 5. Geike Slide and Hebrides Slope MPA; 6. East Rockall Bank SAC; 7. Hatton-Rockall Basin MPA; 8. North-west Rockall Bank SAC; 9. Anton Dohrn Seamount SAC; 10. West Rockall NEAFC Closure; 11. The Barra Fan and Hebrides Terrace Seamount MPA; 12. South-west Rockall NEAFC Closure; 13. South-east Rockall Bank SAC; 14. Logachev Mounds NEAFC Closure; 15. Porcupine Shelf SAC; 16. North-west Porcupine Bank SAC; 17. Hovland Mound Province SAC; 18. Porcupine Bank Canyon SAC; 19. South-west Porcupine Bank SAC; 20. Belgica Mound Province SAC; 21. Southern Canyons SAC; 22. The Canyons MCZ. Purple lines are the boundaries of the Exclusive Economic Zones of both Ireland and the UK, and yellow lines are the Extended Continental Shelves of these countries, which were sourced from Flanders Marine Institute (2019). Map visualised using ArcGIS Pro v 2.8 (Esri Inc. 2020).



In the north of the region, parts of the Rockall-Hatton Plateau fall outside the jurisdiction of both the Republic of Ireland and the UK, leading to difficulties relating to the management and governance of ecosystems in these areas (see Johnson et al. 2019). States and Regional Fishery Management Organisations (RFMOs, which have jurisdiction in the ‘High Seas’ and ‘The Area’, and not within EEZs) are encouraged by the United Nations to protect areas identified as VMEs. Specifically, United UNGA resolution 61/105 calls for the mitigation of significant adverse impacts on VME habitats from destructive fishing practices. Significant impacts are defined as those that alter ecosystem function or structure, cause a loss of species richness or habitat on “more than a temporary basis”, or reduce the ability of natural populations to replenish themselves (FAO 2009).

The North-East Atlantic Fisheries Commission (NEAFC) has implemented fisheries closures at Edoras Bank, Hatton Bank, Rockall-Hatton Basin, North-west Rockall, West Rockall, SW Rockall (Empress of Britain Bank), Logachev Mounds, and the Haddock Box Closure (Figure 15). NEAFC also uses a move-on rule, which requires vessels to move on after contact with a VME, where contact is defined as catching more than 30 kg of live coral or 400 kg of sponges (Article 9, Recommendation 19:2014 on the Protection of Vulnerable Marine Ecosystems in the NEAFC Regulatory Area). As of October 2020, the move-on rule has never been triggered in the NEAFC Regulatory area; it is not known whether there has ever been an encounter or whether threshold limits are too high, since NEAFC does not require by-catch of VME indicator species below the threshold to be reported (Fuller et al. 2020).

## Anthropogenic impacts on VMEs and their constituent species

### *Scleractinian reefs*

Allegations of deliberate damage to coral habitats off Ireland that included intentionally crushing reefs using trawl chains, doors, and other fishing gear were well founded after flattened coral rubble with sharp breaks consistent with mechanical damage were observed in the water depth range of 600–1000 m along the Porcupine Bank (Grehan et al. 2004). Trawl scars have been observed in the region in depths of 200–1400 m (Rogers 1999, Bett 2000, Roberts et al. 2000, Bett 2001, Grehan et al. 2004, Wheeler et al. 2005a, Huvenne et al. 2016, Vieira et al. 2020) and scleractinian corals up to 1 m<sup>2</sup> have been reported as by-catch (Hall-Spencer et al. 2002). Scleractinian corals have been caught from fishing activities at the Hatton Bank in the years 2005–2008 (Muñoz et al. 2011, 2012). *Desmophyllum pertusum* was reported as by-catch from two bottom trawls along the summit, 1.2 kg and 7.7 kg per trawl, respectively, and *Solenosmilia variabilis* was recovered at a much higher rate along the summit and eastern slope of the Hatton Bank (1–25 kg per hour) than the west and south-western bank (0.1–2.8 kg per hour, Muñoz et al. 2012). *Desmophyllum pertusum*, *M. oculata*, and *S. variabilis* were reported as by-catch from 5–13 bottom longlining hooksets deployed at the Hatton Bank with 43 kg, 70 kg, and 1 kg caught, respectively, in total over a 20 day period (Muñoz et al. 2011).

Ocean acidification and global warming are threats to deep-sea scleractinians as these organisms make calcium carbonate exoskeletons, and thus, require the surrounding waters to be saturated with respect to calcium carbonate. Increasing carbon dioxide concentrations and increased carbonate ions will lead to a shoaling of the Aragonite Saturation Horizon – the depth at which over saturated and undersaturated waters meet – which may lead to the dissolution of the skeletons of calcifying organisms (Orr et al. 2005) and may cause 70% of global scleractinian habitat to become undersaturated (Guinotte et al. 2006). Large losses in scleractinian habitat are predicted in the North Atlantic by 2100 under both IS92a (worst-case scenario ‘business as usual’ resulting in an increase in global mean surface temperature of 4.3°C above pre-industrial levels) and S650 climate projections when modelled using Maxent (Tittensor et al. 2010). *Desmophyllum pertusum* and *M. oculata* are predicted to lose 79% and 55% of habitat, respectively, by 2100 under scenario RCP8.5

(worst-case scenario ‘business as usual’ resulting in an increase of 4.3°C above pre-industrial temperatures by 2100, Morato et al. 2020). There is a predicted climate refugium for both species in the North-east Atlantic, which includes the Bay of Biscay, the Irish Continental Margin, Rockall, and the Faroe-Shetland area (Morato et al. 2020). *Desmophyllum pertusum* and *M. oculata* are predicted to inhabit deeper waters and the median of the latitudinal distribution of *M. oculata* is expected to shift about 1.9–4.6° northward. *Solenosmilia variabilis* inhabits deeper waters than *D. pertusum*, so a loss in shallow habitat for *D. pertusum* may put it in competition for space with *S. variabilis*, which itself may not be able to shift deeper due to the aragonite compensation threshold or to an insufficient quantity of organic matter reaching deeper habitats. Previous habitat suitability models found that when reef occurrence data was modelled instead of just colony occurrences, there was a 12-fold reduction in the predicted extent of reef habitat (Howell et al. 2011). Therefore, reef habitat should be used when modelling projected changes under future climate change scenarios. An alternative model (Jackson et al. 2014), using the scleractinian reef distribution predicted by Ross & Howell (2013), suggested that climate change (using the IPCC IS92a scenario, considered a ‘business as usual’ scenario characterised by continued increasing emissions) would not impact deep-sea reefs in the best-case scenario, but in the worst case, 85% of NE Atlantic reef habitats would be exposed to corrosive waters by 2060.

### *Coral garden forming species*

Most sea pens are adapted to live in soft sediment environments where trawling preferentially occurs making them more vulnerable to fishing pressures than octocorals that live on hard substrata. For example, sea pen fields comprising *Balticina finmarchica* and cup-coral gardens of *Flabellum alabastrum* were recently found at densities reaching 3.47 colonies m<sup>-2</sup> and 4.64 ind. m<sup>-2</sup> within the halibut fishery area off Western Greenland making them immediately threatened by trawling in the area (Long et al. 2021). Different groups of sea pens withdraw at different speeds making some more vulnerable than others, an aspect of their morphology that is not considered when assessing their perceived vulnerability. When disturbed by an ROV arm, *Protoptilum* cf. *carpenteri* can completely withdraw into the sediment in 0.6 seconds without the need to retract its polyps (Ambroso et al. 2021). *Virgularia mirabilis* also withdraws with its polyps extended in a couple of seconds (Ambroso et al. 2013). In comparison, *Pennatulula rubra* takes 310–440 seconds, as it has to retract all of its polyps before withdrawing into the sediment (Chimienti et al. 2018).

Using an ensemble modelling approach of Maxent, Random Forest algorithm models, and General Additive Models, three species of octocorals (*Acanella arbuscula*, *Paragorgia arborea*, and *Acanthogorgia armata*) are predicted to lose >80% of their habitat by 2100 under climate scenario RCP 8.5. *Paragorgia arborea* would be worst affected and was projected to lose 99% of all habitat since much of its known current distribution occurs in higher latitudes where ocean acidification will be enhanced due to the increased absorption of CO<sub>2</sub> by colder waters (Sweetman et al. 2017). The distributions of *A. arbuscula* and *A. armata* are projected to shift towards shallower depths. The most important factor affecting the future distribution of octocorals is thought to be the shoaling of the aragonite and calcite compensation depths (Morato et al. 2020).

### *Sponge aggregations*

While climate change is predicted to drastically reduce the habitat for both octocorals and scleractinians, its effect on sponge aggregations may not be as severe. The extent of suitable habitat for *Vazella pourtalesii* reefs on the Scotian Shelf is predicted to increase 4-fold and shift to deeper waters (Beazley et al. 2021) compared with their present day distribution when modelled under both RCP 4.5 and RCP 8.5. Both scenarios predicted loss of habitat primarily in shallower waters and at the southern end of the Scotian Shelf where temperatures became too high, with greater losses under

RCP 8.5. Owing to a lack of basic information on the autecology and synecology of the species, we cannot predict how other habitat-forming sponges will react under future climate conditions. For example, mass mortality events of *Geodia barretti* at Tisler Reef were initially thought to be caused by a rapid increase in temperature (Guihen et al. 2012); however, recent incubation experiments have revealed that while these sponges experienced thermal stress, they quickly recovered and so rapid temperature increase was unlikely to be the sole cause of mass mortality (Strand et al. 2017).

### Non-VME megabenthic habitats

VME habitats occur where complex hydrodynamics lead to increased organic matter input, but other parts of the slope may have extensive habitats rich in either biomass or biodiversity that are not typically classified as VMEs and are poorly understood. Howell (2010) described many benthic assemblages that are not currently considered VMEs and later grouped them into ‘biotope complexes’ by their characterising species (Parry et al. 2015).

While aggregations of stalked crinoids are considered VMEs, aggregations of mobile crinoids do not fall into this category. When reviewing known crinoid distributions (Howell 2010), it was found that an assemblage of stalkless comatulid crinoids (*Thaumatocrinus jungersenii*) was present at 3580 m in the Rockall Trough (Hughes & Gage 2004), and an assemblage of the stalkless crinoid *Leptometra celtica* was present on coarse sediments at water depths of 190–699 m at the heads of Explorer and Dangaard Canyons (Howell et al. 2010) and on the Goban Spur (Lavaleye et al. 2002).

Owing to the dominance of the echinoderm fauna in the deep-sea megabenthos, many habitats are characterised by holothurian, ophiuroid, or urchin-dominated assemblages. For example, aggregations of primarily sedentary holothurians (*Ypsilothuria talismani talismani* and *Echinocucumis hispida*) are found between 1200 m and 1400 m in the Porcupine Seabight (Billett 1991), just below the *Pheronema carpenteri* belt. They are hypothesised to thrive in this narrow bathymetric zone due to the low current speeds depositing suspended organic matter (White 2003). On the south-east flank of Anton Dohrn Seamount, ophiuroids (*Ophiomusium lymani*) and cerianthids on mixed substrata form a distinct biotope at water depths of 1791–1889 m and are associated with solitary corals, stalked crinoids, holothurians, and actinurians (Davies et al. 2015). In the upper region of Dangaard and Explorer canyons, ophiuroids are a major component of three separate biotopes from 184 m to 1094 m, two of which are found in soft sediment environments. These soft sediment environments both contain burrowing ophiuroids, with the first associated with cerianthids, and the second associated with surface-dwelling ophiuroids. A biotope of ophiuroids and squat lobsters *Munida sarsi* has been found in incised channels and mini-mound features with coral rubble. Urchin-dominated assemblages are very common throughout the UK and Irish Margin and on all features in the region. They include assemblages dominated by *Cidaris*, *Echinus*, or Echinothurioida, usually on soft sediments. Howell (2010) also recognised barnacle-dominated assemblages on the Wyville-Thomson Ridge, the summit of Anton Dohrn Seamount and in Explorer and Dangaard Canyons at water depths of 200–950 m, and brachiopod-dominated assemblages on the summit of Anton Dohrn Seamount.

In the Western Hatton Bank, two main geomorphic features are present. The first is an outcrop, described as a non-depositional area that extends down to approximately 1100 m (or 1600 m in the presence of ridges) and the second is the Hatton Drift, an area of thick sediment located just below the outcrop (Sayago-Gil et al. 2012). The outcrop is characterised by an uneven surface with many ridges and escarpments. Octocorals found along the slope of this outcrop (but at insufficient densities to be considered as coral gardens) include bamboo corals (*Acanella* sp.), and corals belonging to the families Paramuriceidae (*Acanthogorgia* sp.), Primnoidae (*Callogorgia verticillata*, *Primnoa resedaeformis*), Plexauridae, Capnellidae (*Capnella florida*),

and Nephtheidae. Black corals found along this outcrop include *Stichopathes* sp., *Parantipathes* sp., and other unidentified antipatharian species. Stylasterids are also present (Sayago-Gil et al. 2012). Where the outcrop is covered in a layer of soft sediments, there are also sea pens (*Pennatula* sp., *Anthoptilum murrayi*, and *Halipterus* sp.; Sayago-Gil et al. 2012). Increased biodiversity on the outcrop is associated with the presence of coral rubble. Fewer families of coral are reported from the Hatton Drift (Coralliidae, Plexauriidae, Anthoptilidae, and Balticinidae; Sayago-Gil et al. 2012) and there is no information on the species present. While the list of families occurring in the Hatton Drift includes at least two that are not adapted to sediment dwelling (Coralliidae and Plexauriidae), Sayago-Gil et al. (2012) noted that these were found in areas very close to, or actually on the edge of, the outcrop.

### Megabenthic biodiversity trends

In the North Atlantic, biodiversity patterns of species and communities have been affected by the changing circulation patterns of water masses in the ocean basin (Puerta et al. 2020). The drivers of deep-sea biodiversity are scale-specific with temperature controlling the distribution of species on a basin and global scale (Watling et al. 2013), while at medium scales (10s of kilometres), it is the presence of geomorphic features (Henry & Roberts 2007), while substratum type affects local distributions. Common octocoral species such as *Paragorgia arborea*, *Primnoa resedaeformis*, and *Acanella arbuscula* have a continuous distribution from Nova Scotia, into Baffin Bay, south of Iceland and around the Faroe Islands (Buhl-Mortensen et al. 2015), and into Irish and UK waters.

Globally, it is hypothesised that there are 14 lower bathyal (801–3500 m) and 14 abyssal (3501–6500 m) seafloor biogeographical provinces (Watling et al. 2013). These provinces have been suggested using oceanographic proxies such as temperature, particulate organic carbon, salinity, and dissolved oxygen levels. The bathyal North Atlantic province was characterised by a high average temperature (5.58°C) and high particulate organic carbon availability (4.92 g m<sup>-2</sup> yr<sup>-1</sup>) which was highly variable and extended across both the North-west and North-east Atlantic. A follow-up study on just bathyal biogeography using occurrence records of anthozoans (Watling & Lapointe 2022) found that the North Atlantic province can be divided into the North-east Atlantic, the Boreal North-west Atlantic, and the Central North-west Atlantic.

Within the region of this review, six proxy biogeographic zones have been identified (Parry et al. 2015) using oceanographic variables depth, salinity, temperature, dissolved oxygen, and particulate organic carbon flux. These broadly correspond to water masses in the region and are used by the Joint Nature Conservation Committee (JNCC) in the upper classifications of biotopes. Using environmental proxies for biogeographic zones can be useful in the absence of faunal occurrence data, but the latter type of data can be used to better delineate potential provinces.

Within the Whittard Canyon, ensemble modelling indicated that there was increased biodiversity of corals in areas where interactions between complex topography and local hydrodynamics led to a local increase in organic matter availability (Pearman et al. 2020). This ensemble model, which used Random Forest, Generalised Additives Model, and Boosted Regression tree approaches with a horizontal resolution of 50 m, identified depth as an important variable for coral presence and for species richness, but overall model performance was always better when physical oceanography variables were included (Pearman et al. 2020).

Maxent species distribution modelling of all octocoral suborders below a water depth of 50 m, constructed from 1 km gridded environmental variables, revealed that all suborders have a predicted habitat along the continental shelf on both sides of the North Atlantic (Yesson et al. 2012). Calcite saturation state and temperature were the most important variables affecting the distribution of octocorals including the pennatuloids, respectively.

## Knowledge gaps and future considerations

Although we are beginning to better understand the biophysical interactions that give rise to habitats that are considered important biological hotspots, the oceanographic/hydrographic controls on the distribution of sponge aggregations, xenophyophores aggregations, and most VMEs other than cold-water coral reefs have rarely been studied. The lack of observational data has severely impaired our ability to understand the ecology of these systems, which in turn hampers our understanding of their vulnerabilities to human impacts, including climate change.

We are lacking even spatial distribution information and basic species-level knowledge for most of the lesser-studied VME habitats (e.g., stalked crinoids, tube-dwelling anemone aggregations). These biological communities are less likely to be retained as by-catch and may be associated with seabed features less frequently targeted by both ROV and AUV surveys, leading to under-reporting of their occurrence and extent. Only systematic surveys that explore a wider variety of environments will reveal this. Deficiencies in distribution data can be partly overcome by habitat models, for example, in directing surveys to potential sites of distribution.

Deep-sea taxonomic knowledge lags that of shallow-water taxa, impacting the quality of ecological studies and policy-driven conservation. The constituent taxa of many VMEs, such as in coral gardens, are rarely identified to species level (Morris et al. 2013, Davies et al. 2014, 2015, Robert et al. 2015, de Clippele et al. 2019). This taxonomic imprecision also restricts the development of autecological knowledge of these key species, limiting our ability to appropriately gauge specific threats, including climate change, to vulnerable habitats.

More generally, there has been little research into the autecology of any deep-water habitat-forming species in the North-east Atlantic, except for the scleractinian corals (particularly *Desmophyllum pertusum* and *Madrepora oculata*). Among other groups that comprise Marine Animal Forests, autecology has been studied for only a handful of species. Habitat-forming species belong to a wide range of taxa (Porifera, including both demosponges and hexactinellids; Cnidaria, including stony corals, black corals, octocorals, tube-dwelling anemones, and hydrozoans; Echinodermata, particularly stalked crinoids; and bivalve molluscs) with corresponding life-history strategies. Knowledge of autecology is vital to understand the vulnerability and potential resilience of these taxa to future climatic conditions. Studies of *in situ* settlement and growth rates, parameters key to understanding vulnerability and recovery potential, require long-term monitoring – a goal frequently difficult to fund without major national or international programmes of research.

Our understanding of the identification and distribution of deep-sea ecosystems is hampered at multiple points. In the North-east Atlantic, there is a limited window of operation for ROV work, extending from about May to August, outside of which the likelihood of weather downtime makes surveys less attractive. While AUVs represent a solution to this, the deployment and recovery of these vehicles require the use of a specialised research vessel. Image analysis of benthic fauna gathered from both ROV and AUV surveys is hindered by the lack of a standardised and open-access image guide. Most research groups have institute-specific species guides, built up over years of research, to consistently distinguish between species and morphotypes, but guides differ between institutes. This leads to a lack of comparability among studies that reference specific morphotypes, where it is unclear whether different studies are referring to the same taxon. Embracing initiatives such as SMaR-TaR-ID (Howell et al. 2020) and the formal use of open nomenclature in image-based studies (Horton et al. 2021), particularly in groups where there is high taxonomic uncertainty, could help standardise studies, as could supplying images of morphotypes in ecological manuscripts, supplementary materials, or other digital repositories. Development of Artificial Intelligence to identify fauna (e.g., Durden et al. 2021, Katija et al. 2022) could further help overcome this barrier.



## Conclusion

The biodiverse fauna observed on the Irish–Scottish Margin is a direct result of the unique topography and oceanography in the region: numerous canyons systems, coral mounds, seamounts, and escarpments are found along the slope and interact with the overlying water to create diverse habitats for megabenthic communities. Despite being one of the most well-explored areas of deep sea in the world, this review highlights how little we still know about the constituents of this biome. The primary research focus among the megabenthos has been on *Desmophyllum pertusum*, both reefs and coral mounds, leading to more information on the controls of reef and mound formation and distribution. Other major habitats such as coral gardens comprise taxa that are either currently undescribed species or have not been identified to species level (either due to lack of expertise or due to difficulties in identifying species from images). This lack of taxonomic information on such a prolific group limits our capability to further understand the species-specific drivers of these habitats and answer fundamental questions. The distributions of both *Phoronema carpenteri* and xenophyophore aggregations are relatively well documented (Roberts et al. 2000, Bett 2001, Narayanaswamy et al. 2006, Howell et al. 2014b, Davies et al. 2015, La Bianca et al. 2019, 2020, Piechaud & Howell 2022) – with species distribution modelling helping to fill probable gaps – but the biophysical controls on distribution remain poorly documented particularly for xenophyophores. Other lesser-studied VMEs such as stalked crinoid fields are present along the Irish and Scottish margin, but they are rarely reported in the literature.

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## Note

- 1 *Lophelia pertusa* was synonymized to *Desmophyllum pertusum* based on molecular evidence of both mitochondrial genomes and 30 microsatellites (Addamo et al. 2016). The name *Desmophyllum pertusum* is widely accepted now, but there is still doubt over the legitimacy of this reclassification. The primary difference between the two genera is that *Desmophyllum* is solitary and *Lophelia* is colonial. Some taxonomic experts believe that this is an important distinction and that until further evidence is provided, the

name *Lophelia pertusa* should continue to be used to prevent taxonomic confusion should the name revert to the original in the future (Cairns & Hoeksema 2022). Throughout this review, we use the most up to date nomenclature in the World Register of Marine Species (WoRMS) and so we refer to this species as *D. pertusum*. We only refer to it as *L. pertusa* where that name has been used in legislation and policy documents.

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