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Ollscoil na hÉireann, Corcaigh
National University of Ireland, Cork



**Understanding Cold-Water Corals' Health and
Ecosystems on the Irish margin, NE Atlantic; A
Critical look into the Ecology, Geology,
Hydrodynamic Processes and Human Impacts**

Thesis presented by

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for the degree of

Doctor of Philosophy

University College Cork

School of Biological, Earth and Environmental Sciences

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Lim

August 2022

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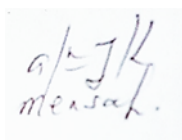
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List of Abbreviations

ASH.....	Aragonite Saturation Horizon
AUV.....	Autonomous Underwater Vehicle
BEES.....	Biological, Earth and Environmental Sciences
BMP.....	Belgica Mound Province
CTD.....	Conductivity-Temperature-Depth
DIC.....	Dissolved Inorganic Carbon
ENAW.....	Eastern North Atlantic Water
ESRI.....	Environmental Systems Research Institute
EU.....	European Union
HD.....	High Definition
LS.....	Labrador Seawater
MBES.....	Multibeam Echosounder
MOW.....	Mediterranean Outflow Water
MPA.....	Marine Protected Area
MYA.....	Million Years Ago
PBC.....	Porcupine Bank Canyon
PRSR.....	Porcupine Ridge and the Slyne Ridge
PS.....	Porcupine Seabight
ROV.....	Remotely Operated Vehicle
SAC.....	Special Area of Conservation
SSS.....	Side Scan Sonar
USBL.....	Ultra-Short Baseline
WoRMS.....	World Register of Marine Species

Declaration

The research presented here is the authors own work and has not been submitted for another degree at University College Cork or elsewhere.

Handwritten signature of John Appah Kwame Mensah in blue ink.

Signed

John Appah Kwame Mensah

Handwritten signature of Prof. Andrew Wheeler in blue ink, followed by the printed name "PROF. A. WHEELER".

Prof. Andrew Wheeler, co-supervisor of research

Signed

Prof. Ruth Ramsay, co-supervisor of research

Signed

Dr Aaron Lim, co-supervisor of research

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Abstract

Cold-water corals (CWCs) have come under threat from climate change and anthropogenic activities such as fishing and marine litter pollution despite, being ecological engineers that support high biodiversity, and as a result are protected in Europe under the EU Habitats Directive with some designated as Special Areas of Conservation (SACs). Abiotic (low pH, macro and microplastics) and biotic (pathogens and harmful microbes) factors, due to climate change and human activities, can stress CWCs, disrupting the coral holobiont with dire consequences on the energy allocation processes, coral health and diseases, growth and survival, resilience as well as biodiversity in deep sea corals. CWCs are azooxanthellate, filter feed and exist withing temperature limits of 4-13 °C. Using a habitat mapping approach, coupled with CWC histology and studies of the coral microbiome, this PhD research investigates the CWCs' ecosystem health and environmental processes that influence biodiversity in the two SACs, upper Porcupine Bank Canyon (uPBC) and the western Belgica Mound Province (wBMP), on the Irish continental margin, northeast Atlantic. Chapter one provides a general introduction to cold-water corals, the objectives of the research and the threats to ocean environmental health and consequent organismal health, while chapter two maps the spatial distribution of CWCs within one of the largest submarine canyons on the Irish margin, the uPBC, highlighting importantly habitat heterogeneity in reef habitats and the hydrographic factors that influence the pattern of CWCs distribution in the canyon. Chapter three mapped the distribution of marine litter in two special areas of conservation (PBC and BMP) on the Irish margin and its impact on CWCs' distribution as well as to determine if the SACs are serving their purpose and their usefulness against litter entry. In chapter four, the study assessed the distribution and roles of the coral holobiont in the uPBC using molecular techniques whilst chapter five uses a combination of histological and molecular techniques to

assess Haplosporidia and *Vibrio* spp. in main framework-forming corals in the uPBC. Chapter six synthesizes the data obtained and concludes on the distribution and status of the cold-water corals in the uPBC in the face of climate change and anthropogenic pressures.

In the analysis, five different substrates were characterized in the uPBC and resolved into non-reef (sediment, sediment & dropstones and bedrock) and reef and rubble (live/dead coral and coral rubble) habitats, including the terrain features observed in the canyon, and these generally contributed to the high biodiversity. High benthic megafaunal diversity (higher number of taxa identified), although not significantly different from the Shannon's diversity observed in reef and rubble habitats, was detected in the non-coral habitats compared to the reef and rubble habitats in the upper PBC. Percentage estimates of Shannon's diversity for non-coral and reef and rubble habitats were ($H'_{\text{non-reef}} = 2.38$; $H'_{\text{reef and rubble}} = 2.16$) and Pielou's evenness ($J'_{\text{non-reef}} = 0.71$; $J'_{\text{reef and rubble}} = 0.65$) respectively whilst density estimates of Shannon's diversity for non-coral and reef and rubble habitats were ($H'_{\text{non-reef}} = 1.72$; $H'_{\text{reef and rubble}} = 1.14$) and Pielou's evenness ($J'_{\text{non-reef}} = 0.54$; $J'_{\text{reef and rubble}} = 0.43$) respectively. Geomorphology and hydrography were noted to affect the distribution of litter in the SACs. Another striking finding was that fishing gear (uPBC=80.7%, wBMP = 14.3% buoys) and plastics (uPBC = 11.3%, wBMP = 55.1%) were detected in relatively high abundance, suggesting that anthropogenic activities such as fishing (>60% vessels) are ongoing in the PBC and BMP despite being a SACs. It is unclear, however, if the observed fishing gear in the uPBC and wBMP may have drifted into them by deep-sea currents or were dumped before they were designated an SAC, as the SACs are closed to fishing. Additionally, the results reveal the upper canyon as a high energy environment with sufficient mixing of materials and community composition among the corals, water and sediment samples. Shannon's index ($H = 2.19$, $P = 0.33$) and species evenness ($J' = 1.66$, $P = 0.43$) among the groups of samples, respectively, were not significantly different. A positive note is that the corals generally appear to be in good health with low Haplosporidia

(0.03%) and *Vibrio* (0.03%) infections in a single *L. pertusa* individual from the canyon head respectively, although we risk losing the corals due to bottom fishing and the current trend of climate change. A total of 40% Rickettsiales-like organisms (RLOs), with 26.7% observed in the south branch and 13.3% observed in the canyon head were detected. Despite the many threats and pressures such as marine litter pollution, changing pH, sedimentation and bottom trawling, the CWCs on the Irish margin, are associated with high biodiversity and appear to be resilient, well adapted to the deep-sea environment.

However, regular monitoring campaigns and health screening studies are advocated. Although continuous monitoring through research and management activities would be the way forward, it is recognised that the cost of such deep-sea surveys/expeditions are huge and require sufficient funding from the various funding bodies. It is believed that the findings of this research will inform policy makers and management on how to effectively protect the vulnerable ecosystems of these deep seas.

Chapter 1

Cold-water corals' ecosystems: ecology, geology, hydrodynamic processes and human impacts

1. Introduction to cold-water corals

1.1. What are cold-water corals (CWCs)?

Corals can be defined as, “*animals in the Cnidaria classes Anthozoa and Hydrozoa that produce either calcium carbonate (aragonitic or calcitic) secretions resulting in a continuous skeleton or as numerous microscopic, individualised sclerites, or that have a black, horn-like, proteinaceous axis*” (Cairns, 2007). A coral polyp is described as a simple animal and is composed of an outer ectoderm and an inner endoderm (with a gastrovascular opening or coelenteron) connected by a gelatinous mesoglea (Giribet and Edgecombe, 2020). Cold-water corals (CWCs) are anemone-like polyps connected by a coenosarc overlying a calcareous exoskeleton to form colonies, but can exist as a solitary animal (Roberts et al., 2009; Giribet and Edgecombe, 2020). They do not form symbiotic relationships with algae (azooxanthellate), occur between 4-13 °C and generally live in the darkness of the deep ocean, without the capacity to make their own food for growth and survival. As such, these sessile animals feed on particulates, plankton and crustaceans by using their tentacles to trap and direct food material into their body in a process called filter feeding (Scharf et al., 2006; Huvenne et al., 2011; Bell, 2012; Giribet and Edgecombe, 2020).

CWCs do not have a true reproductive organ and exhibit both asexual and sexual modes of reproduction (Roberts et al., 2009; Giribet and Edgecombe, 2020). Asexual reproduction occurs through the budding and fragmentation of a new polyp off from a parent polyp during favourable conditions, whilst sexual reproduction occurs in February and March (Larsson et

al., 2014), with the development of sexual gametes in the mesoglea which are dispersed into the surrounding water (where fertilised eggs develop into larvae) through the coelenteron (Freiwald and Wilson, 1998; Roberts et al., 2009; Giribet and Edgecombe, 2020). Certain CWCs are slow growing animals with growth rates typically between 5 - 25 mm yr⁻¹ (*Lophelia pertusa*; Orejas et al., 2008; Roberts et al., 2009) and 3 - 18 mm yr⁻¹ (*Madrepora oculata*; Orejas et al., 2008) and take a long time to recover from destruction. These two species are of particular interest in the current research, due to being ecosystem engineers capable of building biogenic habitats in the northeast Atlantic region. In 2019, in the world register of marine species (WoRMS), Cairns noted that given the significant morphological difference between the solitary *Desmophyllum* and colonial *Lophelia*, one should be rather cautious, concerning the immediate need for a taxonomic change that would synonymize *Lophelia*, although the molecular results seem convincing. Further studies to consolidate this finding may be required to avoid the confusion that may come along with the change in nomenclature in the future. Cairns also notes that so far not many genes have been sequenced and advises more phylogenetic results are obtained before such a major taxonomic change. As such, *Lophelia pertusa* (syn. *Desmophyllum pertusum* (Addamo et al. (2016))) is rather used throughout the thesis.

Cold-water corals (CWC) create complex habitats, which are formed through the interaction of geological, biological and hydrodynamic processes (Roberts et al., 2006, 2009). CWC ecosystems are highly diverse and complex, existing at depths between 7 - 5,000 m where abiotic, such as geology and currents, as well as biotic factors are suitable (Försterra et al., 2005; Wheeler et al., 2005; Roberts et al., 2009; Henry et al., 2014; Vertino et al., 2014; Appah et al., 2020; Lim et al., 2020). CWCs can be characterised according to their ability to form

bathyal mounds, reefs and depth of occurrence (e.g., Schuhmacher and Zibrowius, 1985; Zibrowius, 1988; Roberts et al., 2009).

1.1.1. Diversity of cold-water corals

CWCs are framework-forming anthozoan corals and can be categorised into scleractinian (hard or stony corals), zoanthids, antipatharian (black corals), octocorals (soft corals or gorgonians) and stylasterids or hydrocorals (Giribet and Edgecombe, 2020). The same species of a CWC (e.g. *L. pertusa*) generally may occur with different colours and show a global distribution with a wide range of environmental/ecological tolerances (Roberts et al., 2009). Framework forming scleractinian corals possess anastomosing, rigid calcareous skeletons while stylasterids make rigid and non-flexible calcareous skeletons composed of either calcite or aragonite (Roberts et al., 2009). Both antipatharian and octocorals possess a non-calcareous internal axial skeleton which may be rigid or non-rigid (Roberts et al., 2009). Zoanthids on the other hand are soft bodied cold-water corals with a few of them possessing a skeleton (Cairns, 2007).

Coral taxonomy is rapidly evolving and has been studied using morphological and molecular data, including phylogenomic data (Cairns, 2007; Zapata et al., 2015; Quattrini et al., 2018; McFadden et al., 2022), with modern understanding of the systematics of Cnidaria derived from Daly et al. (2007). Most recent revision of Octocorallia, using phylogenomic data, elevates the anthozoan sub-classes Octocorallia and Hexacorallia to the rank of class (McFadden et al., 2022). According to Fukami et al. (2008), the taxonomy of Hexacorallia, the stony corals, also may require additional studies, using novel markers that can produce results with higher resolution.

Phylum Cnidaria

Subphylum Anthozoa

Class Octocorallia

Order Malacalcyonacea

Order Scleralcyonacea

Class Hexacorallia

Subclass Ceriantharia

Order Penicillaria

Order Spirularia

Order Actiniaria

Order Antipatharia

Order Corallimorpharia

Order Scleractinia

Order Zoanthidea

Certain CWCs are important in palaeoenvironmental research whilst others are exploited for jewellery as well as assessing variations in marine productivity (Druffel et al., 1995; Smith et al., 1997; Grigg, 2002; Sanchez et al., 2004; Roberts et al., 2009).

1.1.2. Calcareous scleractinians and reef builders

Recent advances in ocean floor exploratory methods and techniques, including the use of remotely operated vessels (ROVs) and multibeam echosounder (MBES) have contributed to our current knowledge especially the distribution of reefs composed of CWCs (Freiwald, 2002). CWCs that form reefs can be associated with 1,300 species of the deep ocean (Freiwald, 2002; Roberts et al., 2006). They form three-dimensional habitat structures that make the ecosystem a “hotspot for biodiversity” (Roberts et al., 2006). The most abundant reef forming species in the northeast Atlantic are the scleractinian *Lophelia pertusa* and *Madrepora oculata*

(Davies et al. 2008; Roberts et al., 2009). Their skeleton is made up of either aragonite or calcite (mineral polymorphs of calcium carbonate) which exhibit different stability and tensile strengths (Stolarski et al., 2007, 2021). Aragonite is durable but chemically less stable while calcite is fragile but more chemically stable. CWCs' occur at different depths (Calcium Compensation Depth (CCD) and Aragonite Compensation Depth (ACD)) in the ocean where different physical and chemical conditions affect the distribution of the corals. CWCs' made of calcite will dissolve at the CCD whilst CWCs' made of aragonite will dissolve at shallower depths. The dominant composition of the carbonate species in a CWC skeleton determines its capacity to form reef frameworks. Regrettably, these complex, dynamic and highly diverse CWC ecosystems have suffered and continue to suffer damage from climate change and anthropogenic activities such as fisheries, hydrocarbon exploration and marine litter (Roberts et al., 2006).

1.1.3. Cold-water coral nutrition

Cold-water corals are sessile, filter feeding organisms that lack symbiotic associations with zooxanthellae (Freiwald, 2002). They are distributed in areas in the deep sea where physical and chemical processes generally support high production of food materials and carbon sources for CWCs growth and survival (Frederiksen et al., 1992; Roberts et al., 2006; Duineveld et al., 2007). Two dominant theories exist to explain CWCs' growth and survival with Hovland and Thomsen (1997), firstly, proposing in the early 1990s that CWCs' growth is supported through hydrocarbon seepage and a chemosynthetic food chain. However, isotopic studies on food materials ingested by *L. pertusa* indicate that the carbon source incorporated into the tissues of the corals is modern rather than from older thermogenic sources (Kiriakoulakis et al., 2001; Wheeler et al., 2007). Recent study by Osman et al. (2022) indicates that CWCs (e.g. *Callogorgia delta* and *Paramuricea* sp. type B3) derive their food source from a mixed

chemosynthetic and photosynthetic origins (heterotrophic filter feeding) as they grow in close proximity near active seeps in the Gulf of Mexico, revealing local adaptations.

A second and a more recent theory note that physical and hydrodynamic properties such as current speed, internal waves and up/downwelling processes favour CWCs' growth and survival in particular regions of the ocean. Optimal flow speeds of 2 - 6 cm s⁻¹ in the ocean facilitate a maximum uptake of food particles and particulates (Kiriakoulakis et al., 2007; Mienis et al., 2007; Hennige et al., 2021) whilst current velocities of 10 cm s⁻¹ and beyond can make feeding less effective as the corals close their polyps to avoid damage (Orejas et al., 2016). Higher current speeds however prevent corals from becoming clogged with fine particles (Wheeler et al., 2007).

Internal waves form at the interface of density differences within the water column and as they impinge on seafloor features such as submarine canyons, seamounts and cliffs (associated with CWC communities; Wienberg et al., 2009; Mazzini et al., 2012; Guihen et al., 2013; Davies et al., 2014) they break and overturn, causing sufficient mixing of ocean water. These hydrodynamic processes can cause upwelling and downwelling, that are necessary for entraining significant amounts of nutrients and organic materials (Allen and Durrieu de Madron, 2009). Increased sheer stress around reef areas can locally resuspend particulate matter and/or cause high current advected particulates into the reef system (Guihen et al., 2013), thereby increasing the feeding capacity of the corals. Nepheloid layers are defined as water typified by high concentrations of suspended particles including particulate organic matter (POM) with high velocity contour currents producing basal nepheloid layers through resuspension (Faugères and Mulder, 2011), and intermediate nepheloid layers trapping nutrients and particulates that become entrained in mid-water through equalized density

properties, often at water mass boundaries, which can supply sufficient food to CWCs for growth and survival (Kenyon et al., 2003). Similarly, dense nutrient rich water observed in summer above the Porcupine Bank is rapidly released through boundary layers to nourish the CWC community (White et al., 2005; Davies et al., 2009).

Based on the size of their polyps, tropical scleractinian corals exhibit resource partitioning and discriminate between prey sizes despite the organic materials and nutrient supply available (Porter, 1976), with large polyps feeding on large zooplankton whilst small polyps feed on small zooplankton. Different feeding strategies have been observed in CWCs, including omnivorous feeding strategy (Mortensen, 2001; Duineveld et al., 2007). In their investigation, Duineveld et al. (2004) used stable isotope analysis to identify the diet of the CWCs on the northwest Atlantic margin and found a variation between the $\delta^{15}\text{N}$ of coral tissue and $\delta^{15}\text{N}$ phytodetritus to be > 1 , from which they concluded that the corals were having a mixed diet involving zooplankton and algae. A similar feeding habit to CWCs is found in obligate filter feeders (Duineveld et al., 2007). *Lophelia pertusa* with its large polyps was observed to be feeding on live calanoid copepods in the field (Freiwald, 2002; Duineveld et al., 2004; Kiriakoulakis et al., 2007).

1.2. Physical-chemical processes that affect cold-water coral distribution

The skeleton of *L. pertusa* is composed of aragonite crystals so its growth is affected by the chemical composition of the surrounding water with aragonite saturation of $\Omega_{\text{arag}} > 1$ being an optimal condition for growth in *L. pertusa*-dominating CWC reefs (Guinotte et al., 2006; Gomez et al., 2018), although other studies have shown that corals can grow in environments with $\Omega_{\text{arag}} < 1$ (Hennige et al., 2015; Baco et al., 2017). Corals growing in regions with low

aragonite saturation however must invest high amount of energy in calcification and growth (Hennige et al., 2015).

A threshold dissolved inorganic carbon (DIC) of $2,170 \mu\text{mol kg}^{-1}$ is optimal for CWCs growth in the northeast Atlantic, although high levels of DIC as a result of more CO_2 dissolving and mixing through the ocean drives progressive ocean acidification (Flögel et al., 2014). However, the exact rate of acidification depends on the ocean buffering capacity.

Low dissolved oxygen content of between $2.7 - 2.8 \text{ ml l}^{-1}$ can be stressful to the growth of CWCs (Brooke and Young, 2009; Davies et al., 2010) and can cause CWCs' extinction at 2.0 ml l^{-1} (Jorissen et al., 2007; Fink et al., 2012). A dissolved oxygen content of $6.0 - 6.6 \text{ ml l}^{-1}$ is recognised for CWCs' optimal growth and distribution (Davies et al., 2008; Dullo et al., 2008), whilst oxygen levels below the critical value of 3.26 ml l^{-1} at 9°C can significantly affect the metabolic activities of CWCs (Dodds et al., 2007). However, mixed results of CWCs' mortality and/or survival at low oxygen concentrations of $1.5 - 3.2 \text{ ml l}^{-1}$ (Schroeder, 2002; Davies et al., 2010; Georgian et al., 2014; Lunden et al., 2014) reveal that CWCs can be regionally adapted.

Water mass is a volume of seawater that is defined by a range of temperature and salinity (with T-S plots characterising water density) with properties different from the surrounding water (Liu and Tanhua, 2021) and can affect the growth of CWCs. Temperatures between $4 - 13^\circ\text{C}$ and salinity limits of $32 - 38.8$ respectively are required for optimal growth of CWCs (Freiwald, 2002; Mortensen and Buhl-Mortensen, 2004; Roberts et al., 2006; Kellogg et al., 2016; Lawler et al., 2016). Density limits of $27.35 - 27.65 \text{ kg m}^{-3}$ and $27.74 - 27.84 \text{ kg m}^{-3}$ (at near vertical cliffs of 120 m high) have been noted to affect coral growth and distribution (Dullo et al., 2008;

Huvenne et al., 2011), although density as an hydrographic property that supports larval and coral growth are still under contention. Water mass is characterised based on its physical-chemical properties and where it is located in the global ocean. The major water masses bathing the mounds on the Irish margin are the Eastern North Atlantic Water (ENAW) and Mediterranean Outflow Water (MOW) (Mienis et al., 2007; Appah et al., 2020). The ENAW is observed at depths between 600 - 800 m and characterised by reduced salinity and increased temperature whilst the MOW relatively is colder, more saline and found at depths between 750 - 1,200 m (Mienis et al., 2007).

1.3. Cold-water coral growth and reef development

The different stages of mound formation have been described by Squires (1964) and have been modified (e.g. Figure 1.1) by other researchers to adequately describe the interglacial-glacial processes of mound growths and the erosional/depositional phases including the variety of morphological growth forms such as coral ridges (Roberts et al., 2006; Foubert et al., 2007, 2011; Correa et al., 2012; Douarin et al., 2013, 2014). Coral banks are formed progressively over time through complex, dynamic interactions of CWCs with their surrounding environment. Four distinct stages characterise the process and dynamics of mound formation: colony, thicket, coppice and bank stages (Squires, 1964; Wilson, 1979). The development of a CWC reef or mound starts with a coral planular larvae settling on a hard, stable and firm substrate that favour its growth.

The colonisation of a new environment by *L. pertusa* and *M. oculata* is influenced by the reproductive and the life history strategies of the species. CWC reproduction in the northeast Atlantic is seasonal (Waller, 2005; Larsson et al., 2014) and most likely driven by the seasonal surges of phytodetritus and particulates. Gametes produced by the planular larvae have greater

chance of survival and can disperse over long distances (Dullo et al., 2008; Giribet and Edgecombe, 2020). High current speed of 10 - 50 cm s⁻¹ has been recognised to provide suitable substrate for larval settlement and favour the growth of CWCs (White, 2006; Mienis et al., 2007; Correa et al., 2012; Lim et al., 2018, 2020). The larvae can survive at 6 °C for 64 days and at 11 °C for 35 days respectively (O'Connor et al., 2007), dividing mitotically into a single colony (Wilson, 1979).

The initial growth of a single colony ranges from a millimetre to about 60 cm and attaches to a pebble or cobble, with further growth, vertically and laterally, increasing the size (> 1 m in diameter) of the colony, and facilitating its attachment to more than two pebbles (Squires, 1964; Wilson, 1979). The colonies can remain isolated from each other or form patches/aggregates including colonizing the entire area (Squires, 1964; Douarin et al., 2013) to modify the flow of water to trap and deposit species-poor sediments to enhance as well as strengthen the coral/reef environment (Roberts et al., 2009; Douarin et al., 2013). The intermixing of other colonies growing in the vicinity forms a thicket (aggregation of closely related colonies; Squires, 1964).

The thicket can provide habitat for the reef building polychaete worm *Eunice norvegica* or the reef disintegrating sponge, *Cliona* sp. at its base (Squires, 1964; Roberts, 2005; Wisshak et al., 2012; Büscher et al., 2019). The base of a reef thicket is described as a substrate of debris (Squires, 1964). The activities of these thicket-related species contribute to the development of the reef structure. *Eunice* can induce further calcification and subsequent strengthening of the colony frameworks including garner rubble to form microhabitats and patchy reefs (Roberts, 2005) whilst the sponge can attack and topple the dead exposed basal skeleton of the framework in a process called bioerosion (Squires, 1964; Wilson, 1979). A ring-like matrix of

dead coral debris and fine sediment sometimes found at the base of a thicket further support and strengthen the thicket (Squires, 1964).

The matrix evolves the coral thicket into a coppice when a significant amount of debris accumulate at the base of the thicket, providing new microhabitats (Squires, 1964; Roberts et al., 2006). The new microhabitats are a mixture of bioeroded corals, skeletal debris, shelly debris, organic and inorganic materials that provide shelter and supply food to the associated benthic fauna (Squires, 1964; Wilson, 1979). The sufficient food supply at the substrate of debris can now support diverse animals as does the surface of living corals. The coppice stage is typically characterised by a large proportion of exposed dead coral layers compared to the surface of living cap of corals.

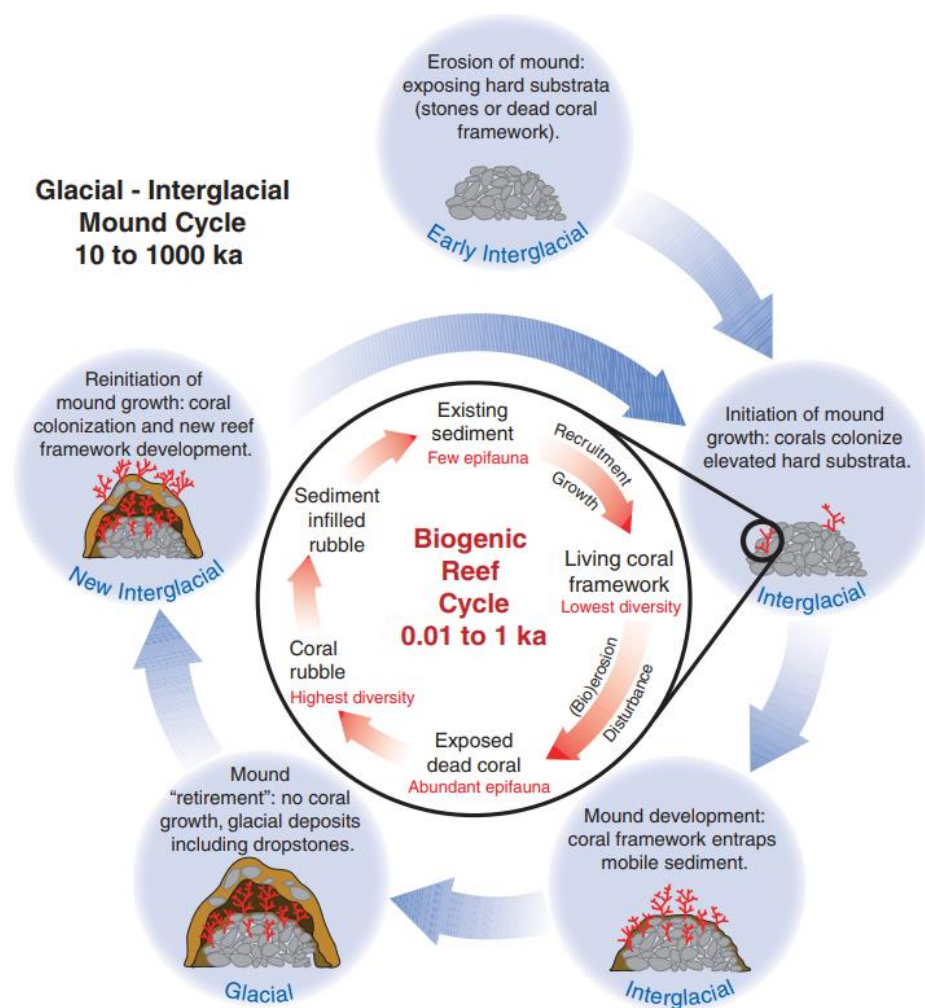


Figure 1.1. A modified model of cold-water coral reef mound formation, showing the initiation, development, retirement, and recolonization stages, including reef microhabitats and biodiversity (Roberts et al., 2006).

Further growth of the coppice through the continual addition to the substrate of coral debris from the surface of living cap of corals eventually develops into a coral bank/mound (bathymetric biogenic features on the seabed) under favourable conditions (Squires, 1964). Sediment build-up gets to a considerable thickness and the interstices of the open mat of coral debris become filled as flow current is modified and traps finer sediment that can also be generated from the biological activities of animals within the mat (Squires, 1964). At this stage, the interior solid mass of skeletal debris finally become impacted with mud that is compacted and lithified, providing home for substrate boring organisms with further compaction. Framework-forming scleractinian CWCs *Lophelia pertusa* and *Madrepora oculata* are generally associated with carbonate mounds/coral banks (De Mol et al., 2002; Thierens et al., 2010; Wheeler et al., 2011; Lim et al., 2017, 2018).

1.4. Cold-water coral biodiversity

Biodiversity can be inferred from the local (alpha diversity), regional (gamma diversity) and the turnover (beta diversity) diversities. Alpha diversity accounts for within habitat variations of species distribution while beta diversity accounts for between habitat variations of species distribution. Gamma diversity investigates evolutionary processes at broader scales of distribution and spatial patterns with the aim of setting biogeographical boundaries (Sepkoski, 1988; Roberts et al., 2009; Walters and Martiny, 2020). Biodiversity in the deep seas is characterised and driven by the geological and hydrographic interactions existing in that environment. The ecology and life history strategies of CWCs such as reproduction, mode of feeding affects CWCs growth and survival in their habitats (de Juan et al., 2022).

Varying patterns of distribution are due to the complex sources of temporal and spatial changes in that environment with different scales of measurement having different inherent sources of variation that affect species distribution (Henry et al., 2014). A study carried out by Quattrini et al. (2012), off the coast of North Carolina, to investigate how different scales of measurement impact the distribution of fish species in a reef habitat, showed that at a fine scale of 30 x 30 m the reef fish alfonsino *Beryx decadactylus*, conger eel *Conger oceanicus* and the brisingid sea star *Novodinia antillensis* were favoured, while at a broader scale of 170 x 170 m supported the distribution of *Echinus* spp. and the red squat-lobster *Euminida picta*, including *N. antillensis* and *B. decadactylus*. Coral reefs offer habitat to a range of organisms with different strategies with coral rubble showing higher biodiversity than live coral as there is more food on a rubble habitat (Mortensen and Fosså, 2006). The habitat-specific distribution of the species on CWCs showed that *Conger oceanicus* and *N. antillensis* uses live corals as foraging grounds whilst *B. decadactylus* uses live corals as refuge against predators and strong flow velocities (Quattrini et al., 2012). Filter/suspension feeders show high affinity for live coral habitat while deposit feeders associate more with coral rubbles (Jonsson et al., 2004; Henry and Roberts, 2007). High habitat heterogeneity in CWC reefs accounts for the high species diversity in the northeast Atlantic (Henry and Roberts, 2007) with faunal diversities generally decreasing with depth in the northeast Atlantic (Vincx et al., 1994). Ecological/environmental conditions such as organic matter, anoxic conditions, and surface productivity in a CWC reef habitat can also influence the distribution of benthic communities (Vincx et al., 1994; Gaever et al., 2004).

1.5. Marine litter in cold-water coral habitats

Cold-water corals (CWCs) have come under threat from anthropogenic activities such as fishing and marine litter (Chapron et al., 2018) despite their ecological significance and importance to biodiversity. Marine litter is found in all the world's oceans and poses a threat to marine species (Rochman et al., 2016). Marine litter is common in shallow waters compared to the deep seas (Galgani et al., 2000; Ryan et al., 2014; Van Franeker and Law, 2015) with the sources of marine litter being land-based sources and marine-based sources (Galgani et al., 2000, 2010). Marine litter can be characterised as macro-, meso- and micro litter based on size (Thompson, 2015; Kershaw et al., 2019).

Marine litter can change the chemical and the physical composition of the benthic habitats (Goldberg, 1994; Barnes et al., 2009; Galgani et al., 2010). Litter can also transport harmful and invasive species into the deep-sea, increasing CWCs' risk to diseases by 85% (Barnes et al., 2009; Lobelle and Cunliffe, 2011; John et al., 2022), as well as posing threats to marine organisms, causing entanglement, disrupting feeding behaviour, and impeding movement (Phillips et al., 2010; Chapron et al., 2018; John et al., 2022). According to Chapron et al. (2018), marine litter reduces the rate of skeletal growth, decrease the rate of food capture and affect the resilience of CWCs' and their associated marine species.

1.6. Cold-water coral microbiome and the damage threshold of coral holobiont susceptibility

Microbial diversity and its interaction with the CWCs and the environment facilitates identification of important linkages existing between the microbial communities and macroecological change (Ainsworth et al., 2010). Microbial community composition on and within CWCs affect coral physiology and immunity, with coral immunity being revealed in the growth and survival of the coral holobiont. The different array of microbial organisms that are

in complex symbiotic associations with the coral host constitute a CWC holobiont that forms the structural and functional foundation of CWCs reef habitats (Bourne et al., 2009; Pogoreutz et al., 2021). Restoring a coral holobiont symbiotic interactions and functioning in the face of climate change and human pressures establishes coral holobiont integrity (Palmer., 2018). The ability of CWCs to accept useful microbes whilst preventing pathogens/harmful microbes from entering them maintains holobiont integrity (Gavish et al., 2018; Palmer, 2018). Pathogens can breakdown the coral symbiotic interactions and cause energy loss, leading to diseases in CWCs whilst useful microbes/mutualists favour and support CWCs health and growth (Palmer, 2018; Pogoreutz et al., 2021; Appah et al., 2022). Abiotic factors such as low pH, macro and microplastics have been found to affect energy allocation in CWCs, with plastics increasing the risk of diseases in corals (Chapron et al., 2018; Palmer, 2018; Weinnig et al., 2020; John et al., 2022). Coral holobiont integrity can be achieved through the available resources that the CWCs use to expunge/fight pathogen infections or to cope with stress conditions in the environment. Coral stress response is linked to its immunity, through the maintenance of holobiont integrity. Damage threshold of coral holobiont susceptibility then is the point at which coral immunity is broken down, leading to CWCs diseases and mortality (Palmer, 2018).

1.7. Submarine canyons

1.7.1. Submarine canyon origin and geomorphology

Submarine canyons are geomorphological features incised into continental slopes and margins, sometimes with the head extending well onto the continental shelf (Harris and Whiteway, 2011). Based on the “V-shaped” morphological definition of submarine canyons (Shepard, 1972, 1981), two main types of submarine canyons are recognised, notably shelf-incised types of canyons, which either connects to or do not connect to a river system and the slope-confined or headless types of canyons. Submarine canyons generally evolve from processes such as

sediment gravity flows, slumping and mass wasting events, turbidity flows and tectonic processes (Shepard, 1972, 1981; Shannon, 1991; Shannon et al., 2007; Normark et al., 2009), that results in the differences in canyon morphologic features such as heads, walls, terraces, interfluves, branches, thalwegs that we observe today (Harris and Whiteway, 2011; Puga-Bernabéu et al., 2013; Mulder et al., 2012; Paull et al., 2013; Harris et al., 2014; Huang et al., 2014; de Almeida et al., 2015), with shelf-incising canyons generally being larger, greatly sinuous, more dendritic and closely spaced (Harris and Whiteway, 2011; Puga-Bernabéu et al., 2013; Huang et al., 2014). Submarine canyon heads are thought to be depositional sites of the canyon (Gamberi et al., 2017), with its closeness to the coastline affecting canyon hydrodynamics and how the submarine canyon channels sediment from nearby rivers or storm induced turbidity flows through it (Puig et al., 2014).

1.7.2. Hydrodynamic processes and sediment transport

The morphology and position of submarine canyons on the continental shelf affect the ocean hydrodynamic processes such as storm events, dense shelf-water cascading, internal waves, hyperpycnal flows and canyon-flank failures that influence sediment transport through canyons (Puig et al., 2014). Sediment transport processes in submarine canyons generally deposit sediments in the upper and middle stretches of the canyon (Lastras et al., 2009) for many years before being flushed into deeper parts of the canyon by large sediment failures (Puig et al., 2014). Upwelling and downwelling processes generated in submarine canyons enhances bioproductivity (Klinck, 1996; Allen et al., 2001; Jordi et al., 2005) with significantly higher concentrations of suspended particulate matter at the benthic boundary layer, which decreases from the upper to the lower sections of the canyon (Tyler et al., 2009). Similarly, chlorophyll-*a* and organic carbon concentrations have been detected in higher concentrations in submarine canyons (García et al., 2008; Ingels et al., 2009; Pusceddu et al., 2010). Storm events can affect

turbidity currents down submarine canyons (Shan et al., 2014) with the transport of sediment along canyon and across slope in a pulse-like process (de Stigter et al., 2007; Oliveira et al., 2007).

Dense shelf-water cascading can also distribute large amounts of sediment and organic matter in submarine canyons (Canals et al., 2006; Puig et al., 2014). The rapid cooling and/or evaporation of shelf water increases the density of the ocean water that can be transported down a submarine canyon with its head extending to the shore as a dense shelf cascading water (Ribó et al., 2011).

Internal waves occur due to the differences in density and salinity of ocean water that behave like different fluids (Carter and Gregg, 2002; Kunze et al., 2002; Puig et al., 2014). Internal tides of the ocean within submarine canyons creates internal waves in the dense lower ocean waters (Carter and Gregg, 2002) which can periodically resuspend sediments along the canyon axis, with coarse sediments commonly found in the canyon heads and becoming progressively finer with depth (Paull et al., 2005; de Stigter et al., 2007; Gamberi et al., 2017).

Hyperpycnal flows are usually associated with high rainfalls and floods that discharges large amount of sediment-laden water with significantly higher bulk density (Zavala, 2020). The resuspension of sediment materials from river discharges after flood events into submarine canyons also creates highly turbid waters that are typically warmer and fresh at shallower depths in the canyon (Mulder et al. 2001; Puig et al., 2014).

Large slope failures evolve into turbidity currents that are channelised through submarine canyons (Puig et al., 2014) carrying finer sediments with higher carbonate and total organic

carbon content (Vincx et al., 1994). Slope failures can be caused by earthquakes, river discharges, storm events and internal waves (Heezen et al., 1964; Okey, 1997; Puig et al., 2014; Paull et al., 2010). Slumps and other submarine mass movements can also occur when there is considerable increase in the sediment's pore pressure on the seafloor, reducing seafloor sediment shear resistance and internal cohesion (Iverson, 1997; Lee et al., 2007).

1.7.3. Submarine canyon ecology and human impacts

Submarine canyons serve as channels where sediments, nutrients and organic matter as well as litter and chemical pollutants from the continental shelves are transported into the abyssal zone (Huvenne and Davies, 2014; Fernandez-Arcaya et al., 2017).

Submarine canyons are hotspots of biodiversity due to their dynamic interactions with the hydrological and geological components of the deep ocean (Vetter et al., 2010; Davies et al., 2014) and offer different habitats including vertical CWC habitats (Huvenne et al., 2011; Appah et al., 2020). A heterogeneous habitat is more stable and resilient (Tilman, 1999), can be related to topography, current flow, the type of substrate and is responsible for enhanced benthic biodiversity (Smith et al., 2008; Vertino et al., 2010). *Lophelia pertusa* and *M. oculata* are associated with habitat heterogeneity in a submarine canyon off the Irish margin and show a high biodiversity in the northeast Atlantic (Appah et al., 2020).

Submarine canyons provide spawning, feeding, nursery and refuge sites for marine species (De Leo et al., 2010; Fernandez-Arcaya et al., 2017), although they have come under pressure from anthropogenic activities such as fishing (Orejas et al., 2009; Puig et al., 2012), oil and gas extraction (Harris et al., 2007) and dumping of land-derived mine tailings (Hughes et al., 2015; Ramirez-Llodra et al., 2015).

1.8. Marine data acquisition and cold-water coral habitat mapping

Deep-sea survey techniques can use motion sensitive multibeam echosounders (MBES) that can be coupled to remotely operated vehicles (Huvenne et al., 2011; Lim et al., 2017) or hull mounted (Appah et al., 2020; Lim et al., 2020; De Oliveira et al., 2021; Summers et al., 2021) for bathymetry studies. Ground truthing of acoustic surveys have become possible using box cores and ROVs equipped with high definition (HD) video camera systems. An ultra-short baseline (USBL) beacon coupled to the ROV allows for accurate positioning and coring or sampling for ground truthing purposes.

Regional oceanography and hydrodynamic profiles can be collected with an SBE 911plus Conductivity-Temperature-Depth (CTD) profiler (Sea-Bird Electronic Inc.) which is used to characterise the different water masses of a location in the global ocean by creating a T-S diagram (Appah et al., 2020; Lim et al., 2020) whilst Acoustic Doppler Current Profilers (ADCPs) are deployed at different monitoring stations to measure the different current regimes and their impact on the biotic (biodiversity) and abiotic components of the deep ocean (Lim et al., 2020).

ROV-videos (vertical or oblique angled) of the seafloor are collected for ground truthing data and to aid megafaunal species identification, with the video frames extracted at specified intervals using available software. Although, image-based identification is non-destructive, the taxonomic resolution of individuals is often limited, with the meiofauna and infauna as well as the highly motile organisms generally being overlooked.

Habitat mapping is an approach to determine the spatial and temporal distribution of key species and their biological assemblages. Different mapping strategies have been carried out to achieve different research objectives and results and widely applied to map CWC reef habitats (Vertino et al., 2010; De Clippele et al., 2018). Maps are a way of quantifying and evaluating changes in these habitats with time through monitoring programmes and are generated for effective management and conservation of CWC habitats. Habitat maps indicate a habitat's resilience and function in relation to environmental processes, climate change and anthropogenic invasions.

Sound can travel great distances through water and makes it suitable for collecting seafloor data by measuring the intensity of and time for sound waves reflected from the seafloor to be received on a hydrophone (Roberts et al., 2009). The pattern of the reflected waves depends on the features on the seafloor with soft substrates generating weak reflectance whereas hard substrates produce strong reflectance. Generally, low frequency sounds can travel deeper into the seabed but with low resolution while high frequency acoustics have wider coverage with higher resolution making it possible to determine the depth of the seabed.

High resolution seabed mapping and video surveys have revealed the destructiveness of litter, trawl fishing and industry on deep sea CWCs, indicative of the negative anthropogenic influences in the deep ocean (Roberts et al., 2006; Ragnarsson et al., 2017; Chapron et al., 2018; Pierdomenico et al., 2019).

1.9. Threats to ocean environmental health and consequent cold-water coral health

The rapid expansion of human activities into the deep ocean started since the introduction of steam engines for fishing in the 1860s for the growing human populations. Bottom trawling

occurs when fishing gears with heavy metallic doors are dragged along the seafloor to extract fish, resulting in the destruction and/or removal (i.e. CWCs habitats are fragmented or become patchy, crushed and dislodged) of the fragile and vulnerable CWCs that support large number of benthic organisms and high biodiversity. Trawling activities can cause slope failures in submarine canyons and can also resuspend large amounts of sediment materials that can clog the feeding apparatus of suspension or filter feeders (Martín et al., 2008). Resuspended sediments that persist in the water column high above the seafloor for long periods of time result in high turbidity (Ragnarsson et al., 2017).

Marine litter can be observed globally in the oceans, affect ocean aesthetics and health, with several threats to marine life including deep sea organisms. The sources of marine litter pollution are difficult to identify and generally thought to be marine-derived, land-derived or both. Marine litter can change the chemical composition of the immediate environment (Barnes et al., 2009; Galgani et al., 2010; Goldberg, 1994), bacterial community structure (Lobelle and Cunliffe, 2011), entangle and impede the movement of other marine organisms, as well as disrupt the feeding behaviour of marine species (Phillips et al., 2010).

The global carbon dioxide (CO₂) concentration has been increasing in the atmosphere since the industrial revolution and this has dire consequences for the global ocean. The absorption of high concentrations of CO₂ changes the ocean chemistry and causes an increase in hydrogen ions (which can result in low ocean pH) as well as a reduction in carbonate ions in the ocean. CWCs and other marine organisms that incorporate carbonate ions in their calcareous skeletons and shells become threatened as these growth structures can dissolve in acidic environments. It is predicted that if the current rate of CO₂ emission, particularly by the wealthy and developed nations (40% of the global total emissions), is not reduced, the global temperature is set to

increase at an average of 2.4 °C by the end of the century with consequent warming of the oceans, increase in the suitability of novel pathogen infections, rare diseases and the acidification of the ocean (Romanello et al., 2021). High temperatures in the deep sea because of climate change/global warming can reduce the availability of dissolved oxygen to marine organisms and also affect the physiological processes of CWCs (Dodds et al., 2007; Ragnarsson et al., 2017).

1.10. Study sites

1.10.1. The Porcupine Bank Canyon

The Porcupine Bank Canyon (PBC) is located on the southwestern coast of Ireland (Figure 1.2). It is cut off from terrestrial inputs, making it an ideal model to investigate and understand oceanographic changes in the northeast Atlantic waters. The PBC is on the western margin of the Porcupine Bank (PB) and covers an area of 2,055 km² with the canyon head at 430 m water depth and exits into the Rockall Trough at 3,300 m water depth (Appah et al., 2020; Lim et al., 2020; De Oliveira et al., 2021; Wheeler et al., 2021). The PBC is the largest submarine canyon on the Irish continental margin with a gentle western wall and a relatively steep eastern wall. It is a double canyon, tectonically controlled and asymmetric in orientation with a series of elongate canyon-parallel ridges of carbonate mounds of heights between 50 to 250 m occurring at water depths of 500 - 1,200 m (Mazzini et al., 2012; Lim et al., 2020) in the canyon head, canyon flank and south branch (Appah et al., 2020). There are two deeply cut channels with many adjoining shallow dendritic channels existing within the canyon with the main channels exiting into the Rockall Trough. Common scleractinian CWC species in the PBC include *L. pertusa*, *M. oculata* and *Desmophyllum cristagalli* (Mazzini et al., 2012; Appah et al., 2020). The PBC provides different habitats at different scales and has been designated a Special Area of Conservation (SAC) under the EU Habitat Directive (92/43/EEC).

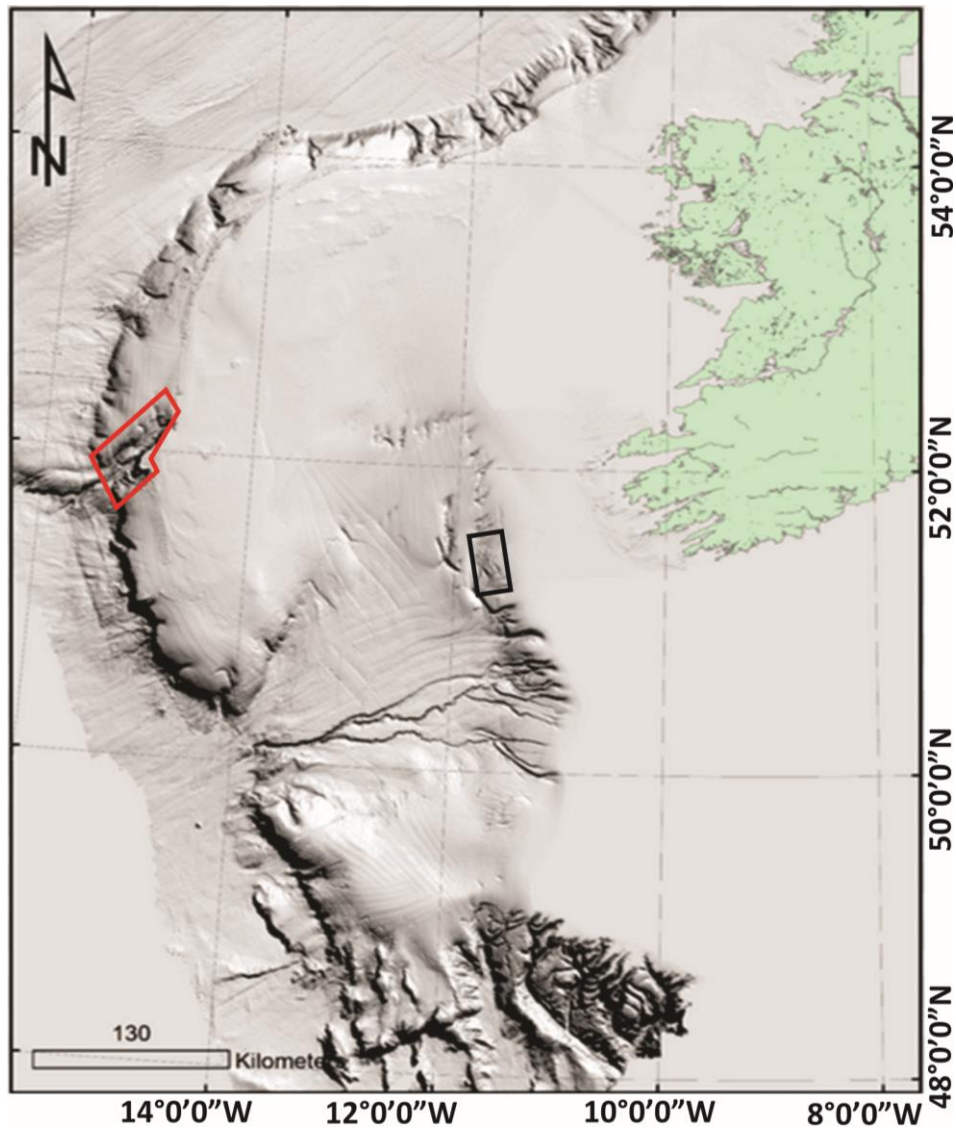


Figure 1.2. Location map showing the Porcupine Bank Canyon (red polygon) and the Belgica Mound Province (black rectangle) on the Irish continental margin

1.10.2. *Western Belgica Mound Province*

The Belgica Mound Province (BMP) is located to the southwest of Ireland and is on the eastern edge of the Porcupine Seabight (Figure 1.2). Several relatively small CWC mounds and active sediment deposition processes characterise the western Belgica Mound Province (wBMP). The eastern BMP is characterised by giant carbonate mounds such as Therese Mound, Galway Mound and Challenger Mound not present in the wBMP (see De Mol et al., 2002, 2007; Eisele et al., 2008; Thierens et al., 2010). Sediment waves of wavelength ~ 10 m and height 20 - 75

cm occur in the wBMP (Lim et al., 2017, 2018). The CWC mounds are restricted by the continental shelf to the east and the Arwen Channel to the west (Murphy and Wheeler, 2016). Shallow downslope channels exit into the Arwen channel at the northern bounds of the BMP (Wheeler et al., 2007). Small and elongated coral mounds (Moirs Mounds) are observed between 800 - 1,100 m. The Piddington Mound, one of the larger Moirs Mounds, is located within the less sediment-stressed area. Current speeds from 30 cm s^{-1} to $> 41 \text{ cm s}^{-1}$ in the northern part of the wBMP have been recorded (Lim et al., 2018). Benthic features such as seabed striations, comet marks and sediment waves suggest strong bottom currents in the BMP (Wheeler et al., 2005). The slope of the seabed in the BMP is between $0 - 55.7^\circ$ with a regional slope angle of 1.2° (Lim et al., 2017).

1.11. Objectives of the research

The general objective of the thesis is to investigate the key control processes that affect benthic megafaunal distribution including CWCs health and environmental threats in two CWC rich habitats (Porcupine Bank Canyon (PBC) and Belgica Mound Province (BMP)) off the Irish margin that have been designated special areas of conservation under the EU Habitat Directive (92/43/EEC) as well as assess the health status of the CWCs by looking histologically for parasites and the health of the coral microbiome in the PBC.

1.11.1. Specific objectives

- a)** To determine the processes and environmental controls that influence the distribution of benthic megafauna in the newly discovered CWC-habitat zones, including vertical habitats in the upper PBC. Here I answer two important questions: 1) what are the patterns of distribution of benthic taxa in the PBC, and 2) what are the factors that influence the distribution of benthic fauna in the canyon?

- b)** To evaluate, identify and quantify potential anthropogenic impacts in two Irish SACs, the upper PBC and western BMP, to make recommendations for sustainable use deep-sea resources and efficient management of these SACs.
- c)** To characterise habitats and species distribution linking them to stress conditions in the Porcupine Bank Canyon as well as determine factors that allow the benthic fauna to cope with stress in the canyon.
- d)** To evaluate the CWC microbiome, diversity and coral health in the uPBC.

The specific objectives listed above have been organised into chapters (2, 3, 4 and 5) which highlight the general objective of the thesis. Each specific objective seeks to answer different questions that explain the processes occurring throughout the canyon and allows one to observe the pattern of benthic megafauna distribution in the canyon. These chapters have been written as research papers and have been published already or are under review in peer-reviewed scientific journals of international repute at the time of writing this thesis.

Chapter two assesses the importance of *Lophelia* reef and rubble habitats to biodiversity in an isolated canyon (Porcupine Bank Canyon) on the Irish continental margin in the face of climate change, by specifically, looking at benthic megafauna and its relationship to environmental conditions that are changing due to climate change and may therefore be a source of stress. Remotely operated vehicle-based videos of the seafloor, including data on conductivity-temperature-depth, current speeds, particulate organic matter and bathymetry were collected to determine the drivers and patterns of distribution of the benthic megafauna in the canyon. The study revealed that biodiversity is high in the canyon, and to this effect, I looked at marine litter as additional source of stress in the third chapter. In particular, I looked at how litter is distributed, its influence on benthic organisms and how litter relate to flow patterns (from

bedform evidence and current speed) and anthropogenic activities such as trawling – from VMS data. Here also, remotely operated vehicle-based videos of the seafloor including data on current speeds, and bathymetry were collected, to determine the drivers and patterns of distribution of litter in the canyon and the western Belgica Mound Province. Although marine litter affects CWC growth and survival, including biodiversity and resilience, biodiversity is high in the PBC as noted in the previous chapter. However, there is the risk of litter increasing CWC disease, including the tendency to transport harmful pathogens such as Haplosporidia to the corals.

As a result, chapter four evaluates the microbial communities in the corals (and particularly pathogens that could not be detected with standard PCR by using advanced diagnostic techniques) as a proxy for coral health, as well as assess the microbial communities in the sediment and the water samples and determine the canyon wide implications in the face of climate change. Coral samples from the seafloor were collected, along with data on current speeds, particulate organic matter and bathymetry, using a remotely operated vehicle-based collection, in order to characterise the composition and diversity of microbial community in the Porcupine Bank Canyon.

Additionally, chapter five was undertaken to detect pathogens (genus *Vibrio* and Haplosporidia) infections, using histology and molecular experiments, in the coral samples to determine their health status in the Porcupine Bank Canyon. This study also evaluates the mechanisms that enable the benthic organisms to cope with stress in the canyon and determine the canyon-wide implications in the face of climate change. Coral samples were collected from the seafloor, using a remotely operated vehicle, along with data on current speeds, particulate organic matter and bathymetry.

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Chapter 2

Are non-reef habitats as important to benthic diversity and composition as coral reef and rubble habitats in submarine canyons? Analysis of controls on benthic megafauna distribution in the Porcupine Bank Canyon, NE Atlantic

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Abstract

Submarine canyons support high biomass communities as they act as conduits where sediments, nutrients and organic matter from continental shelves, or those that are carried along by slope currents, are transported into the abyssal zone. The Porcupine Bank Canyon (PBC), located on the Irish continental margin and isolated from terrigenous inputs, reveals a complex terrain and substrate variation that affect the distribution of benthic fauna. Here, ROV-based benthic video, Conductivity-Temperature-Depth (CTD), current velocity profiles, suspended particulate organic matter (POM) and bathymetric data were assessed to determine the controls on the distribution of benthic megafauna throughout the canyon. Multivariate analysis of the benthic community reveals significant differences in community structure among habitats and site locations throughout the canyon. Furthermore, these results show that non-reef habitats exhibit more variation in the composition of benthic taxa than coral reef and rubble habitats, with the following species contributing most to the structural differentiation between habitats: *Leiopathes glaberrima* (12.46%), *Hexadella dedritifera* (10.37%), *Cidaris cidaris* (9.31%), *Aphrocallistes beatrix* (9.33%), *Araeosoma fenestratum* (9.11%), *Stichopathes cf. abyssicola* (7.39%), *Anthomastus grandiflorus* (4.66%) and *Benthogone rosea* (3.84%). In addition, greater diversity, taxa evenness and high abundance of motile fauna were observed in non-reef habitat and the canyon flank. Seabed terrain features (depth, slope) are the most important environmental drivers that affect benthic taxa distribution while site locations and habitat type are the categorical variables that influence taxa distribution in the PBC. The highest mean current speed was observed on the canyon flank where the highest Shannon's diversity was recorded while mean current speed ranged from 18.2 - 31.3 cm s⁻¹. As the PBC is cut off from

direct terrigenous input, this research contributes to understanding cold-water coral habitat responses to natural Northeast Atlantic environmental conditions. The findings of the current study will inform key stakeholders on how to responsibly interact with the canyon benthic habitats and can help inform policy makers on the effective conservation and management of the cold-water coral habitat in the PBC and other canyons.

Keywords: Biodiversity, Porcupine Bank Canyon, POM, cold-water coral, non-reef habitat, species distribution, habitat variability

1. Introduction

Submarine canyons are geomorphic features incised into continental margins and shelves (Shepard, 1972; Harris and Whiteway, 2011; Harris et al., 2013; Puig et al., 2014), including slopes of oceanic Islands (Vetter et al., 2010). They can be connected to landward river systems (Huang et al., 2014), terrestrially disconnected or tectonically controlled (Greene et al., 1991; Liu et al., 1993; Lo Iacono et al., 2014). Canyons have complex topographies and morphologies that affect hydrographic, oceanographic and biological processes (Allen et al., 2001; Bosley et al., 2004; Trotter et al., 2019). They are conduits for organic matter, nutrients and sediment transport to the abyssal zone (de Stigter et al., 2007; Kiriakoulakis et al., 2011; Mazzini et al., 2012; Puig et al., 2013) as well as litter and organic pollutants (de Jesus Mendes et al., 2011; Mordecai et al., 2011; Schlining et al., 2013; Tubau et al., 2015). Storm events may also affect circulation and current regimes along the rims of submarine canyons (Shan et al., 2014). Sedimentation processes in submarine canyons can affect the distribution of the benthic community through increased disturbance and modified turbidity (Huvenne and Davies, 2014; Martín et al., 2014) with hydrographic and oceanographic processes affecting food supply (Canals et al., 2006; Kenchington et al., 2014) which in turn affects benthic

community structure (Kiriakoulakis et al., 2007; De Leo et al., 2010). Seabed terrain and substrate variation provide a variety of suitable habitats for benthic communities in submarine canyons (Schlacher et al., 2007; McClain and Barry, 2010; Vetter et al., 2010; Cunha et al., 2011; Davies et al., 2014; De Mol et al., 2011; Paterson et al., 2011; Fanelli et al., 2018) with submarine canyons recognized as areas of significant ecological importance.

They are considered ‘hotspots’ for biodiversity (De Leo et al., 2010; Vetter et al., 2010; Cunha et al., 2011; Martín et al., 2011; Puig et al., 2014, 2013) and are able to support cold-water coral ecosystems (Canals et al., 2006; Orejas et al., 2009; Huvenne et al., 2011; Khripounoff et al., 2014; Morris et al., 2013; van den Beld et al., 2017; Aymà et al., 2019), with which can be associated more than 1,300 marine species (Roberts et al., 2006; Henry and Roberts, 2015). In particular, *Lophelia pertusa* (syn. *Desmophllum pertusum*: Addamo et al., 2016; taxonomic status pending scientific community consensus) reefs are able to form geologic features called coral mounds on the interflaves of submarine canyons (De Mol et al., 2011; Stewart et al., 2014). Coral mounds can be tens of meters tall and several kilometers wide (Wheeler et al., 2007) and can affect local hydrographic processes (Mienis et al., 2007). It has also been noted that cold-water corals show slow growth and recovery after anthropogenic disturbance (Fabri et al., 2014; Huvenne et al., 2016).

The Porcupine Bank Canyon (PBC) is incised into the western margin of the Porcupine Bank, 300 km west of Ireland (Figure 2.1) (Dorschel et al., 2010) and is cut off from direct terrestrial inputs, making it an ideal model system to investigate oceanographic influences on coral habitats in the Northeast Atlantic. It is situated between the Porcupine Seabight to the southeast and the Rockall Trough to the west into which the canyon drains. The Porcupine Bank Canyon (PBC) is tectonically controlled (Shannon, 1991; Shannon et al., 2007) and is the largest

submarine canyon on Ireland's western margin (63 kilometres in length) and incises higher up into the Porcupine Bank than neighbouring canyons, to 420 m water depth crossing the

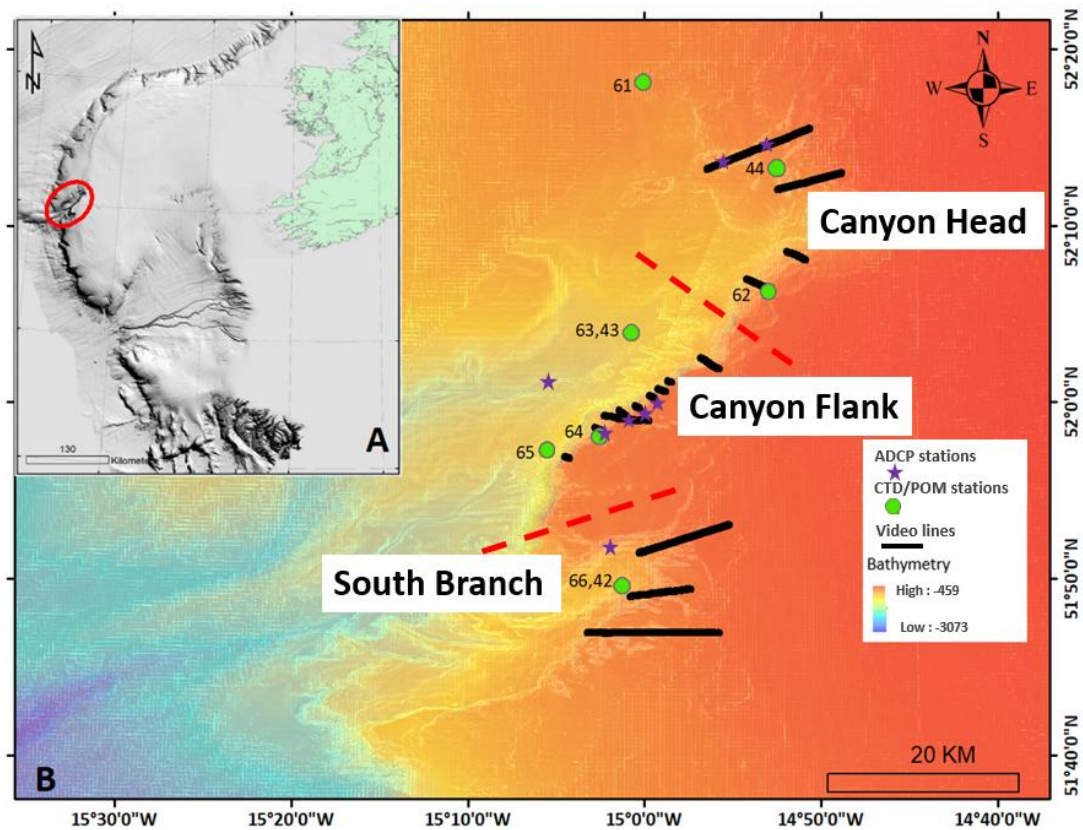


Figure 2.1. Map showing the location of A) the Porcupine Bank Canyon (red ellipse) on the Irish-Atlantic margin, B) ADCP stations, CTD/POM stations, benthic video lines and ship-based MBES bathymetry. Different site locations of the canyon are separated by red broken lines.

cold-water coral habitable zone (Davies et al., 2008). Elsewhere on the Porcupine Bank, cold-water coral reefs are located upslope of canyon heads on the open margin (Akhmetzhanov et al., 2003; van Weering et al., 2003; Wheeler et al., 2005; Dorschel et al., 2009). The Porcupine Bank Canyon is a geological feature that can be described as an area of high habitat heterogeneity that supports a high biomass (Wheeler et al., 2017; Lim et al., 2018). It has been designated as a Special Area of Conservation (SAC; Figure 2.2) under the EU Habitat Directive (92/43/EEC) as a submarine canyon with cold-water corals and closed to fishing. *Lophelia pertusa* is the main framework-forming cold-water coral in the canyon. The slow growth rate

of this scleractinian coral (Gass and Roberts, 2006; Orejas et al., 2008) demands that the ecosystems in canyons be managed and protected in the face of continued anthropogenic activities such as trawl fishing. To this effect, the present study investigated: (a) the benthic megafauna distribution and variability within site locations and habitats, and (b) the environmental drivers of the benthic faunal distribution and variability in the PBC. These questions are addressed using a rich dataset (including 46.81 km of HD ROV video data), characterising megafauna distribution in the PBC for the first time. Due to the isolation of this major submarine canyon on the European Atlantic margin, the relationships discovered here act as a “natural barometer” for oceanic controls of benthic diversity in submarine canyons including for cold-water corals.

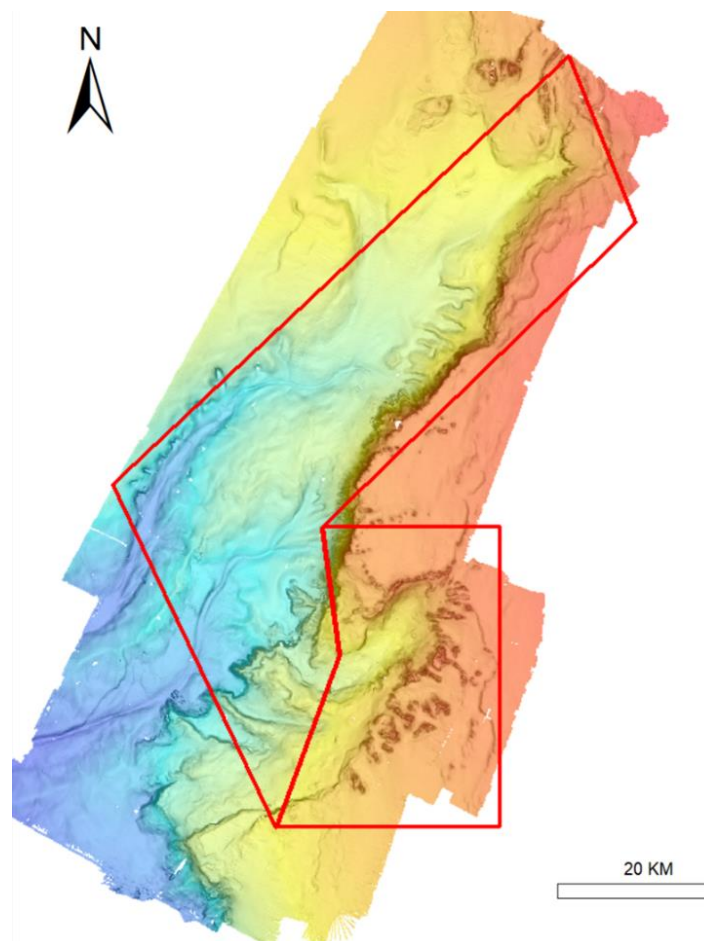


Figure 2.2. A map showing the area of the Porcupine Bank Canyon and the Southwest Porcupine Bank designated as special area of conservation (SAC) (demarcated by red polygon).

2. Materials and Methods

Survey, oceanographic and sample data from the PBC (Table 2.1; Figure 2.1) were collected on board the RV Celtic Explorer with the Holland I ROV (www.marine.ie) in 2017 (CoCoHaCa I: Wheeler et al., 2017), 2018 (CoCoHaCa II: Lim et al., 2018) and 2019 (MoCha_Scan I: Lim and Shipboard Party, 2019). The ROV (made by Soil Machine Dynamics Limited) was equipped with two 400 Watt Deep-sea Power and Light SeaArc2 HMI lights, two 25,000 lumen Cathx Ocean APHOS LED lights, a pair of Deep-sea Power and Light lasers 10 cm apart, an Insite Mini Zeus forward-facing high definition (HD; 1080p) video camera and a Kongsberg 14 - 208 digital stills tilt camera systems to collect benthic video data at a speed of 0.2 knots. ROV navigation was recorded with a coupled Sonardyne Ranger 2 USBL (ultra-short baseline positioning system) and RDI workhouse doppler velocity logger.

Table 2.1 . ROV transects in the PBC, length (km), mean depth and depth range and date for each transect

Video lines	Depth range (m)	Mean depth (m)	Length (km)	Co-ordinates of video lines		Date of dive
				Start (Lat/Long)	End (Lat/Long)	
5	582 - 1019	822	5.02	52.2004755/-14.8749045	52.2162493/-14.8134502	23/06/2017
4	582 - 1054	936	8.43	52.2199477/-14.9410820	52.2587293/-14.8434248	22/06/2017
8	654 - 1233	936	2.56	52.1160897/-14.9035102	52.1049630/-14.8781872	24/06/2017
7	709 - 1039	878	1.78	52.1418340/-14.8656937	52.1340797/-14.8478487	23/06/2017
10	695 - 1231	905	1.73	52.0417677/-14.9472790	52.0307722/-14.9295458	24/06/2017
11	681 - 1008	789	3.20	51.9872062/-15.0386897	51.9817048/-14.9956017	24/06/2017
12	704 - 1020	813	0.46	52.0060868/-14.9961498	52.0037287/-14.9907723	25/06/2017
16	760 - 967	903	0.39	51.9479248/-15.0758619	51.9468131/-15.0706514	26/06/2017
20	701 - 972	827	0.78	51.9920744/-15.0246131	51.9866632/-15.0175038	26/06/2017
21	762 - 995	849	0.35	51.9966081/-15.0090888	51.9949090/-15.0072242	26/06/2017
21a	740 - 922	793	0.31	51.9955653/-15.0073699	51.9935245/-15.0042819	27/06/2017
22	686 - 1021	790	0.64	52.0124273/-14.9877423	52.0094863/-14.9797737	27/06/2017
23	729 - 1026	860	0.32	52.0196988/-14.9786440	52.0183787/-14.9746790	27/06/2017
19	715 - 969	782	0.68	51.9756827/-15.0473160	51.9722080/-15.0391987	26/06/2017
15	622 - 1070	744	9.11	51.7817563/-15.0542793	51.7818997/-14.9290390	26/06/2017
14	567 - 1039	769	4.37	51.8159363/-15.0136093	51.8229947/-14.9559127	25/06/2017
13	596 - 1043	772	6.68	51.8571415/-15.0047455	51.8840042/-14.9196713	25/06/2017

2.1. Seabed terrain and substrata characterisation

Ship-based 30 kHz multibeam echosounder (EM302) data were acquired using parallel sets of lines following depth contours over the canyon and gridded at 25 m resolution. The minimum swath overlap was 25% at c. 8 knot and swath width was 2000 m. The acquired data were managed and processed with Seafloor Information System, cleaned with Fledermaus Qimera and tidal corrections were applied. A sound velocity probe was applied to the data to correct it for water sound velocity variations. The data were imported into ArcMap v10.4 and projected in UTM zone 28N. A total area of 1,800 km² of seabed was surveyed. Terrain variables (slope, aspect and rugosity) were obtained using ESRI's Spatial Analyst Extension Tool in ArcMap, and values were extracted using the extract values to points tool incorporated in ArcMap. According to Guinan et al. (2009), slope is “*a plane tangent to a digital terrain model surface at the centre of an analysis window*” while aspect is “*the azimuthal direction of the steepest slope at the centre of the analysis window*”. Rugosity is defined as “*the ratio of surface area to planar area*” (Jenness, 2002). Aspect was transformed into two variables namely northness and eastness in MS Excel. First, aspect was converted into radians ($\pi * aspect(^{\circ})/180$) and then converted into northness (cosine of aspect in rad) and eastness (sine of aspect in rad) to provide a continuous measure from negative one to positive one. Vertical and oblique imagery were used to characterise the seabed as adopted in Lim et al. (2017, 2018), Mortensen and Buhl-Mortensen (2004) and Vertino et al. (2010). In total 1823 images were used to characterise the different seabed types in the PBC. A gridded quadrat of 0.25 m² (with 25 individual squares) created based on the 10 cm laser scale was overlaid on each image, and the percentage cover was estimated as the ratio of grids overlying a seabed type to the total number of grids in the grid quadrat. The point count method (applied in the present study) for estimating the percentage cover of a seabed type yields accurate results (Mortensen and Buhl-

Mortensen, 2004). Five substrata were identified (Table 2.2 and Table A.3) and resolved into coral reef and rubble (dead/live corals and coral rubble) and non-reef habitats (sediment dominated, sediment & dropstone and bedrock) (Table A.3) at each of the three site locations in the canyon (Figure 2.1). Live/dead coral is characterised by a cell coverage of >50% observable living and dead parts while coral rubble is dominated by a cell coverage of >60% observable biogenic materials. Hermatypic corals and ahermatypic coral polyps are biological organisms which can build coral reefs (physical features or habitats made from secretions of calcium carbonate and other associated biological and non-biological materials). Therefore, coral presence was determined when the coral polyp's corallite skeletal casing (usually bright, white or orange in colour in the NE Atlantic) was easily noticeable while dead coral was identified as darker, grey or brown skeleton. Smaller fragments of dead skeleton were identified as coral rubble.

Table 2.2. Seabed classification system used for this study

Seafloor type	% cell coverage	Environment
Live/dead coral (DL)	>50% cell coverage	Coverage with observable living or dead parts
Coral rubble (R)	>60% cell coverage	Coverage with observable biogenic materials
Sediment & dropstone (SD)	>60% cell coverage	Coverage with observable dropstones
Sediment (S)	>90% cell coverage	Coverage with no observable biogenic material and dropstones
Bedrock (B)	>60% cell coverage	Coverage with observable bedrock

2.2. Megafaunal analysis

A series of regularly spaced, but randomly located, ROV-video transects from the deep-waters to the shallow-waters in the PBC were run to cover the different substrata and habitats throughout the canyon. ROV-based video frames were extracted at 60 second intervals using the online software Free Video to JPG converter available from DVDVideoSoft. Poor quality

images and those captured at sub-optimal angles were removed. The survey depth ranged between 582 - 2126 m from the canyon head to the south of the canyon traversing the canyon slope. As described for the seabed terrain and substrata characterisation, a gridded quadrat of 0.25 m² was created based on a 10 cm laser scale and overlaid on each image. The abundance of benthic taxa was estimated following Boolukos et al. (2019) and Doyle et al. (2005). Colonial taxa (e.g. *Hexadella dedritifera*, *Parantipathes* sp. and *Leiopathes glaberrima*) were estimated as percentage cover while discrete organisms (e.g. Asteroidea species, squat crab and the true crab *Chaceon affinis*) were counted. The percentage cover was estimated as the ratio of grids overlying a taxon to the total number of grids in the grid quadrat. However, the hit point method (Doyle et al., 2005) was used to estimate the percentage cover of colonial taxa in the present study. With the hit point method, a point of intersection is made in each of the 25 grids by joining the 4 vertices in each grid with two straight diagonal lines. An organism is counted if the point of intersection touches it, and the process is repeated for each of the quadrats in particular habitat (coral reef and rubble - non-reef) or location (flank - head - south). The percentage cover then is the ratio of the number of hits of a taxon to the total number of possible hits multiplied by 100. All the images used to characterise the seabed types were used to characterise the benthic fauna. The density (i.e., individuals m⁻²) of discrete taxa was determined by multiplying the mean number of each taxon (within N number of 0.25 m² grid quadrat) by four. Individual organisms were taxonomically resolved to species level where possible although this was not achievable for most taxa, given the limitations associated with identifying benthic organisms from ROV-images. As such, many organisms were identified as morphotypes or species, using best practice for habitat analysis (Henry and Roberts, 2013; Henry et al., 2014).

2.3. Statistics

Most of the survey data were analysed with R (R Core Development Team, 2014). Shannon's diversity (H') ($H' = -\sum_{i=1}^S P_i \ln P_i$) (Shannon, 1948) and Pielou's evenness ($J' = H'/\ln S$) (Pielou, 1966) were estimated for the studied habitats (coral - non-reef) and locations in the canyon (flank - head - south). P_i is the proportion of the i th taxa while S is the total number of taxa within each community. Pielou's index evaluates the relative abundance of the benthic taxa (species evenness) while Shannon's index calculates the diversity of the community, considering the relative abundance of each taxon. Significant differences between taxa evenness and Shannon's diversity index for the variable habitats and site locations were evaluated using z-test. Z-test is less conservative than Student's t test and can be used when the population variance is known or unknown, but the sample size is large (Derrick et al., 2015). The z-test could also be used when the population is normally distributed. It is worthy to note that Geary's C test (for spatial autocorrelation; Bivand et al., 2008; Dubé and Legros, 2014) estimates a z-value (by randomisation or normalisation). Also, a Bonferroni correction was applied to assess significance of the taxa evenness and Shannon's diversity among site locations throughout the PBC. *Lophelia pertusa* data were excluded from the diversity indices since it is the main framework-forming coral and occurs everywhere in the canyon. *Lophelia pertusa* percentage cover was however estimated for the three site locations existing within the canyon. Significant differences between *L. pertusa* percentage cover in each of the three site locations within the PBC were determined by performing a pairwise z-test as there were only three levels for site locations. A z-test is suitable for testing proportional data and data from a large sample size (Krishnamoorthy and Thomson, 2002). Preliminary test of spatial autocorrelation of sample points among habitats and site locations by randomised Geary's C test was made in ROOKCASE (Sawada, 1999). Rarefaction curves were made to standardize the sample size (on each substrate, habitat and site location) (Fussey, 1995; Belgrano and Reiss,

2011). Rarefaction curves were made in PAST ver 2.17c (Hammer et al., 2001). Presence/absence data of the benthic taxa were used for multivariate analyses and again *L. pertusa* data were excluded in the analyses since, as previously mentioned, this species occurs everywhere in the canyon and is the main framework-forming coral. All sample points without data were removed, leaving 799 sample points for the multivariate analyses. Multivariate analyses were performed using the **vegan** package incorporated in R. Bray-Curtis dissimilarity distance was estimated and used to perform analysis of similarity (ANOSIM), similarity of percentages (SIMPER) and non-metric multidimensional scaling (nMDS) ordination (Oksanen, 2011). The nMDS plot was made using the *metaMDS* function and the stress (measure of goodness-of-fit) calculated. Significant differences in the dissimilarities between the benthic taxa grouped into habitats and site locations were evaluated using the function *adonis*. nMDS scores (x,y coordinates) were extracted and put into a new data frame. Lastly, employing the **ggplot2** package, an aesthetic nMDS plot was made from the extracted nMDS scores. ANOSIM estimates significant differences in community structure. Also, ANOSIM is a method in *vegan* which can handle only class predictors and is less robust than *adonis* while *adonis* on the other hand is a function that partitions dissimilarities for the sources of variation and uses permutation tests to examine the significances of those partitions (Oksanen et al., 2014). SIMPER analysis computes the taxa that most contribute to the observed differences in taxa composition. nMDS ordination is a rank-based approach which allows dissimilarities between objects to be viewed in reduced dimensional space. The stress value (< 0.2 indicates a good representation) indicates a measure for the goodness-of-fit of the ordination (Clarke and Gorley, 2001; Clarke and Warwick, 2001).

Furthermore, canonical correspondence analysis (CCA) was used to determine the relationship between seabed terrain features (depth, slope, rugosity and aspect), habitats, site locations and

the distribution of the benthic taxa. CCA accounts for the patterns of taxa distribution by estimating taxa centroids (ter Braak, 1986; Quattrini et al., 2012). The analyses were made employing the *cca* function of the *vegan* package incorporated in R (Oksanen et al., 2014). In order to perform CCA, sample points with no taxa were excluded from the analysis. Model choice was made by calculating the Akaike's information criterion (AIC) (which is based on the measure of goodness-of-fit) using the *step* function. Also, the *ordistep* function which incorporates a random component in the model choice was run. In addition, the variance inflation factor (VIF) which determines multicollinearity amongst variables was estimated. A VIF of 1 indicates complete independence of variables while a $VIF > 10$ indicates high multicollinearity. A permutation test was performed to determine the significance of the overall CCA model. Similar permutation tests were run to determine the significance of the environmental variables and the axes that explain the variability in the species distribution.

2.4. Ecological composition

The benthic fauna were classified into functional groups, motility and mode of feeding. The benthic fauna were classified into functional groups based on their biological and life strategies (Jonsson et al., 2004; Henry and Roberts, 2007; Macdonald et al., 2010). Presence/absence data were used to estimate the percentage composition of functional groups within the variable habitats and site locations in the PBC. Motility comprised of motile and sessile taxa while mode of feeding consisted of suspension/filter feeders and detritivores (Macdonald et al., 2010; Massironi, 2016). Also, the percentage composition of predators and non-predators were determined for the different habitats and site locations (Scharf et al., 2006; Bell, 2012; Thiel and Watling, 2015). Some of the benthic fauna identified exhibit more than one mode of feeding. As such, the present study focused mainly on predators, suspension/filter feeders and detritivores to observe possible trends of distribution.

2.5. Environmental context

During summer months of 2018 and 2019, a CTD (Sea-Bird 911 plus) was used to characterize the water masses around the benthic habitats throughout the canyon (Table 2.3; Figure 2.1). Seawater samples were collected at different depths from 20 – 500 m above the seabed within the benthic boundary layer (McCave et al., 2001; Lueck et al., 2009) reflecting the dynamic sedimentary (organic and inorganic) processes that occur in the bottom and intermediate seawaters. A 10 litre (l) Niskin bottle rosette unit on the CTD system was used to collect water.

Samples at different depths at different stations and POM data were determined via an ashing method, outlined in Lysiak-Pastuszak and Krysell (2004) and Strickland and Parsons (1972). In addition, eight 1Hz Nortek Aquadopp Acoustic Doppler Current Profilers (ADCP), were deployed in different macrohabitat types throughout the canyon (see locations on Figure 2.1). Each ADCP was vertically mounted (upward-facing) onto metal frames ('landers') to ensure they did not move. The ADCPs, once deployed (15-19/05/2019), continuously collected data (25 m above the transducer for a period of 1 min every 10 min) for a period of approx. 2.5 months (retrieved on 27-28/07/2020).

Table 2.3. Seawater samples from the PBC collected on 08-08-2018 showing Time (UTC), station number, sample depth and coordinates

Time	Station number	Sample depth (m)	Lat	Long
6.45am	61	599	52°13.295	14°52.569
6.45am	61	550	52°13.298	14°52.572
7.52am	62	519	52°05.66	14°51.61
9.16am	63	894	52°03.82	15°00.50
9.16am	63	992	52°03.81	15°00.49
9.16am	63	695	52°03.84	15°00.52
9.16am	63	1050	52°03.80	15°00.48
9.16am	63	592	52°03.85	15°00.53
9.16am	63	795	52°03.83	15°00.51
12.52pm	65	797	51°56.69	15°05.96
12.52pm	65	994	51°56.67	15°05.94
12.52pm	65	599	51°56.71	15°05.98
12.52pm	65	895	51°56.68	15°05.95
12.52pm	65	697	51°56.70	15°05.97
15.37pm	66	696	51°49.68	15°01.24
15.37pm	66	994	51°49.65	15°01.21
15.37pm	66	597	51°49.69	15°01.25
15.37pm	66	894	51°49.66	15°01.22
15.37pm	66	796	51°49.70	15°01.26
21.36pm	42	1093	51°49.66	15°01.13
21.36pm	42	993	51°49.66	15°01.13
21.36pm	42	843	51°49.66	15°01.13
21.36pm	42	747	51°49.66	15°01.13
21.36pm	42	599	51°49.66	15°01.13
7.58am	43	1044	52°03.88	15°00.77
7.58am	43	976	52°03.88	15°00.77
7.58am	43	849	52°03.88	15°00.77
8.05am	43	750	52°03.88	15°00.78
8.08am	43	620	52°03.88	15°00.77
8.10am	43	560	52°03.88	15°00.77
10.04am	44	892	52°13.23	14°52.52
10.06am	44	850	52°13.23	14°52.52
10.08am	44	750	52°13.23	14°52.52
10.09am	44	630	52°13.23	14°52.52
10.12am	44	580	52°13.23	14°52.52
10.12am	44	490	52°13.23	14°52.52

3. Results

3.1. Seabed terrain and substrata

Forty-eight percent of the observed seabed was classified as sediment dominated, 37% was coral rubble and the rest of the classifications were less than 10% (Table 2.4). Coral reef and rubble habitat comprised 91% coral rubble and 9% live/dead coral while non-reef habitat comprised 79% sediment, 13% bedrock and 8% sediment & dropstone (Table 2.4). Percentage composition of sediment was highest on the canyon head while coral rubble was highest on the flank (Table 2.4). Twenty-five percent of bedrock was exposed in the flank but there was no exposed bedrock in the south (Table 2.4). Seabed terrain variables (depth, slope, rugosity and aspect), the different habitats and site locations are presented in Table A.3.

Table 2.4. Percentage composition of the five substrata in the different habitats and site locations in the PBC

Substrata	Percentage (%) composition					
	PBC	Coral reef and rubble habitat	Non-reef habitat	Flank	Head	South
Bedrock (B)	7.70	0.00	12.90	24.70	0.70	0.00
Dead/Live coral (DL)	3.60	8.90	0.00	2.30	1.60	6.40
Coral rubble (R)	36.50	91.10	0.00	42.00	26.60	41.20
Sediment (S)	47.60	0.00	79.40	28.60	64.50	47.70
Sediment & dropstone (SD)	4.60	0.00	7.70	2.30	6.50	4.70

3.2. Benthic taxa composition

A total of 60 benthic taxa from four different phyla were observed in the total survey area in the PBC. Examples of benthic fauna identified in the PBC are shown in Figures 2.3, 2.4 and 2.5. The four phyla occurred in the order: Cnidaria (50.8%) > Echinodermata (23.7%) > Porifera (15.3%) > Mollusca (10.2%), in the 0.25 m² gridded quadrats. In addition, the percentage composition of the different phyla distributed in the different habitats and site locations within the canyon were estimated (Table 2.5).

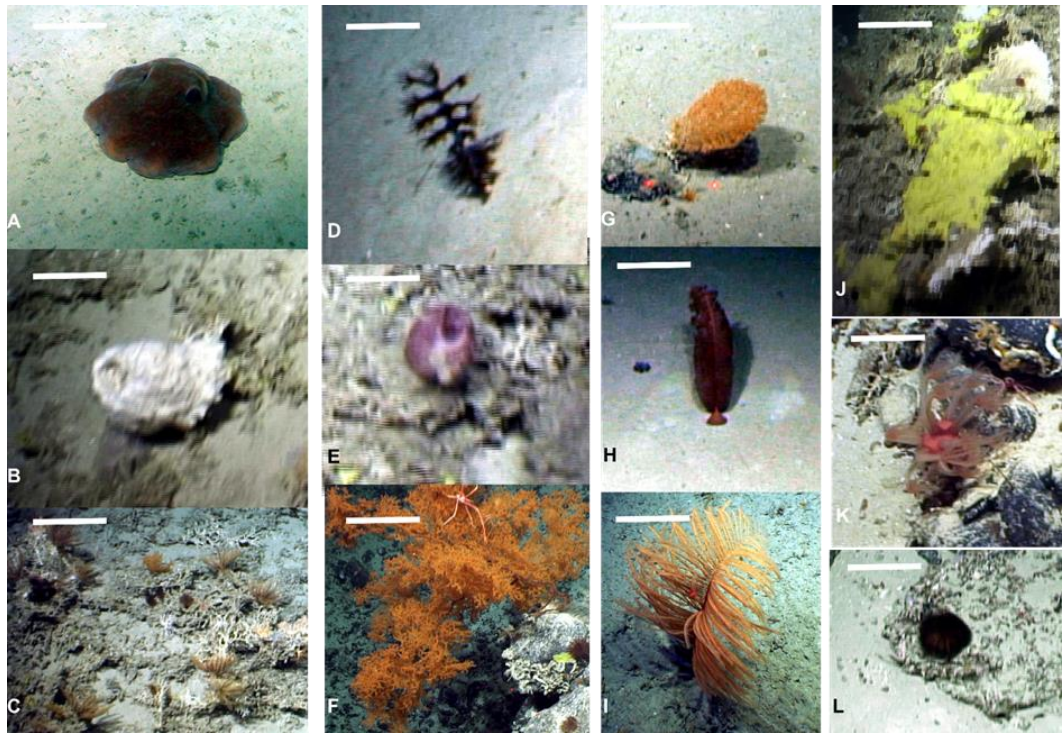


Figure 2.3. Benthic taxa in the PBC. Scale bar = 10 cm: A) *Opisthoteuthis agassizii* B) *Porifera* sp. C) *Crinoid* D) *Kophobelemnnon* sp. E) *Geodia* sp. F) *Leiopathes glaberrima* G) *Chrysogorgia* sp. H) *Pennatula* sp. I) *Bathypathes* sp. J) *Hexadella dedritifera* K) *Anthomastus grandiflorus* L) *Araeosoma fenestratum*

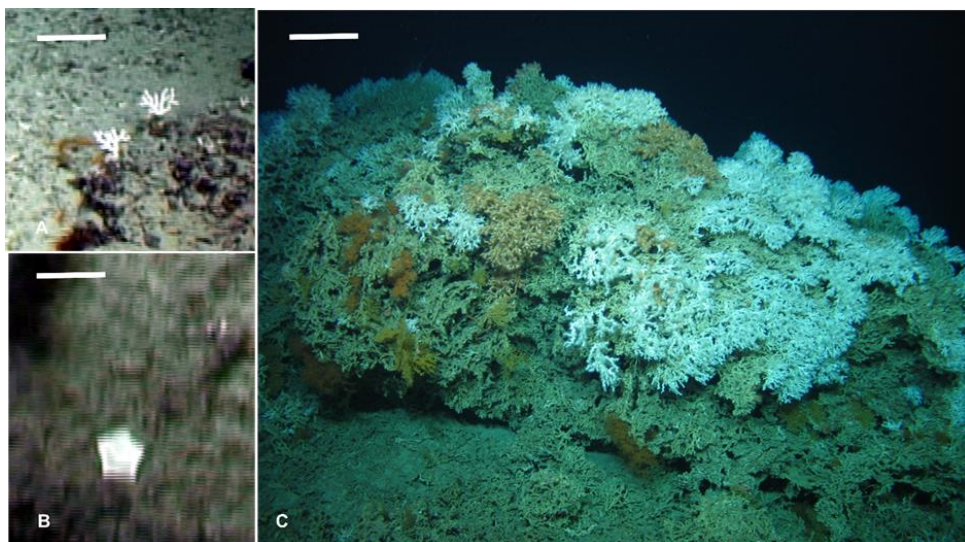


Figure 2.4. Benthic taxa in the PBC. Scale bar = 10 cm: A) *Pliobothrus symmetricus* B) *Asteroidea* sp. C) *Lophelia pertusa*

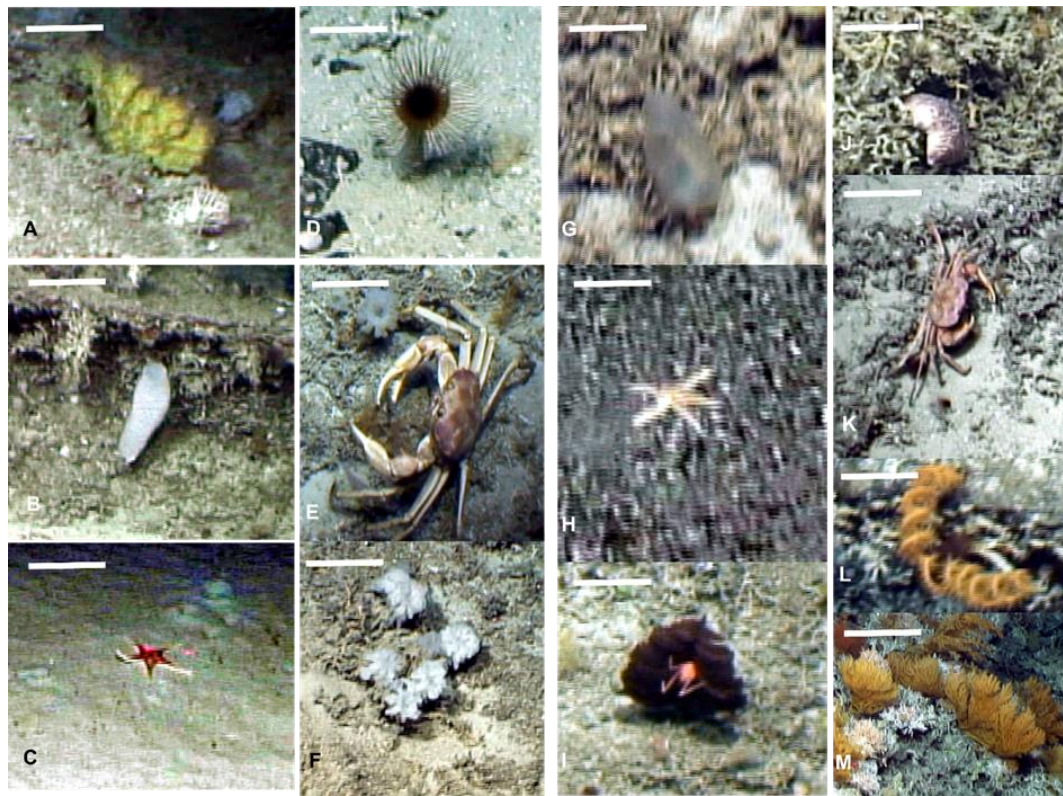


Figure 2.5. Benthic taxa in the PBC. Scale bar = 10 cm: A) Unidentified sp. B) Euplectellid sp. C) Asteroidea sp. D) Actiniaria sp. E) *Chaceon affinis* F) *Aphrocallistes beatrix* G) Ascidian sp. H) Asteroidea sp. I) *Bathypathes* sp. with squat crab J) *Porania* sp. K) Decapoda sp. L) *Stichopathes* cf. *abyssicola* M) *Paramuricea* sp.

Table 2.5. Percent composition of each of four phyla on the different habitats and site locations in the PBC

Habitat and site locations	Percentage (%) composition			
	Cnidaria	Echinodermata	Mollusca	Porifera
Coral reef and rubble habitat	53.659	17.073	9.756	19.512
Non-reef habitat	56.863	25.490	7.843	9.804
Flank	52.273	25.000	13.636	9.091
Head	51.282	25.641	5.128	17.949
South	55.172	17.241	6.897	20.690

Mean percentage cover of benthic colonial taxa on coral reef and rubble habitat was four times greater than the mean percentage cover on non-reef habitat (Table 2.6). The glass sponges *Hexadella dedritifera* (26%) and *Aphrocallistes beatrix* (27%) and the black coral *Leiopathes glaberrima* (17%) were the most common and dominant colonial species in the coral reef and

rubble habitat while the echinoderm *Cidaris cidaris* (73%) was the most common discrete species in the coral reef and rubble habitat. However, taxa distribution in non-reef habitat exhibited low dominance as the most common discrete taxa abundances were the echinoderms *Araeosoma fenestratum* (27%), *Cidaris cidaris* (26%), *Psolus squamatus* (16%) including the holothurian *Benthogone rosea* (21%) while highest abundances of common colonial taxa were *Leiopathes glaberrima* (19%) and *Stichopathes cf. abyssicola* (16%). The percentages of the species listed are proportions of quadrats (0.25 m²) in which the species were seen. Meanwhile, benthic taxa mean percentage cover in the flank was twice as much as taxa mean percentage cover in the canyon head and south (Table 2.6). The rarefaction curve shows higher number of species on non-reef habitat (Figure 2.6B).

Table 2.6. Number of taxa, mean percentage cover of colonial taxa and mean density of discrete taxa (mean $\pm$ s.e)

Habitat and site locations	Benthic taxa abundance		
	Number of taxa	Mean % cover	Mean density (m ⁻²)
Coral reef and rubble habitat	41	0.30 $\pm$ 0.25	2.53 $\pm$ 0.22
Non-reef habitat	51	0.07 $\pm$ 0.11	3.58 $\pm$ 0.25
Flank	44	0.25 $\pm$ 0.28	2.18 $\pm$ 0.28
Head	39	0.10 $\pm$ 0.16	5.11 $\pm$ 0.36
South	29	0.14 $\pm$ 0.15	2.16 $\pm$ 0.16

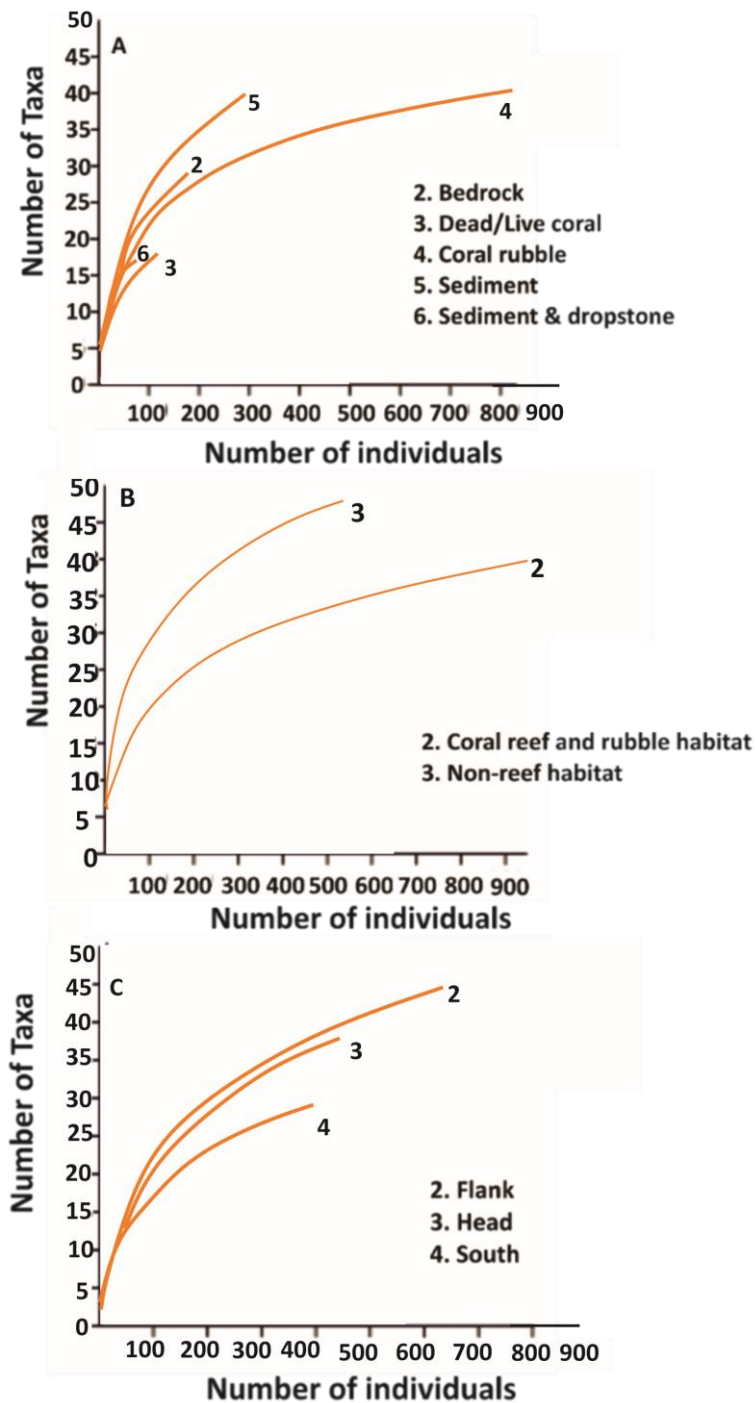


Figure 2.6. Rarefaction curves for pooled data on: A) substrata, B) habitats and C) site locations. Sample size for substrata, the different habitats and site locations are: bedrock ($n = 141$), dead/live coral ($n = 65$), coral rubble ($n = 666$), sediment ($n = 867$), sediment & dropstone ($n = 84$), coral reef and rubble habitat ($n = 731$), non-reef habitat ($n = 1092$), canyon flank ($n = 555$), canyon head ($n = 612$) and canyon south ($n = 656$) respectively.

3.3. Benthic taxa and biodiversity

Diversity was highest on the canyon flank and in non-reef habitats, although no significant ($P > 0.05$) differences were observed in benthic taxa diversity within the different habitats and site locations (Table 2.7). In relation to canyon site locations, taxa dominance (uneven distribution of species in a community) was highest in the flank and lowest in the canyon south while non-reef habitat exhibited high evenness (the relative abundance of species) and low dominance (Table 2.7). There was no significant ($P > 0.05$) difference observed in taxa evenness within the different habitats and site locations. Calculated P-values after applying Bonferroni correction among site locations and after performing a pairwise z-test among site locations for Shannon's diversity and taxa evenness were compared (and found not to be significant in both cases). Also sample points in the different site locations did not show spatial autocorrelation (Geary's $C_{\text{flank}} = 1.1992$, $z = -10.510$; Geary's $C_{\text{head}} = 1.1993$, $z = -11.039$; Geary's $C_{\text{south}} = 1.1993$, $z = -11.431$) as well as in the different habitats (Geary's $C_{\text{coral reef and rubble}} = 1.1994$, $z = -12.068$; Geary's $C_{\text{non-reef}} = 1.1996$, $z = -14.759$).

Table 2.7. Estimates of Shannon's diversity and Pielou's evenness obtained from percentage and density abundance data in the different habitats and site locations in the PBC

Habitat and site locations	Percentage estimate		Density estimate	
	Shannon's diversity (H')	Pielou's evenness (J')	Shannon's diversity (H')	Pielou's evenness (J')
Coral reef and rubble habitat	2.16	0.65	1.14	0.43
Non-reef habitat	2.38	0.71	1.72	0.54
Flank	2.36	0.74	1.97	0.65
Head	2.23	0.67	1.44	0.56
South	1.83	0.59	0.80	0.38

3.4. Benthic faunal composition

Analysis of similarity (ANOSIM) estimate ($0.091 < R < 0.166$; $P < 0.05$) revealed that there were significant differences in the benthic taxa composition in the different habitats and site

locations in the canyon. Similarity of percentages (SIMPER) revealed the taxa that most contributed to the observed structure in the benthic community within the PBC. The first seven taxa that most contributed to the observed compositional differences between habitats are *Leiopathes glaberrima*, *Hexadella dedritifera*, *Cidaris cidaris*, *Aphrocallistes beatrix*, *Araeosoma fenestratum*, *Stichopathes* cf. *abyssicola* and *A. grandiflorus*. Also, the first four species that contributed to the compositional differences between canyon head and flank are: *Leiopathes glaberrima*, *Hexadella dedritifera*, *Cidaris cidaris* and *Stichopathes* cf. *abyssicola*; between canyon head and south are *Leiopathes glaberrima*, *Cidaris cidaris*, *Aphrocallistes beatrix* and *Hexadella dedritifera*; and between flank and south are *Leiopathes glaberrima*, *Aphrocallistes beatrix*, *Hexadella dedritifera* and *Stichopathes* cf. *abyssicola*. Non-reef habitats are more variable than coral reef and rubble habitats (habitats are represented by the different shapes of the objects— triangles and circles) while the canyon head and south is more variable than the flank (site locations are represented by the different colours in the legend— red, blue and green) as supported by non-metric multidimensional scaling (nMDS) ordination. Also, objects closer together are more similar (and tend to cluster) than are those farther apart. The nMDS analysis showed the dissimilarities among the benthic taxa grouped into habitats and site locations in the Porcupine Bank Canyon (Figure 2.7).

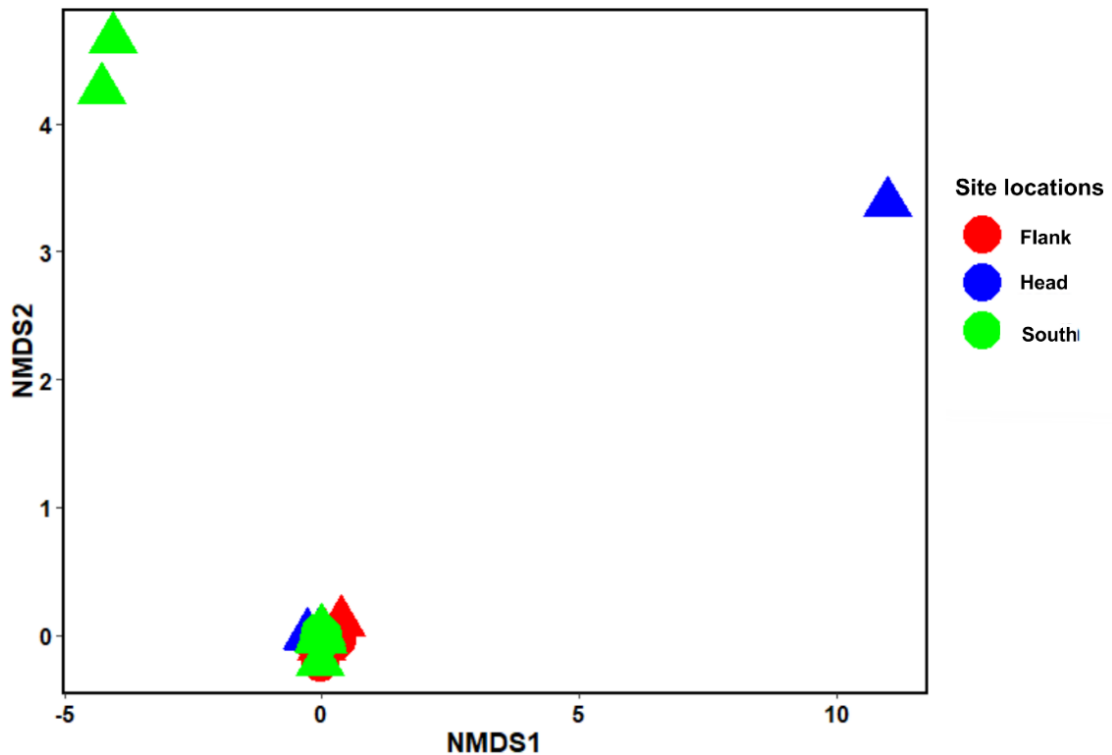


Figure 2.7. Non-metric multidimensional scaling (nMDS) ordination using Bray-Curtis distance. Stress = 0.035. nMDS (n = 799) represents the dissimilarities between the benthic taxa grouped into habitats and site locations in the Porcupine Bank Canyon. Circles: coral reef and rubble habitat; Triangle: Non-reef habitat.

3.5. Relationship between seabed terrain, habitats, site locations and benthic fauna distribution

Aspect (northness and eastness) and rugosity were removed from the model because they were not significant ($P > 0.05$). The significance of the permutation test ($P = 0.001$) revealed the utility of the CCA model to evaluate the relationships among the terrain variables, habitats, site locations and the benthic fauna, although only 5.39% of the total variation was captured in the CCA. A similar permutation test also revealed that the terrain variables, habitats and site locations significantly ($P = 0.001$) accounted for the variation in benthic fauna distribution. The test also revealed the first two axes, CCA1 and CCA2, significantly ($P = 0.001$) accounted for the variation between the variables and taxa distribution respectively (Figure 2.8). Axis

CCA1 accounts for 46.95% of the variation while CCA2 accounts for 26.50% of the variation (Figure 2.8). Length of the arrow determines the degree of influence of the terrain variables, habitats and site locations on taxa distribution while a stronger relationship exists between taxa closer to the arrow than for those farther away (Figure 2.8). Furthermore, arrow lengths correlate to the ordination axes, where a longer arrow suggests a stronger correlation and potentially more variation being explained. Also, the perpendicularity between the arrows reveals the vital variables that contributed to benthic taxa distribution. Depth and slope were the most important terrain features, although depth exhibited greater influence on benthic taxa distribution (Figure 2.8). The categorical variables, habitat and site locations, were also important in the distribution of the benthic fauna in the PBC (Figure 2.8).

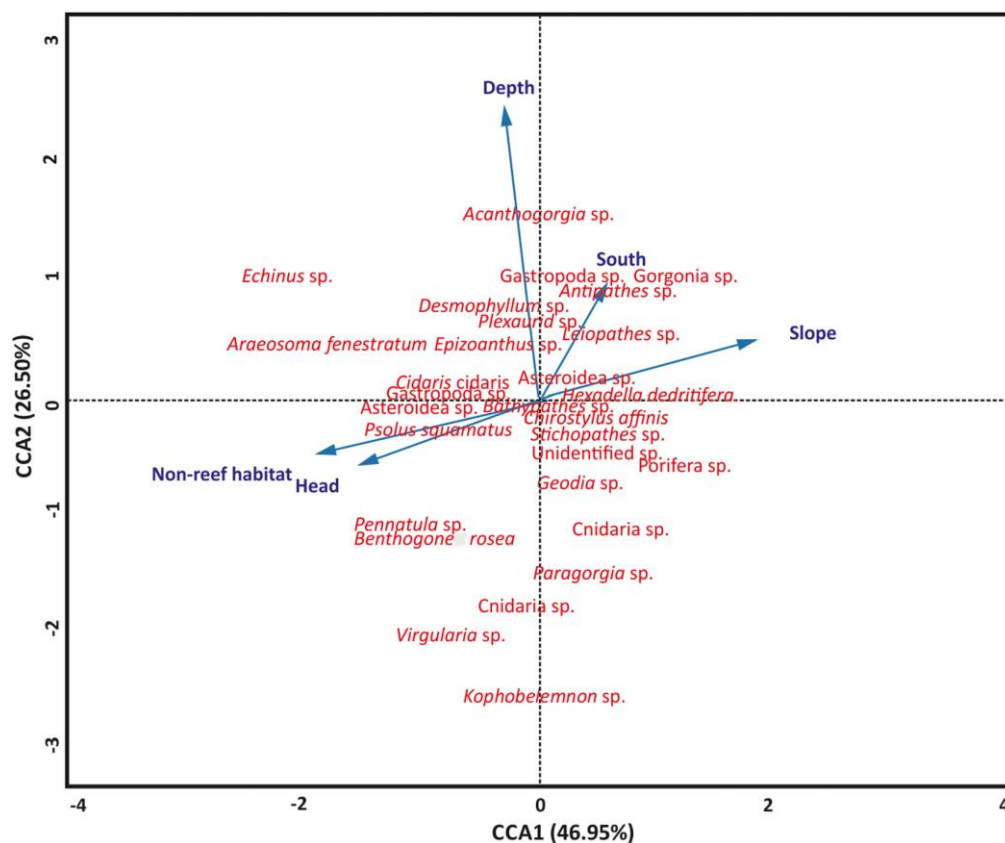


Figure 2.8. Canonical-correlation analyses showing the relationship among terrain features (slope and depth), habitat, site locations and benthic taxa distribution (n = 799). CCA = canonical correspondence analysis. Blue arrows are terrain variables, habitats and site location represented as vectors.

3.6. Ecological composition

3.6.1. Motility

Classification of the motile and sessile groups was made based on the biology of the organisms (Table 2.8). Sessile taxa were more abundant than the motile fauna in the two habitats and three site locations in the canyon (Table 2.8). Sessile fauna were high in abundance in each of the three site locations with the characteristic most common coral species *Stichopathes* cf. *abyssicola* and *L. glaberrima* and sponges *Aphrocallistes beatrix* and *Hexadella dedritifera*. The most common motile fauna on coral reef and rubble and non-reef habitat was *Cidaris cidaris*, while *Araeosoma fenestratum* constituted the most common motile species in non-reef habitat. Crinoid and *Epizoanthus paguriphilus* respectively were the only motile (organisms that move on their own accord) echinoderm and cnidarian taxa observed in the canyon. Motile fauna were highest on the flank (Table 2.8).

3.6.2. Mode of feeding

Classification of the suspension/filter feeders, predators and detritivorous was made based on the biology of the organisms (Table 8). Suspension/filter feeders constituted a greater percentage in the different habitats and site locations in the canyon (Table 8). Cnidarians identified in the canyons also demonstrate predation mode of feeding (Scharf et al., 2006; Bell, 2012; Massironi, 2016). The percentage composition of predators and non-predators for habitats were coral reef and rubble (40.68% and 59.32%) and non-reef (57.63% and 42.37%) whilst the percentage composition for the site locations were flank (50.85% and 49.15%), head (38.98% and 61.02%) and south (30.51% and 69.49%) respectively. Some benthic organisms have adopted other modes of feeding such as grazing and scavenging (Macdonald et al., 2010; Massironi, 2016). For instance, the echinoderm *Cidaris cidaris* and *Porania* sp are grazers (Macdonald et al., 2010; Massironi, 2016). Suspension/filter feeders (e.g. the sponges

Aphrocallistes beatrix and *Hexadella dedritifera*) were observed where the sclerectinian *Lophelia pertusa* and the black coral *Leiopathes glaberrima* appeared well developed and actively growing (i.e., making new polyps and accumulation of skeletal mass) (e.g. Figure 2.6C).

Table 2.8. Percent composition of the functional groups in the different habitats and site locations in the PBC

Habitat and site locations	Percentage (%) composition			
	Motility		Mode of feeding	
	Motile	Sessile	Suspension/filter feeder	Detritivore
Coral reef and rubble habitat	26.00	74.00	76.00	24.00
Non-reef habitat	35.00	65.00	67.00	33.00
Flank	38.00	62.00	62.00	38.00
Head	27.50	72.50	75.00	25.00
South	27.00	73.00	77.00	23.00

3.7. Bathymetry, oceanography, POM and hydrodynamics

Ship-based multibeam bathymetry data (Figure 2.1 and 2.4) reveals the PBC as a double canyon with two branches separated by a ridge. Both branches exit into the Rockall Trough separately. The southern branch (Figure 2.1 and 2.4) is smaller with its head reaching to 1900 m water depth near to station 65 and has an arm that cuts into the southeastern margin of the canyon up to a minimum water depth of 600 m and typically 700 m.

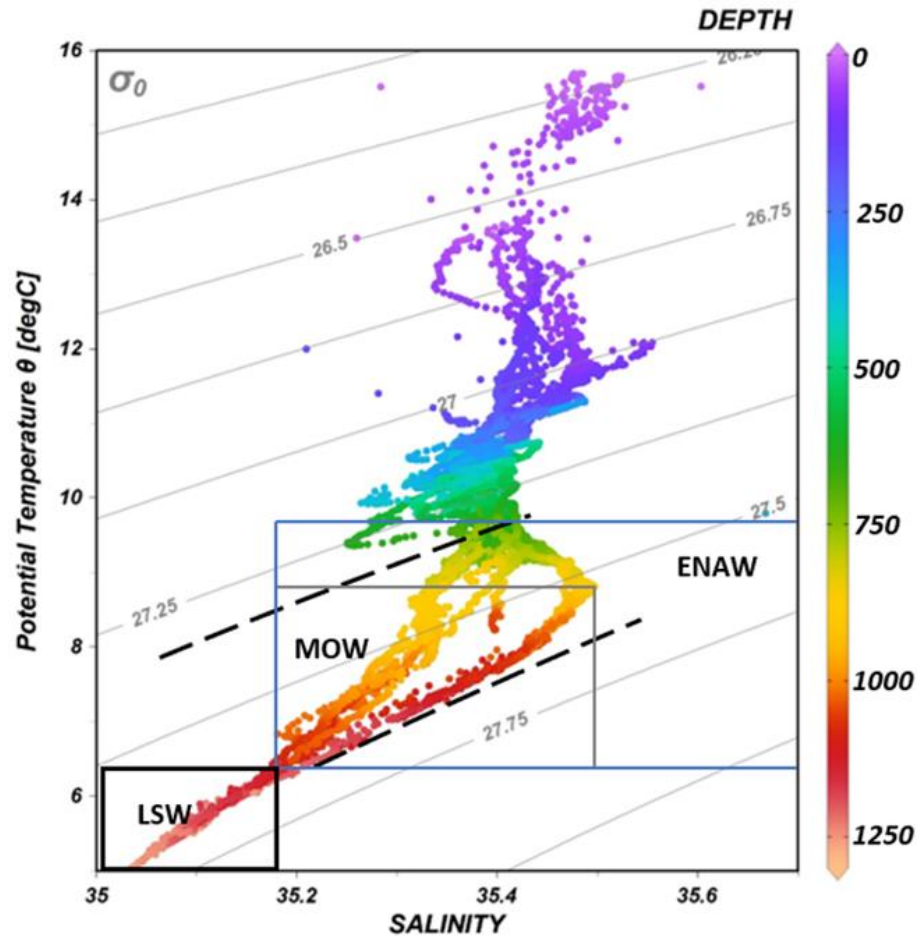
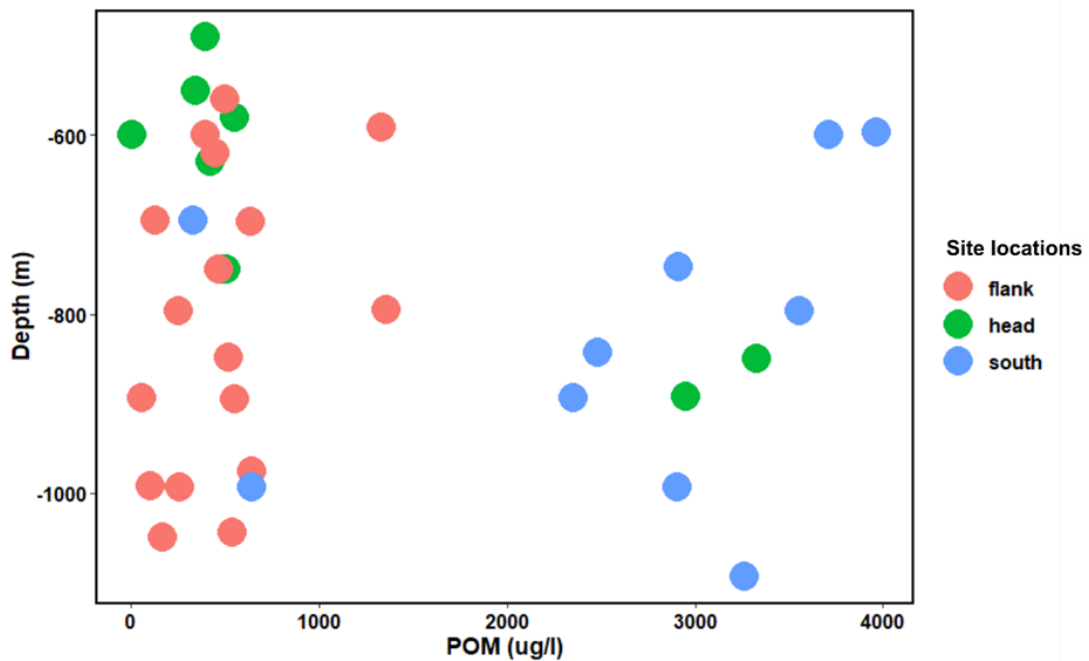


Figure 2.9. T-S plot of CTD data with density contours to characterise the water mass properties through a 1200 m depth from the surface water in the PBC: ENAW (Eastern North Atlantic Water), MOW (Mediterranean Outflow Water), LSW (Labrador Sea Water). Space between broken lines reveal the predicted density envelope for NE Atlantic CWCs (Dullo et al., 2008).

The main branch of the canyon has an asymmetrical profile with the southeastern margin represented by a tectonically faulted, steep cliff from 1600 to 750 m water depth. On the northeastern margin, the head of the canyon is more gently sloping, with even gentler gradients defining the northwestern margin (Figure 2.2). Small gullies around the canyon margins feed into the two branches. The rim of the canyon is plateaued.

CTD data reveals that the Eastern North Atlantic Water (ENAW) was the main water mass generally bathing the benthic community from 600 - 1200 m in the PBC while the Labrador Seawater (LSW) occurred below 1200 m (Figure 2.9). The temperature and salinity limits between 600 - 1000 m are 6.5 - 9.8 °C and 35.18 - 35.5 psu respectively.



4. Discussion

4.1. *Patterns of fauna composition and diversity*

This research presents the findings of an extensive ROV-based survey of the PBC, which includes a detailed analysis of 46.81 km of ROV HD video data detailing the different substrata and habitats within the PBC including a large coverage of coral reef and rubble and non-reef habitats (Table 2.4). Although the quadrat size (0.25 m²) was small, it was necessary to sample a standardised area as both oblique and vertical images were used, and also due to the fact that the number of species is proportional to the area being sampled (Rosenzweig, 1995). According to Clark et al. (2010), substratum characteristics influence benthic taxa composition. Generally, coral rubble and dead/live corals have been reported to support large numbers of species and high Shannon's diversity compared to non-reef habitat (Jonsson et al., 2004; Mortensen and Fosså, 2006; Henry and Roberts, 2007; Wienberg et al., 2008) with a few studies reporting lower taxa richness and diversity on coral rubble habitat (Robert et al., 2014; Buhl-Mortensen L. et al., 2017). Moreover, as the sample size for the substrata varied, it was appropriate to pool them into habitats to mitigate the effect of uneven sample size on taxa number (Figure 2.6). As such, the different substrata in the present study were resolved into potentially more diverse habitats (coral reef and rubble) and less diverse habitats (non-reef) to allow for the evaluation of differences in taxa diversity and richness between the two habitats and the different site locations in the PBC.

Most surveys of cold-water corals are exploratory in nature and tend to focus their survey lines on reefs and/or interesting features which most likely limit their biodiversity assessments (Buhl-Mortensen P. et al., 2017). According to Buhl-Mortensen P. et al. (2017), survey areas which were most likely to support corals were chosen for their study. However, in the present study, a canyon-wide systematic survey pattern was applied covering all habitats proportional

to seabed area. High biodiversity was noted on coral reef and rubble but they are localised hotspots. On balance, there is a higher number of taxa identified in non-reef habitat than coral reef and rubble (Figure 2.6, Table 2.6), and consequently this influences the Shannon's diversity observed in non-reef compared to coral reef and rubble habitat, although this observed difference was not significant (Table 2.7). A more proportional abundance of benthic fauna in the non-reef habitat and the canyon flank resulted in the highest Shannon's diversity and taxa evenness estimated in the canyon flank, but again there was no significant difference observed. Similarly, Ramirez-Llodra et al. (2010) observed high Pielou's evenness and Shannon's diversity in the canyon head and walls of the Blanes submarine canyon in the Mediterranean. In line with the present study, the sponges *Aphrocallistes beatrix* and *Hexadella dedritifera* have been previously noted to colonise coral reef and rubble habitats in high abundance (Pfannkuche et al., 2004; Buhl-Mortensen L. et al., 2017; Boolukos et al., 2019). The ubiquitous and frequent presence of the glass sponges *Aphrocallistes beatrix* and *Hexadella dedritifera* were observed on all substrates in relatively high abundance during each dive. Similarly, the black corals *Leiopathes glaberrima* and *Stichopathes cf. abyssicola* occurred on all substrates in comparatively high abundance during each dive. Faunal dominance was low in the non-reef habitat and canyon flank, but this observation was also not significant (Table 2.7). Non dependence (from Geary's C test) of sample points in the different habitats and site locations was sufficient reason to use either a t- or z-test (both test assumes independence of samples, although a z-test was used in the present study) to assess the level of significance of taxa diversity and evenness among habitats and site locations in the PBC.

There are more exposed hard seabed substrates on the canyon flank (Table 2.4) and the steepness (20 - 60°) of the canyon flank prevents sediment accumulation on this substrate. In addition, this exposed bedrock on the flank and non-reef habitat provides extra substrate for

sessile benthic faunal attachment. According to Vertino et al. (2010) and Wienberg et al. (2008), substrate variability typically gives rise to high biodiversity. In general, hard substrata and dropstones provide suitable habitats for stylasterids (Cairns, 1992). Similarly, our results show a low abundance of the stylasterid *Pliobothrus symmetricus* in coral reef and rubble habitat with higher abundances in non-reef habitat. There is a gradation from a more coral-rich area in the south to a sandier sediment area in the north of the PBC. As a result, high abundance of echinoderms on sediments and sediment & dropstone were observed in the north. Particularly, *Cidaris cidaris* and *Araeosoma fenestratum*, and *Psolus squamatus* are the taxa that influence the abundance of echinoderms on sediments and sediment & dropstone habitats respectively, in the canyon head in the north. In addition, the sea pens *Kophoblemnon* sp. and *Pennatula* sp. are abundant in the deeper parts of the PBC which is mostly sediment (Hogan et al., 2019).

4.2. Benthic fauna composition and POM

High *Lophelia pertusa* abundance in the canyon south (Figure 2.11) may be due to the high concentrations of POM in the south of the canyon (Figure 2.10). Kiriakoulakis et al. (2007) shows that POM is food source for benthic communities. Also, food availability and composition in a submarine canyon structure the spatial distribution of benthic fauna (Huvenne et al., 2011; Leduc et al., 2014). POM in the sediment becomes available to suspension feeders through resuspension by hydrographic or biological activities in the canyon. However, human activities such as trawl fishing and objects (Figure 2.12G) dropped to the seafloor also resuspend POM and make them available to the benthic community (Wilson et al., 2015; Daly et al., 2018). In the PBC, evidence of past fishing activities included fish traps, fishing lines (Figure 2.12) and possible trawl/tool marks (Figure 2.12).

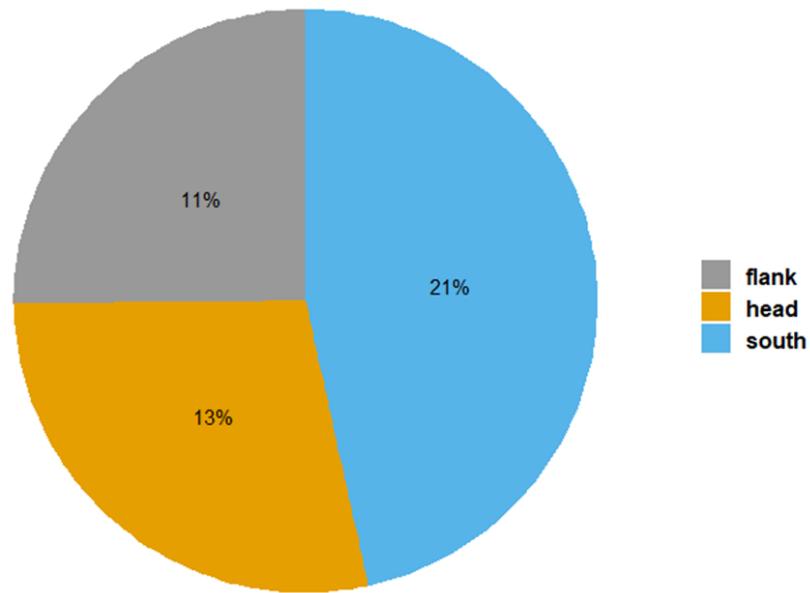


Figure 2.11. *Lophelia pertusa* mean percentage cover among site locations in the PBC. A significant ($P < 0.05$) difference between the canyon south and flank was observed. The sample size for canyon flank, head and south are 555, 612 and 656 respectively.

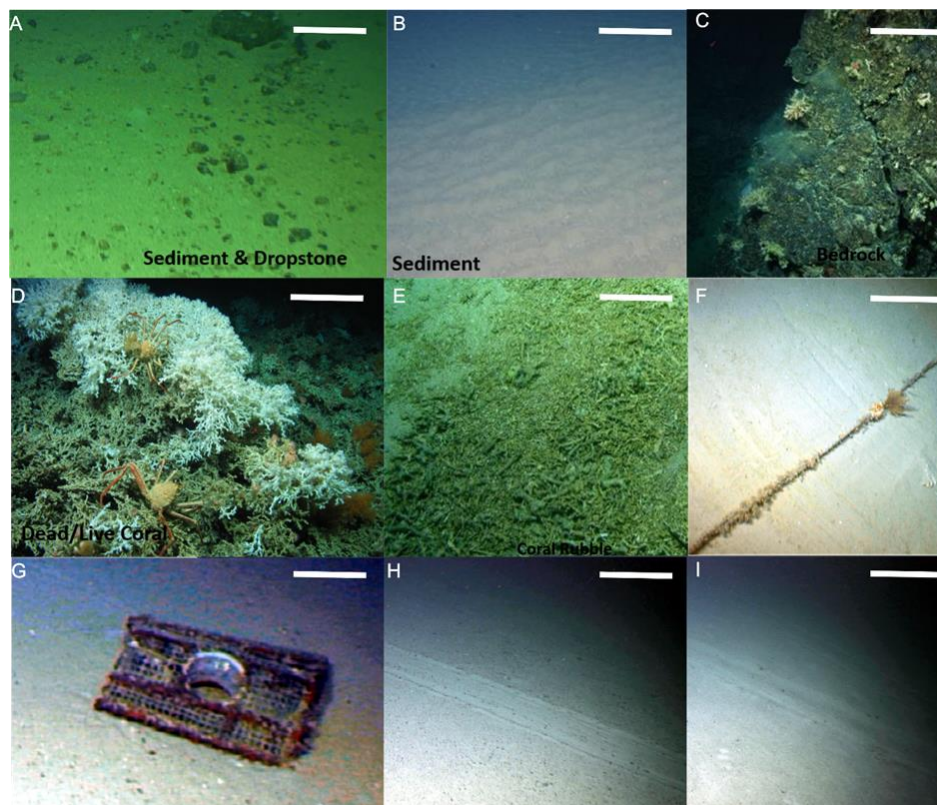


Figure 2.12. Seabed types that exist in the PBC and identified evidence of human activities, scale bar = 10 cm: A) sediment & dropstone (SD) ($n = 84$), B) sediment (S) ($n = 867$), C) bedrock (B) ($n = 141$), D) live/dead coral (DL) ($n = 65$), E) coral rubble (R) ($n = 666$), F) fishing line, G) metal fish trap, H) tool marks (837 m), I) tool marks (774 m)

4.3. Ecological composition

The biology of the benthic taxa influences the ecological composition of benthic organisms in the PBC (Danovaro et al., 2008). The burrowing activities of some benthic taxa can resuspend sediment and POM, affecting structure of the benthic community (Lampitt et al., 1986; Smith et al., 1986). In addition, the variability of taxa composition can be attributed to oceanographic and environmental factors prevailing in the canyon (Henry et al., 2014). High abundances of motile fauna were observed in non-reef habitat and on the flank. The abundance of sessile fauna corresponds with the abundance of suspension/filter feeders in the canyon. Similar observation was made in other deep-sea studies (Jonsson et al., 2004; Henry and Roberts, 2007). In line with Massironi (2016), cnidarians are classified as predators (ambush or passive) in the present study. Massironi (2016) classified cnidarians as predators probably because they get their food by waiting in ambush (and this seems to be the case). The ambush (sit and wait) mode of predation is generally demonstrated by organisms that have low energy requirements and also when their prey (e.g. zooplankton including calanoid copepods, amphipods, euphausiid crustaceans) are dense (Scharf et al., 2006; Bell, 2012). Moreover, the organism's ability to capture live prey by actively focusing the prey through its mouth with the aid of its tentacles constitute and fit the definition for predation. The high abundance of suspension/filter feeders and predators in the Porcupine Bank Canyon could be explained by the high concentrations of resuspended POM ($1,330 - 3,965 \mu\text{g l}^{-1}$) and the low rate of sedimentation in the high energy environment (Jonsson et al., 2004; Henry and Roberts, 2007). According to Gardner (1989) resuspended particle concentrations may exceed $5000 \mu\text{g l}^{-1}$ in high energy environments of submarine canyons.

4.4. Environmental drivers of benthic fauna distribution

4.4.1. Relationship between seabed terrain, habitats, site locations and benthic fauna distribution

Canonical correspondence analysis was performed to evaluate the relationship between the terrain features (depth, rugosity, aspect and slope), habitats, site locations and the benthic megafauna in the PBC. In the present study, seabed terrain features (depth and slope) were the most important terrain features that affected the spatial distribution of benthic fauna while non-reef habitat and canyon head are the categorical variables that affected fauna distribution (Figure 2.8). The contributions of non-reef habitat and site locations on benthic taxa distribution are succinctly observed from the high taxa richness and Shannon's diversity that they support in the PBC. The canyon morphology, revealed by the MBES data (Figure 2.1 and 2.4), contributes to the distribution patterns in the canyon as the CCA analysis showed that the different site locations (which show different morphologies) also influenced taxa distribution. Henry and Roberts (2007) recognised that vertical habitat heterogeneity significantly influences benthic fauna diversity. In addition, depth and other geomorphic canyon features have been found to affect the spatial distribution of benthic fauna (De Mol et al., 2011; Kenchington et al., 2014; Fanelli et al., 2018; Trotter et al., 2019).

4.4.2. Oceanography and hydrodynamics

The low variation in benthic fauna distribution accounted for by the CCA1 and CCA2 axes respectively (Figure 2.8) suggest that in addition to seabed terrain, substrata and the different site locations and morphologic features, other factors such as oceanography and hydrodynamics may contribute to the pattern of benthic fauna distribution observed in the PBC. Cold-water coral distribution is largely influenced by temperature and salinity (Freiwald, 2002; Roberts et al., 2006; Davies et al., 2008; Dullo et al., 2008; Naumann et al., 2014). In the

present study, actively growing and well-developed corals (e.g. Figure 2.12D and 2.6C) are restricted to a bathymetric depth of 600 - 1,000 m and permanently immersed in ENAW (Figure 2.9), suggesting that ENAW influences the distribution of the benthic fauna in the PBC. A similar trend of fauna distribution was observed by Mienis et al. (2007) in the Rockall Trough margins. However, poorly developed corals were observed to coincide with LSW below 1200 m (Figure 2.9). It is noted that high taxa number and Shannon's diversity were observed on the canyon flank where mean current speed was highest (31.3 cm s^{-1}), although no direct link between current speed and benthic fauna distribution was assessed. It is thus highly probable that current regimes influence benthic fauna distribution in the PBC. Deep-sea currents and POM have also been recognised to influence the distribution of benthic fauna (Levin et al., 2001; Cunha et al., 2011; Henry et al., 2014).

4.4.3. Conservation and management of the benthic fauna and habitats in the PBC

The expansion of human activities into the deep-seas, coupled with climate change most likely threaten the coral ecosystem in deep-seas (including the PBC) as human activities impact negatively on species distribution and diversity (Hall–Spencer et al., 2002; Glover and Smith, 2003; Grehan et al., 2004; Gass and Roberts, 2006; Kaiser and Barnes, 2008; Danovaro et al., 2017; Volkov et al., 2017; Durack et al., 2018; Miller et al., 2020). Management and conservation biologists strive to prevent habitats and species from permanent damage and declines. Also, scientists have observed that some proportions of habitat loss and population decline are recoverable while some losses and declines are permanent, although many of these losses and declines could have been prevented (Young, 2000). Therefore, management is required to recover and fix those that can be fixed whilst ensuring that permanent losses and declines do not occur going forward. To this effect, it is believed that the findings of the present study would help conservation and management efforts in regulating the activities of key

stakeholders who interact with the PBC in order to protect the different habitats and benthic fauna therein. Canyon-wide conservation and management of the PBC is advocated here due to the high benthic fauna abundance and consequently high diversity observed in non-reef habitat (although not significant) contrasting to what is usually reported in literature. Scientists have recognised that processes/activities (e.g. increased sedimentation through trawl fishing) happening in one part of the canyon can potentially impact life elsewhere in the canyon (Huvenne and Davies, 2014; Martín et al., 2014) and hence the need to consider canyon-wide conservation and management of the PBC.

5. Conclusions

The Porcupine Bank Canyon is a submarine canyon on the Irish margin disconnected from across-shelf transport and containing cold-water coral habitats. As such, it provides a perfect ecosystem to identify environmental control on cold-water coral and canyon habitats without terrigenous inputs. The present study suggests that the spatial distribution of benthic fauna is associated with the availability of POM, oceanographic and hydrographic processes, seabed terrain (depth and slope), canyon morphologic features at the different site locations and habitats of the PBC. Analysis of the benthic taxa of the PBC has revealed significant structure in the faunal and ecological composition. Habitat heterogeneity evidenced by the different substrata and morphologic features in the canyon contributes to the trend of diversity, evenness and taxa distribution observed in the canyon. The present study also suggests that non-reef habitats have the potential to hold high benthic fauna diversity in submarine canyons. However, there is the need for standardisation of methods for deep-sea community studies, to allow for comparability and effective conservation and management processes in submarine canyons, which in many cases, are limited by the cost of deep-sea research.

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Chapter 3

Accumulation of marine litter in cold-water coral habitats: a comparative study of two Irish Special Areas of Conservation, NE Atlantic

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Abstract

Cold-water corals (CWCs) have come under threat from anthropogenic activities such as fishing despite their ecological significance and importance as biodiversity hotspots and as such are protected in Europe under the EU Habitats Directive with some designated as Special Areas of Conservation (SACs). The present study maps the distribution and sources of marine litter in CWC habitats in two Irish SACs as additional anthropogenic impacts. Data on marine litter were collected during the summer with a remotely operated vehicle (ROV) in the upper Porcupine Bank Canyon (uPBC) and the western Belgica Mound Province (wBMP) in the NE Atlantic. The density, abundance and composition of litter were assessed, with differences observed between the two sites. The regional morphology influences the distribution of litter in the SACs, with CWC reefs and rock exposures trapping more marine litter. A total of 62 litter items were observed in the uPBC while 49 were detected in the wBMP between 600 - 1,200 m and 900 - 1,100 m respectively. Fishing gear (80.7%) was the most abundant litter identified in the uPBC followed by plastics (11.3%), whilst in the wBMP plastics (55.1%), followed by buoys (14.3%) were commonly found. Hence litter in the uPBC appear to be predominantly marine-derived whilst that in the wBMP appear to be predominantly land-derived. A high traffic volume of fishing vessels was observed in both SACs, which may account for some of the recorded litter. The observed deep-sea fishing and the high traffic volume of fishing vessels have contributed to the exceedance (>20% fishing gear as litter) in the SACs of the global rates of fishing related litter (10-20% fishing gear as litter). This

suggests that the SACs appear to offer limited protection to the coral habitats with respect to marine litter.

Keywords: Marine litter, Porcupine Bank Canyon, deep sea, northeast Atlantic, Ireland, bathymetry, Belgica Mound Province, SACs.

1. Introduction

Marine litter, defined as “any persistent, manufactured or processed solid material discarded, disposed of or abandoned in the marine and coastal environments” (Galgani et al., 2010), has become a global threat since it is found in all of the world’s oceans (Rochman et al., 2016). Different techniques of identifying the sources of marine litter have been described (e.g. Tudor et al., 2002; Williams et al., 2003; Koutsodendris et al., 2008) with the two main sources being land-derived and marine-derived sources (Kershaw et al., 2019). Land-based sources are created through tourism activities, illegal dumping, waste from surface run offs and river discharges as well as coastal dumping, while marine-based sources may come from fisheries’ activities, scientific expeditions, accidents at sea, aquaculture and recreational shipping (Galgani et al., 2000, 2010).

Marine litter can be characterised as mega-, macro-, meso- and micro litter based on size (Cózar et al., 2014; Kühn et al., 2015; Thompson, 2015; Kershaw et al., 2019). They can drift long distances in the water column including into deep-sea areas (Large et al., 2009; Ryan et al., 2014), with their fate influenced by microbial activities, hydrodynamics, bathymetry, sedimentology and oceanographic regimes upon entering the ocean (Galgani et al., 2010). Seasonal and temporal trends of marine litter have been reported (Galgani et al., 2000; Ryan et al., 2014; Van Franeker and Law, 2015) and spatially, marine litter is more abundant in bays

than along coastal regions and in shallow waters rather than in the deep seas (Galgani et al., 2000; Ryan et al., 2014; Van Franeker and Law, 2015). Much of this litter has a persistent residence time and takes a long time to biodegrade (Barnes et al., 2009; O’Brine and Thompson, 2010). The litter becomes more bioavailable to marine wildlife when it is broken-down into smaller fragments (Chapron et al., 2018; Botterell et al., 2019; La Beur et al., 2019), which increases the object’s surface area to volume ratio and thus becoming potentially more available and harmful to wildlife than in their non-degraded state. It is estimated that plastic in the northeast Atlantic accounts for approx. 60 - 80% of marine litter (Galgani et al., 2013), while fisheries related litter accounts for 11,000 tons of debris annually in European seas (Kershaw et al., 2019). About 20% of fishing gear is thought to be lost due to abandonment and bad weather conditions in certain regions of the ocean, including the NE Atlantic (Large et al., 2009; Kershaw et al., 2019).

Marine litter impacts benthic habitats physically and can also change the chemical composition of the immediate environment (Goldberg, 1994; Barnes et al., 2009; Galgani et al., 2010). Litter can provide habitats to harmful and invasive species in the marine environment (Barnes et al., 2009; Lobelle and Cunliffe, 2011), as well as reducing the aesthetic value of the ocean, posing threats to human health and marine organisms, causing entanglement, deteriorating visibility, disrupting feeding behaviour, and impeding movement (Derraik, 2002; Sazima et al., 2002; Phillips et al., 2010). However, marine litter can also provide an additional habitat for benthic fauna (Mordecai et al., 2011; Tubau et al., 2015; Haram et al., 2021).

Non-invasive sampling techniques such as remotely operated vessels and submersibles can be used to characterise and monitor marine litter (Spengler and Costa, 2008; Watters et al., 2010;

Miyake et al., 2011; Pierdomenico et al., 2019). Remotely operated vessels can precisely determine the location of litter as well as discriminate between litter types and sizes.

Most studies have focused on litter in the coastal (Rangel-Buitrago et al., 2017) and continental shelf regions (Moriarty et al., 2016), although the deep-sea acts as the biggest sink for marine litter (Pham et al., 2014; van den Beld et al., 2017), with submarine canyons noted for transporting litter from the continental shelves to the abyss (Mordecai et al., 2011; Schlining et al., 2013; Tubau et al., 2015). Research on litter in the deep-sea to date is rather limited (Schluning et al., 2013; Woodall et al., 2015; La Beur et al., 2019; Pierdomenico et al., 2019), since deep-sea research is expensive and sampling is difficult to carry out (Galgani et al., 2010). The present study maps the distribution and abundance of litter in the upper Porcupine Bank Canyon (uPBC) and western Belgica Mound Province (wBMP) to determine its origin, composition and how it may interact with benthic fauna. The effectiveness of the two study sites (designated as areas within Special Areas of Conservation (SACs) under the EU Habitat Directive (92/43/EEC)) to protect vulnerable habitats is assessed considering marine litter entry. SACs are one of many spatial management approaches used to protect vulnerable benthic fauna such as cold-water corals (CWCs) and sponges from potential human activities affecting deep-sea habitats (Muñoz et al., 2020). CWCs and deep-sea sponge ecosystems constitute vulnerable marine ecosystems that are generally significantly impacted by bottom trawling, hydrocarbon exploration and deep-sea mining and are being protected by spatial management tools such as SACs (Muñoz et al., 2020).

CWCs are simple azooxanthellate animals that generally live in the dark and feed on planktons, crustacea and particulates in the water column for growth and survival. They form colonies but can exist as solitary animals and are generally found within temperature and salinity limits

of 4 - 12°C and 32 - 38.8 respectively. They are slow growing S-strategist animals that take a long time to recover from a disturbance in the ecosystem (Orejas et al., 2008; Roberts et al., 2009).

1.1. Study areas

1.1.1. Upper Porcupine Bank Canyon

The Porcupine Bank Canyon (PBC) is situated 310 km off the southwestern coast of Ireland (Figure 3.1A) and is bounded by the Porcupine Seabight to the east and the Rockall Trough to the southwest into which the PBC exits. Its morphology has been influenced by regional tectonics (Shannon et al., 2007; Mazzini et al., 2012) and it cuts higher up into the Porcupine Bank than adjacent canyons, including into the CWC habitable region. The southern branch area is smaller than the main canyon cutting into the southeastern edge with the canyon head reaching to 1,900 m water depth (Appah et al., 2020). The canyon head exhibits a gentler slope at the northeastern and northwestern margins (Figure 3.1).

1.1.2. Western Belgica Mound Province

The Belgica Mound Province (BMP), approx. 150 km southwest of Ireland, consists of several CWC mounds and is located on the eastern edge of the Porcupine Seabight (Figure 3.1A). Giant carbonate mounds are confined by the continental shelf to the east and the Arwen Channel to the west (Murphy and Wheeler, 2016). Shallow downslope channels empty into the Arwen channel at the northern limits of the BMP (Huvenne et al., 2005; Wheeler et al., 2007). Small and elongated coral mounds (Moira Mounds) are found between 800 - 1,100 m (Figure 3.1C). The Piddington Mound, one of the larger Moira Mounds, is located within the less sediment-stressed area (Figure 3.1C). Sediment waves of wavelength ~10 m and height 20 - 75 cm occur in the wBMP (Lim et al., 2017, 2018) operating under current speed from 30

cm s⁻¹ to > 41 cm s⁻¹ in the northern part of the wBMP (Lim et al., 2018). Benthic features such as seabed striations, comet marks and sediment waves suggest strong bottom currents in the wBMP (Wheeler et al., 2005a). The slope of the seabed in the BMP is between 0 - 55.7° with a regional slope angle of 1.2° (Lim et al., 2017).

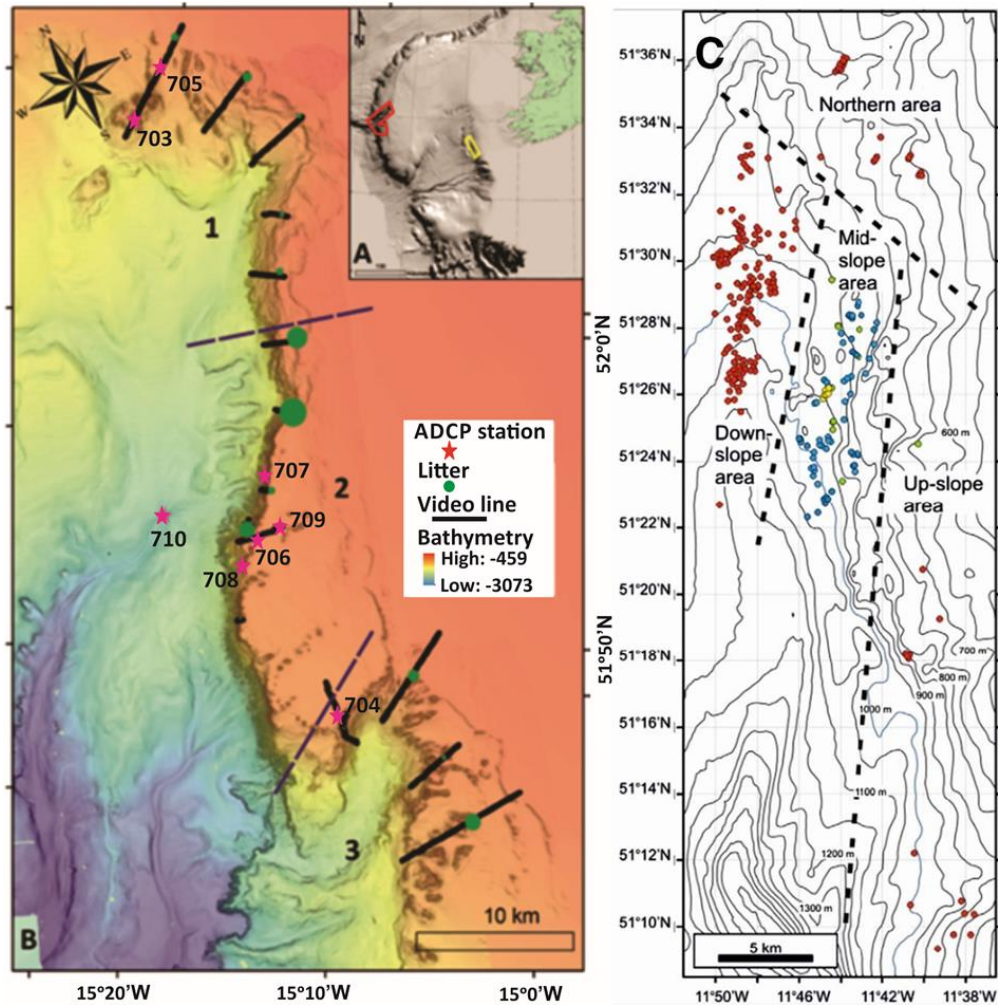


Figure 3.1. Location of: A) Porcupine Bank Canyon Special Area of Conservation (red polygon) and Belgica Mound Province (yellow rectangle); B) geomorphological divisions of the upper Porcupine Bank Canyon (purple broken line). B1, B2 and B3 represent canyon head, canyon flank and south branch, respectively, C) geomorphological divisions of the Belgica Mound Province Special Area of Conservation (black broken line; adapted from Lim et al., 2017). The coloured circles in Figure 1C represent carbonate mounds. The size of the circles is proportional to the abundance of litter observed on each survey in the upper Porcupine Bank Canyon.

2. Methodology

2.1. Hull-mounted multibeam (EM302) echosounder profile

Thirty kHz hull-mounted multibeam echosounder (MBES) data were collected (on board the RV Celtic Explorer in 2017 and 2018) as a contour-parallel series of lines in the uPBC. The minimum swath overlap was 25% at a survey speed of circa 8 knots whilst swath width was typically 2,000 m. The acquired data were processed with QPS Qimera, imported into ArcMap v10.4 and projected in UTM zone 28N. Slope angle and depth were derived from the resulting bathymetric data using the Spatial Analyst Tool in ArcMap. Bathymetric data were reclassified into three slope classes (0 - 10°, 10 - 15°, 15+°) and depth classes (<600 m, 600 - 1000 m, >1000 m) in the uPBC.

2.2. Acoustic doppler current profiler (ADCP) profile

As described by Appah et al. (2020) and Lim et al. (2020), ADCP data were collected in the uPBC using a 1 Hz Nortek Aquadopp upward-facing ADCP vertically fixed onto lander frames (Wheeler et al., 2021). The ADCP data were collected from the mid upper canyon (15°5'16.394"W; 52°1'12.544"N) at 2,125 m depth, including seven other ADCP stations, deployed on the 15-19/05/2019 and recovered on the 27-28/07/2019 respectively (Table 3.1).

Table 3.1. The codes of ADCPs, location, depth, average current speed and dates of deployment and recovery in the upper Porcupine Bank Canyon

ADCP	Depth (m)	Ave. current speed (cm s ⁻¹)	Coordinates		Deployed	Recovered
			Latitude	Longitude		
705	839	18.22	52.24396033	-14.87962033	15/05/2019	27/07/2019
703	719	9.40	52.22728500	-14.92564953	15/05/2019	27/07/2019
707	697	31.30	52.00396042	-14.98886345	15/05/2019	27/07/2019
709	645	17.30	51.98318233	-14.99900400	15/05/2019	27/07/2019
706	719	9.75	51.98373150	-15.01926833	16/05/2019	27/07/2015
708	685	24.00	51.87006383	-15.03355883	18/05/2019	27/07/2019
704	605	25.40	51.97348667	-15.04166500	17/05/2019	28/07/2019
710	2125	9.80	52.02015117	-15.08788717	19/05/2019	27/07/2019

2.3. Remotely operated vehicle (ROV) video survey

The Holland I ROV on board the RV Celtic Explorer was used to quantify litter in the wBMP (Wheeler and shipboard, 2011, 2015) and the uPBC (Wheeler and shipboard, 2017; Lim and shipboard, 2018, 2019, 2020), using forward-facing high definition (HD) pan and tilt camera systems between 800 - 1,100 m in the wBMP and 567 - 2,126 m in the uPBC. ROV speed was maintained at 0.4 knot at approx. 1 m from the seabed although this was not always possible due to variable currents and irregular terrain, providing a mean camera field of view of 3 m. Note the video transects in the western Belgica Mound Province are relatively flat. The video images were scaled with 10 cm spaced parallel laser beams. Vertical imagery was analysed systematically to characterise litter in the uPBC and the wBMP. Video frames were extracted and imported into ImageJ (Rasband, W.S., 1997 - 2014). The scale (in pixels/m) for the images was set with the Analyse Tool incorporated in ImageJ. The known distance of the laser scale on the image (10 cm) was used to determine the distance in pixels. Litter was characterised according to the type of material and primary use as adopted in literature (Mordecai et al., 2011; Hanke et al. 2013; Ramirez-Llodra et al., 2013; Tubau et al., 2015; Fleet et al., 2021; Vered and Shenkar, 2021).

2.4. Abundance estimates of litter

The area and the number of litter items, including fishing lines in the uPBC, were evaluated by depth classes (<600 m, 600 - 1000 m, >1000 m) whilst the area and the number of litter items in the uPBC, including fishing lines, were analysed by slope classes (0 - 10°, 10 - 15°, 15+°). The density of litter on each video transect in the uPBC was estimated as the ratio of the number of litter items to the surveyed area along the video transect. The area of a video transect was

determined from the length of the video transect and the ROV camera's field of view. The density of litter (100 m⁻¹) in the uPBC was calculated as adopted in Tubau et al. (2015):

$$A = L \times F \dots \dots \dots (\text{Eq. 1})$$

$$De = N \times 100/L \text{ (litter } 100\text{m}^{-1}) \dots \dots \dots (\text{Eq. 2})$$

$$D = N/A \text{ (litter.km}^2) \dots \dots \dots (\text{Eq. 3})$$

where, A = area along video line; L = length of video line; F = ROV camera's field of view; D = density of litter in km⁻²; N = number of litter items; De = density of litter 100 m⁻¹.

The mean area of each item of litter in the uPBC was estimated by tracing its outline (5x; Figure 3.2) using ImageJ. Litter in the wBMP was quantified with the density of litter determined as the ratio of the total number of litter items to the total distance of video transects surveyed.

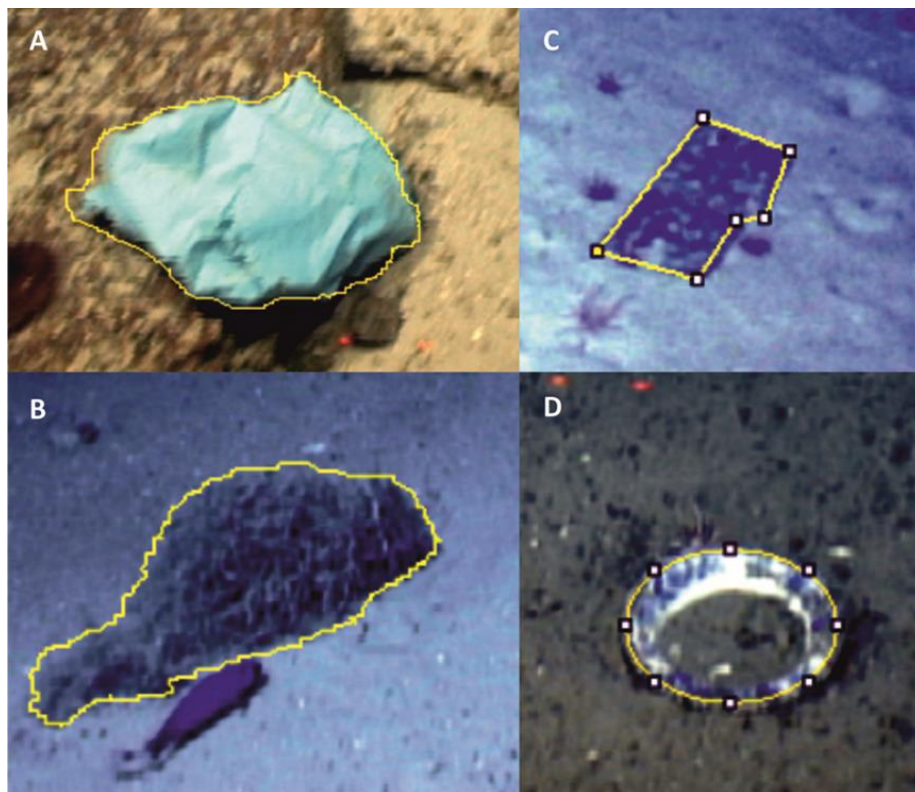


Figure 3.2. Area of different litter items in the upper Porcupine Bank Canyon: A) plastic, B) paper crate, C) fishing net, D) plate

3. Results

3.1. Acoustic doppler current profiler (ADCP) profile in the uPBC

Current speed in the uPBC range from 34.1 cm s^{-1} to 114.2 cm s^{-1} with max mean flow of 31.3 cm s^{-1} . Water flows are mostly unidirectional and bidirectional (Figure 3.3A). Active transport processes (Figure 3.3B) were observed in the mid- upper canyon with flows showing a dominant tidal signal.

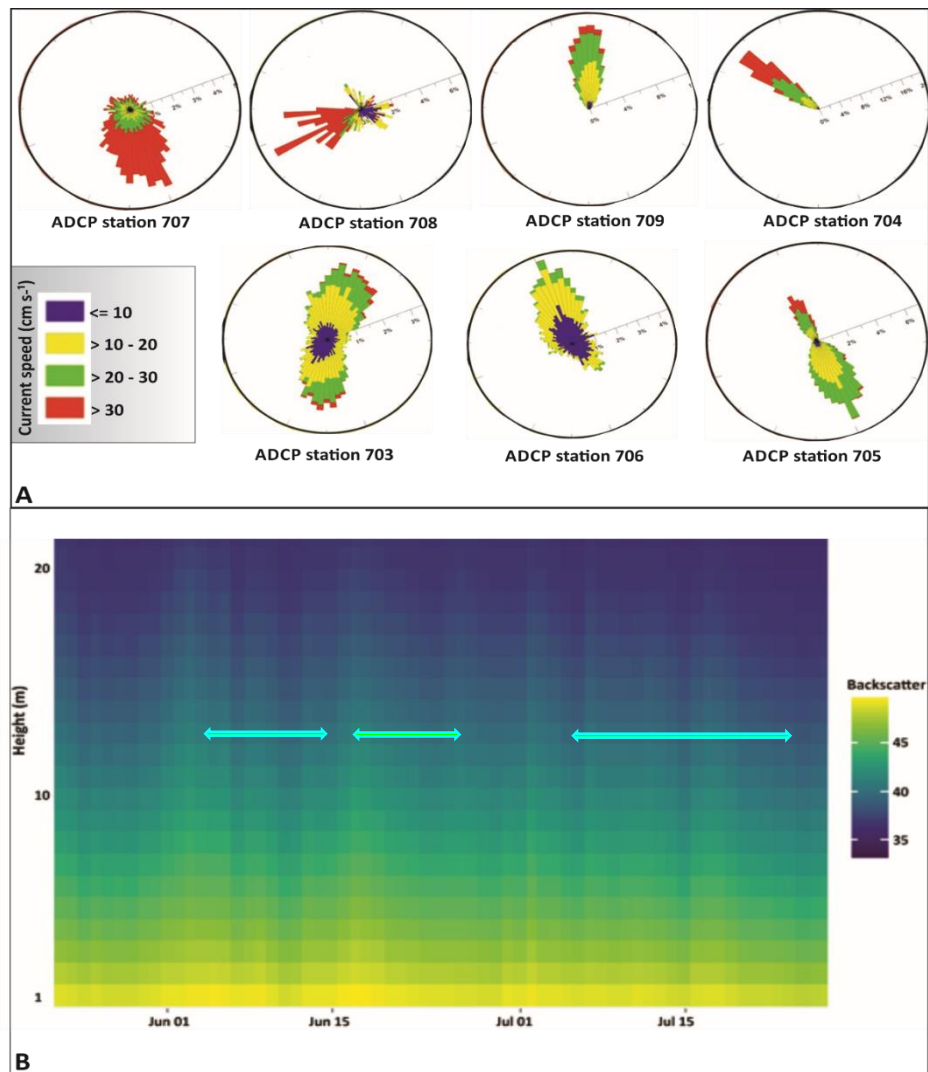


Figure 3.3. ADCP data from eight monitoring stations between 600 - 2,125 m water depth over a period of approx. 2.5 month in the upper Porcupine Bank Canyon showing: A) current speeds and direction, B) acoustic backscatter showing an example of active transport processes. Daily average measurements show pronounced transport activity observed within 10 m above the transducer with periods of considerable activities generally around 1st - 6th and 13th - 19th June 2020 and 1st - 19th July 2020 (arrowed lines). Areas of high backscatter shows high transport activities (Dwinovantyo et al., 2017).

3.2. Distribution of litter in the canyon, bathymetry and slope

A total of 62 litter items were identified in the uPBC whilst 49 were found in the wBMP. Examples of litter identified in the uPBC and wBMP are shown in Figures 3.4 and 3.5. Over the 21 video transects surveyed in the uPBC, litter was observed on 14 of them. The density of litter on each video transect is shown in Table 3.2. The highest litter concentration was observed on video transect 10 (Table 3.2). The mean density of litter in the canyon head was 0.08 litter 100 m⁻¹, in the canyon flank was 0.45 litter 100 m⁻¹ and in the south branch was 0.06 litter 100 m⁻¹ (Table 3.2).

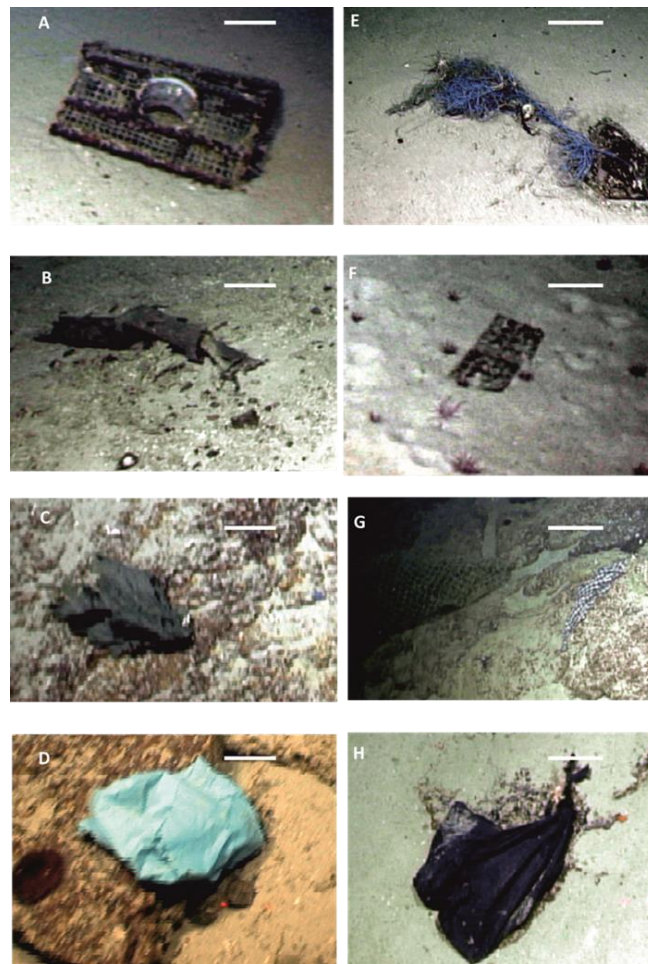


Figure 3.4. Different litter items identified in the upper Porcupine Bank Canyon. Scale bar = 10 cm: A) metal, B) wood, C) fragmented plastic, D) plastic, E) fishing net, F) paper crate, G) fishing net and cloth, H) plastic.

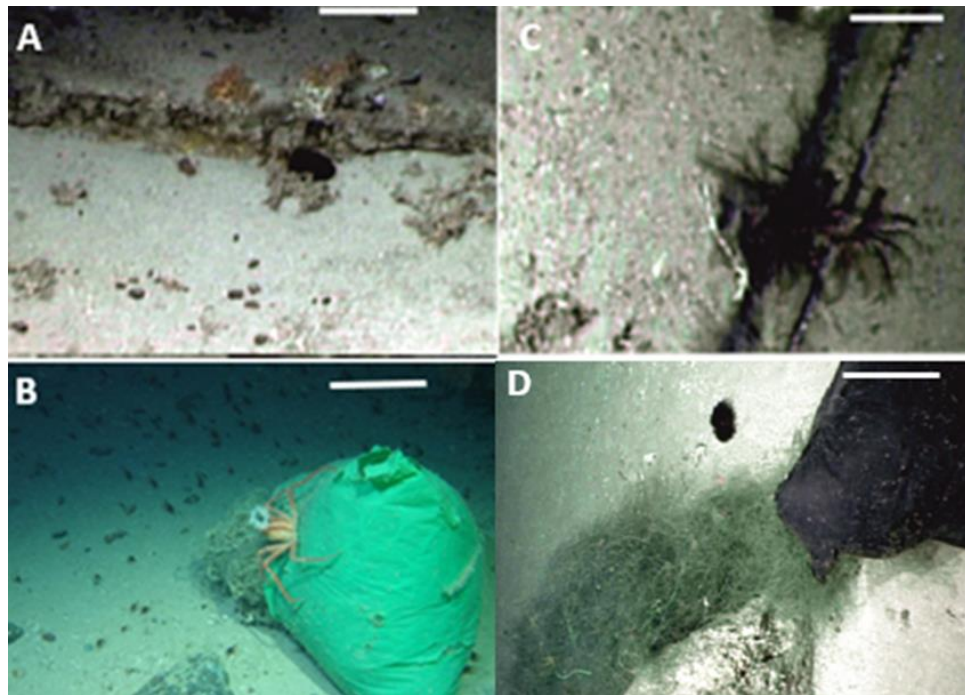


Figure 3.5. Different litter items identified in the upper Porcupine Bank Canyon and western Belgica Mound Province. Scale bar = 10 cm: A) fishing line with corals, B) plastic and fishing net with a crab and a sponge, C) fishing line with crinoids and, D) plastic and fishing net.

Of the 62 litter items identified in the uPBC, 25 (40%) were in the canyon flank, 23 (37%) in the canyon head and 14 (23%) in the south branch (Table 3.3). With respect to the wBMP most of the litter were observed in the northwest (Table 3.3).

Fishing gear (80.7%) was most abundant in the uPBC followed by plastics (11.3%) whereas plastics (55.1%) and buoys (14.3%) were commonly discovered in the wBMP (Figure 3.6). Eight percent of litter in the wBMP were fishing related (Figure 3.6). Forty percent of litter were trapped by the exposed rocks in the uPBC.

Table 3.2. ROV transects in the upper Porcupine Bank Canyon, length (m), depth range (m), number of items of litter, area along video transect (m²) and density of litter items (litter/m²). na = not available

Video transects	Depth range (m)	Length (m)	Litter	Area (km ²)	Start (Lat/Long)	End (Lat/Long)	Area (km ²)	Litter/km ²	Litter 100 m ⁻¹
5	582 - 1019	5020	4	1.51x10 ⁻²	52°12'01.712"N 14°52'29.656"W	52°12'58.497"N 14°48'48.421"W	1.51x10 ⁻²	265.6	0.08
6	662 - 1242	4428	2	1.33x10 ⁻²	52°10'12.550"N 14°51'07.454"W	52°10'44.710"N 14°47'21.709"W	1.33x10 ⁻²	150.6	0.05
4	582 - 1054	8430	3	2.53x10 ⁻²	52°13'11.812"N 14°56'27.895"W	52°15'31.425"N 14°50'36.329"W	2.53x10 ⁻²	118.6	0.04
8	654 - 1233	2560	3	7.68x10 ⁻³	52°06'57.923"N 14°54'12.637"W	52°06'17.867"N 14°52'41.474"W	7.68x10 ⁻³	390.6	0.12
7	709 - 1039	1780	2	5.34x10 ⁻³	52°08'30.602"N 14°51'56.497"W	52°08'02.687"N 14°50'52.255"W	5.34x10 ⁻³	374.5	0.11
9	574 - 1248	2437	9	7.31x10 ⁻³	52°04'37.816"N 14°55'36.195"W	52°04'06.104"N 14°53'39.023"W	7.31x10 ⁻³	1231.0	0.37
10	695 - 1231	1730	12	5.19x10 ⁻³	52°02'30.364"N 14°56'50.204"W	52°01'50.780"N 14°55'46.365"W	5.19x10 ⁻³	2312.1	0.69
11	681 - 1008	3200	7	9.60x10 ⁻³	51°59'13.942"N 15°02'19.283"W	51°58'54.137"N 14°59'44.166"W	9.60x10 ⁻³	729.2	0.22
12	704 - 1020	460	3	1.38x10 ⁻³	52°00'21.912"N 14°59'46.139"W	52°00'13.423"N 14°59'26.780"W	1.38x10 ⁻³	2173.9	0.65
16	760 - 967	390	1	1.17x10 ⁻³	51°56'52.529"N 15°04'33.103"W	51°56'48.527"N 15°04'14.345"W	1.17x10 ⁻³	854.7	0.26
20	701 - 972	780	-	2.34x10 ⁻³	51°59'31.468"N 15°01'28.607"W	51°59'11.988"N 15°01'03.014"W	2.34x10 ⁻³	na	na
21	762 - 995	350	-	1.05x10 ⁻³	51°59'47.789"N 15°00'32.720"W	51°59'41.672"N 15°00'26.007"W	1.05x10 ⁻³	na	na
21a	740 - 922	310	-	9.30x10 ⁻⁴	51°59'44.035"N 15°00'26.532"W	51°59'36.688"N 15°00'15.415"W	9.30x10 ⁻⁴	na	na
22	686 - 1021	640	-	1.92x10 ⁻³	52°00'44.738"N 14°59'15.872"W	52°00'34.151"N 14°58'47.185"W	1.92x10 ⁻³	na	na
23	729 - 1026	320	-	9.60x10 ⁻⁴	52°01'10.916"N 14°58'43.118"W	52°01'06.163"N 14°58'28.844"W	9.60x10 ⁻⁴	na	na
19	715 - 969	680	-	2.04x10 ⁻³	51°58'32.458"N 15°02'50.338"W	51°58'19.949"N 15°02'21.115"W	2.04x10 ⁻³	na	na
15	622 - 1070	9110	7	2.73x10 ⁻²	51°46'54.323"N 15°03'15.405"W	51°46'54.839"N 14°55'44.540"W	2.73x10 ⁻²	256.1	0.08

Table 3.2. ROV transects in the upper Porcupine Bank Canyon, length (m), depth range (m), number of items of litter, area along video transect (m²) and density of litter items (litter/m²). na = not available

Video transects	Depth range (m)	Length (m)	Litter	Area (km²)	Start (Lat/Long)	End (Lat/Long)	Area (km²)	Litter/km²	Litter 100 m⁻¹
14	567 - 1039	4370	2	1.31x10 ⁻²	51°48'57.371"N 15°00'48.993"W	51°49'22.781"N 14°57'21.286"W	1.31x10 ⁻²	152.6	0.05
13	596 - 1043	6680	5	2.00x10 ⁻²	51°51'25.709"N 15°00'17.084"W	51°53'02.415"N 14°55'10.817"W	2.00x10 ⁻²	249.5	0.07
13s	638 - 1180	2360	1	7.08x10 ⁻³	51°51'13.514"N 15°02'12.091"W	51°51'13.547"N 15°02'12.244"W	7.08x10 ⁻³	141.2	0.04
13z	2085 - 2126		1	na	52°01'12.990"N 15°05'12.444"W	52°01'13.357"N 15°05'07.699"W	na	na	na

Table 3.3. Site location, number of litter and mean area $\pm$ S.D in the three different areas of the uPBC and wBMP

Site location	Area $\pm$ S.D (m ²)	Number of litter items (%)	Density (litter/km)
uPBC Canyon head	0.263 $\pm$ 0.013 ^{ac}	23 (37%)	0.63
uPBC Canyon flank	2.306 $\pm$ 0.309 ^b	25 (40%)	4.02
uPBC South branch	0.855 $\pm$ 0.135 ^{bc}	14 (23%)	0.67
wBMP	-	49 (100%)	8.29

$\alpha = 0.05$; superscripts a, b and c denote significance, SD = standard deviation

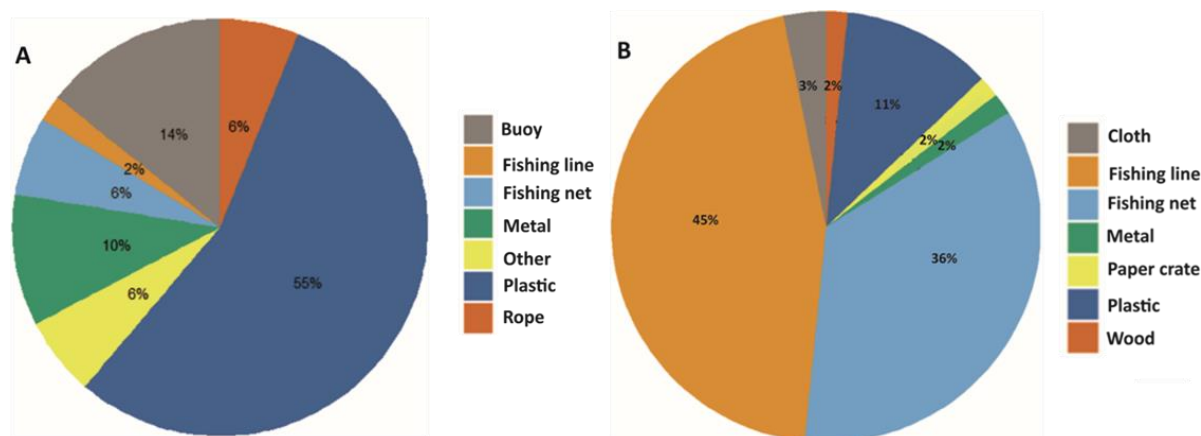


Figure 3.6. Percentage distribution of litter in the: A) western Belgica Mound Province and B) upper Porcupine Bank Canyon.

The reclassified (based on slope and depth) bathymetric data are shown in Figure 3.7. The estimated area and the number of litter items, including fishing lines in the uPBC, evaluated by depth classes, are shown in Table 3.4 whilst the calculated area and the number of litter items, including fishing lines, analysed by slope classes, are shown in Table 3.5. The total distance of video transects where litter was observed in the uPBC was 52.96 km whilst the total distance of video transects that contained litter in the wBMP was 5.91 km (Table 3.2).

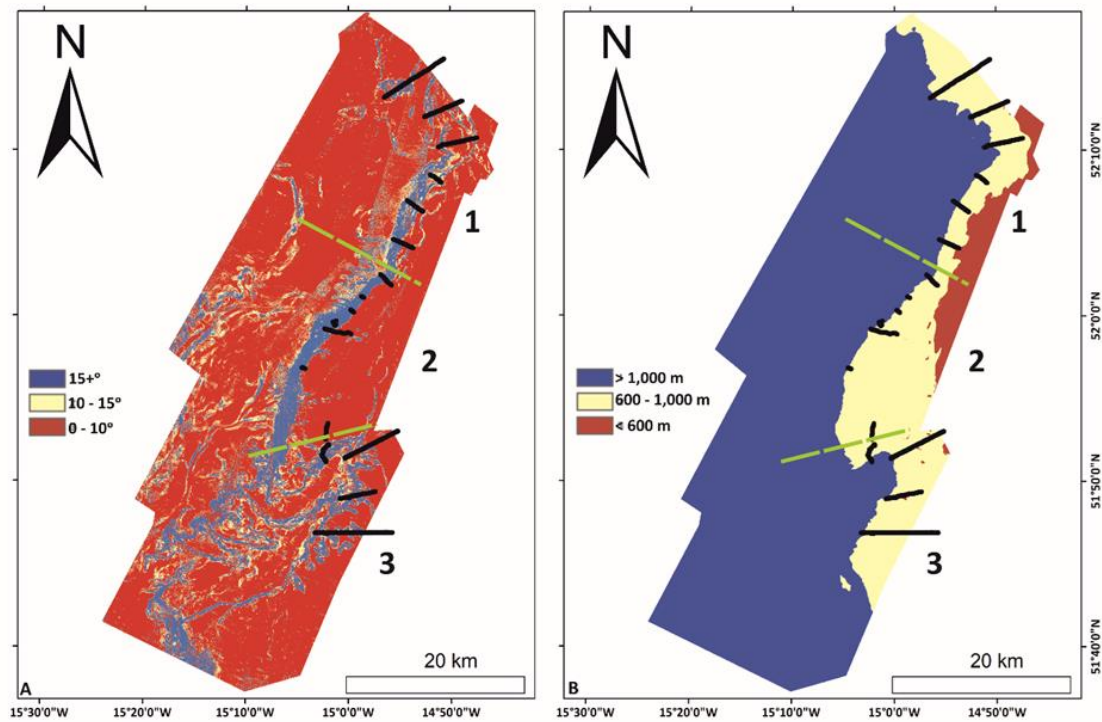


Figure 3.7. Bathymetric map of the upper Porcupine Bank Canyon showing: A) slope zonation, B) depth zonation. The green broken line demarcates the different areas of the upper Porcupine Bank Canyon. 1, 2 and 3 are the canyon head, canyon flank and south branch areas, respectively. The black lines denote video transects.

Table 3.4. Area (mean area $\pm$ S.D) of litter, number of items and percentage of litter in relation to depth in the uPBC.

Depths (m)	Area (m ²)	No. of litter items (%)
< 600	0.210 $\pm$ 0.042	2 (3.23%)
600 - 1,000	2.717 $\pm$ 0.392	50 (80.65%)
> 1,000	0.497 $\pm$ 0.023	10 (16.13%)

$\alpha = 0.05$

There was no significant difference between the depth classes ($P = 0.221$) and the slope classes ($P = 0.094$) for the area of litter assessed in the uPBC. Generally, no apparent trend of litter distribution in relation to depth was observed in the uPBC, although there was a decreasing trend of total area covered by litter from gentle slopes to steeper slopes in the canyon (Figure 3.8). Litter accumulation was observed at a relatively flat seafloor, between 600 - 800 m and slope of 0 - 5° in the uPBC (Figure 3.8).

Table 3.5. Area (mean area $\pm$ S.D) of litter, number of items and percentage of litter in relation to slope in the uPBC.

Slope (°)	Area (m ²)	No. of litter items (%)
0 -10	2.010 $\pm$ 0.198	25 (43.10%)
10 -15	0.465 $\pm$ 0.109	15 (25.86%)
15+	0.484 $\pm$ 0.051	18 (31.03%)

$\alpha = 0.05$

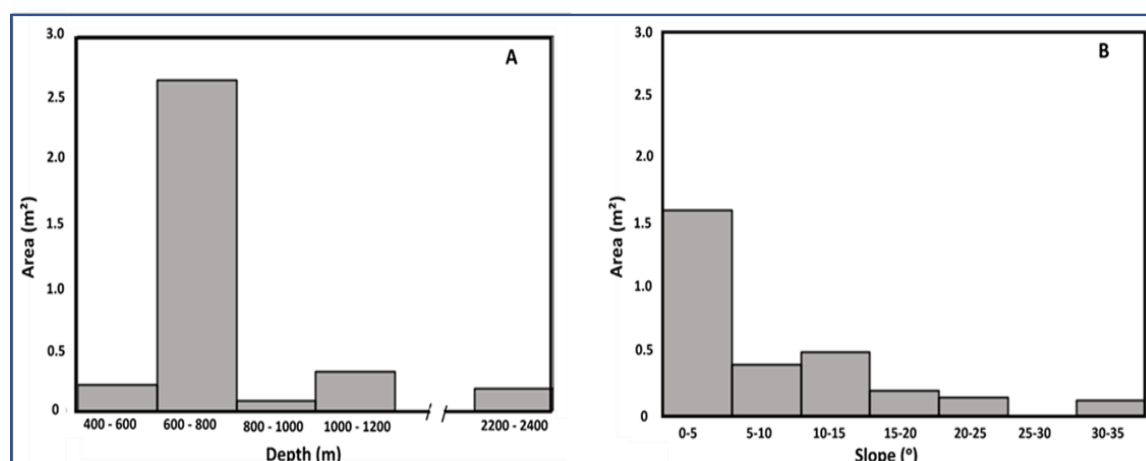


Figure 3.8. Total area covered by litter in the upper Porcupine Bank Canyon in relation to: A) depth (m) and B) slope (°)

3.3. Litter interactions with benthic organisms

Lophelia pertusa and crinoids were observed on fishing lines in the uPBC (Figures S3A, S3C and S3D), whilst a crab and a sponge were seen sitting on a fishing net in the wBMP (Figure S4B).

4. Discussion

4.1. Litter composition, abundance and distribution

Fishing gear and plastics were more abundant in the uPBC while plastics were commonly discovered in the wBMP. The differences in the composition of litter between the two SACs can be attributed to the distance from the coast to the SACs, suggesting different origins of litter. The source of litter in the uPBC most likely is marine-based due to its distance from the coast whilst the source of litter in the wBMP is most likely land-based. Similarly, the

remoteness of the uPBC from land can likely be attributed to the lower density of litter recorded in the canyon than those reported elsewhere (Galgani et al., 2000; Tubau et al., 2015). The distance between the coast and the uPBC creates a barrier that makes it difficult for land-derived litter to reach the canyon. The wBMP however experiences a greater density of litter in a smaller area. The relatively abundant fishing gear in the uPBC can also be attributed to the increasing fishing activities in and around the canyon. Vessel Monitoring Systems data show that many local and international vessels were fishing while in the uPBC as well as the wBMP (CC.By4 from the Marine Institute data catalogue; www.marine.ie) (Tables 3.6 and 3.7).

Generally, a high abundance of litter was found in rubble and coral habitats in the SACs. Given the baffling ability of corals, the branches of the corals may have trapped the rope and fishing lines causing them to become entangled. A substantial amount of litter (e.g. Figure 3.2B, Figure 3.4A and Figure 3.5) detected in rubble habitats indicate the potential influence of litter on the survival of the corals (Wheeler et al., 2005b; Ragnarsson et al., 2017), as many litter items are found where dead pieces of coral are located. Deep sea bottom trawling can result in crushed and dislodged coral frameworks (Ragnarsson et al., 2017) as well as sparsely distributed and/or patchy living coral colonies that generally show as reduced backscatter (Wheeler et al., 2005b). It has been shown that coral rubble increased by 1.5% annually and dead coral framework by 1.4% over a period of four years on the Piddington Mound in the BMP (Lim et al., 2018). The changes in coral facies as noted by Lim et al. (2018), can partly be attributed to the effect of physical processes such as crushing and dislodging of already dead coral framework by marine litter to produce the rubble. It has also been noted that coral abundance negatively correlates with litter (Giusti et al., 2019). Litter was seen entangled in coral reefs in the present study.

Table 3.6. Type of gear, classification of gear, number of the different gears, percentage composition of gear type, vessel country of origin, number of vessels and percentage composition of vessels actively involved in fisheries activities in the uPBC from 2005 - 2018. The Food and Agriculture Organisation (FAO) of the United Nations gear codes can be found at <http://www.fao.org/3/a-bt986e.pdf>.

Gear type	Gear classification	Counts	% Composition	Country	Counts	% Composition
FPO	Shallow	29	0.265106	Germany	467	4.269129
GND	Shallow	2	0.018283	Denmark	3	0.027425
GNS	Shallow	1487	13.59356	Spain	4185	38.25761
GTR	Shallow	46	0.420514	France	3072	28.08301
LHP	Shallow	10	0.091416	Faroe Islands	2	0.018283
LLD	Shallow	401	3.665783	United Kingdom	670	6.124874
LLS	Shallow	3447	31.51111	Ireland	2389	21.83929
LNB	Shallow	9	0.082274	Lithuania	3	0.027425
LTL	Shallow	41	0.374806	NA	37	0.338239
LX	Shallow	2	0.018283	Netherlands	41	0.374806
NA	Not Available	115	1.051284	Norway	15	0.137124
NK	Unknown	3	0.027425	Portugal	3	0.027425
OT	Bottom	3	0.027425	XNE	52	0.475363
OTB	Bottom	1757	16.0618			
OTM	Midwater	375	3.428101			
OTT	Midwater	419	3.830332			
PS	Shallow	426	3.894323			
PT	Midwater	21	0.191974			
PTB	Bottom	75	0.68562			
PTM	Midwater	2213	20.23037			
SDN	Shallow	50	0.45708			
TB	Bottom	8	0.073133			

Total number (1039; 61.07%) of vessels that are likely fishing in the uPBC from 2005 - 2018. Vessels in shallow (54.39%) mid (27.68%) and bottom (16.85%) water while unknown and NA (118; 1.08%). XNE=not determined.

4.2. Litter interactions with benthic organisms

The introduction of litter into the cold-water coral habitats can offer surfaces for attachment by benthic fauna as fishing lines provided habitat for the scleractinian coral *Lophelia* and crinoids in the uPBC (Figures 3.4A, 3.4C and 3.4D), whilst a crab and a sponge were seen sitting on a fishing net in the wBMP (Figure 3.5B). Similar observations of animals associated with litter

have been reported (Mordecai et al., 2011; Schlining et al., 2013; Tubau et al., 2015; Pierdomenico et al., 2019).

Table 3.7. Type of gear, classification of gear, number of the different gears, percentage composition of gear type, vessel country of origin, number of vessels and percentage composition of vessels actively involved in fisheries activities in the wBMP from 2005 - 2018. The Food and Agriculture Organisation (FAO) of the United Nations gear codes can be found at <http://www.fao.org/3/a-bt986e.pdf>.

Gear type	Gear classification	Counts	% Composition	Country	Counts	% Composition
FPO	Shallow	6	0.0717	Germany	11	0.1315
SDN	Shallow	50	0.5977	Portugal	3	0.0358
GNS	Shallow	390	4.6622	Spain	3724	44.5188
GTR	Shallow	8	0.0956	France	2135	25.5230
LHP	Shallow	10	0.1195	Norway	4	0.0478
LLD	Shallow	297	3.5505	United Kingdom	296	3.5385
LLS	Shallow	3033	36.2582	Ireland	2153	25.738194
LNB	Shallow	1	0.0120	Netherlands	9	0.1075
LTL	Shallow	41	0.4901	NA	30	0.3586
PS	Shallow	255	3.0484			
NA	Not Available	75	0.8966			
NK	Unknown	3	0.0357			
TB	Bottom	8	0.0956			
OTB	Bottom	1541	18.4220			
OTM	Midwater	172	2.0562			
OTT	Midwater	316	3.7776			
PTM	Midwater	2063	24.6623			
PT	Midwater	21	0.2510			
PTB	Bottom	75	0.8966			

Total number (8365; 61.57%) of vessels that are likely fishing observed in the wBMP from 2005 - 2018. Vessels in shallow (148.91%) mid- (30.75%) and bottom (19.41%) water while unknown and NA (78; 0.93%).

4.3. Environmental context

Generally, areas with high abundance of litter coincided with areas with the highest mean current speed in the uPBC (Figure 3.1 and 3.3, Table 3.1 and 3.2). The mean abundance of litter in the canyon head is 129.99 litter km⁻² (influenced by current speed of 13.81 cms⁻¹; ADCP stations 703 and 705), canyon flank 304.21 litter km⁻² (influenced by current speed of

16.46 cm s^{-1} ; ADCP stations 706, 707, 708, and 709) and south branch 99.93 litter km^{-2} respectively (Figure 3.1 and 3.3, Table 3.1 and 3.2). However, a northwest current speed of 25.40 cm s^{-1} was observed at ADCP station 704 (Table 3.1), suggesting that the current here is directly influencing litter in the canyon flank rather than those in the south branch. Litter was observed at a depth of 2,125 m in the mid-upper canyon in the uPBC, where active transport processes (Figure 3.3B) were detected, suggesting that sediment flows may likely have transported the litter item to that depth in the canyon. Turbidity and gravity flows can transport large amount of sediment and sediment-borne litter and consequently bury the litter on the seafloor (Paull et al., 2005, 2010; Mordecai et al., 2011; Pierdomenico et al., 2019). Certain litter items were seen slightly buried in sediment (Figure 3.2C) and appear to have undergone fragmentation to various degrees (Figure 3.4C), suggesting the complete burial of some litter which may not have been accounted for in the present study. Furthermore, given the high current speeds within the uPBC and that litter observed herein are typically observed attached to or baffled within objects (e.g. outcrops; Figure 3.4C and H), it is likely that some litter is transported through the canyon, rather than becoming deposited, underestimating the reported litter abundance. The gently sloped canyon head of the uPBC shows many rocky outcrops which tend to trap the litter. Litter was observed between 900 - 1,100 m in the wBMP, implying litter was trapped by corals existing on the carbonate mounds. Litter in the coral habiting depth-zone could be due to the highly branching corals that trap litter while some get stuck as they are being transported by currents. Also, litter was more abundant on slopes between 0 - 10° gradient in the uPBC. More energy is required to move a larger litter on a relatively flattened surface than along a steep slope, explaining the decreasing trend of large litter from gentler slopes to steeper slopes in the uPBC. These means that slope angle is also a factor in concentrating larger sized litter.

4.4. Effectiveness of both SACs to protect cold-water coral habitats from marine litter entry

Management of offshore SACs is far more difficult to carry out compared to onshore SACs due to its limited accessibility and associated costs. Generally, more vessels enter the wBMP than those that entered the uPBC, although fishing related litter in the uPBC was more than in the wBMP. It is most likely that fishing related litter recorded in the uPBC are linked to the type of fishing gear found onboard these vessels. Many fishing nets were found in the uPBC compared to other litter items. However, it is unclear whether fishing nets have drifted to their current locations in the SACs or from vessels fishing in them. Litter was found only in the north of the BMP so there is little to no evidence to suggest that a specific gear type is causing the impacts recorded in this SAC. Further analysis of the south of the BMP SAC is recommended to provide a clearer picture of litter in the entire SAC. More than 60% of vessels in the SACs are fishing while in the SAC and would indicate that both SACs appear to offer limited protection to the coral habitats. It may be that the SAC boundaries are sufficient, but the monitoring of the areas is not effective. This can result in further changes to the CWC habitats in the future as already described (Lim et al., 2018). Marine protected areas (MPAs) protect CWCs (Huvenne et al., 2016). However generally, the low abundance of litter observed in the uPBC and the wBMP, compared to the highly abundant litter observed elsewhere (Mordecai et al., 2011; Tubau et al., 2015; Pierdomenico et al., 2019), could be because the uPBC and wBMP are SACs and closed to fishing.

5. Conclusion

The present study is the first to provide insight into the composition of marine litter found in CWC habitats in two Irish offshore SACs and background data. Bathymetry and hydrodynamics affect the distribution of litter in the uPBC. The source of the litter observed in the uPBC most likely is marine-based, with fishing gear being the majority whilst in the

wBMP, plastic is most abundant and the source of litter is most likely land-based. As the uPBC and wBMP are SACs and closed to fishing, the observed fisheries related litter in the uPBC and wBMP may have been dumped before they were designated an SAC and almost certainly have drifted into them by deep-sea currents, although these claims cannot be substantiated. Fishing related litter is > 20% for both SACs, exceeding the 10 - 18% global rates, making the high percentage of vessels that are fishing while inside the SACs concerning. Additionally, the differences in the composition and abundance of litter between the SACs indicates the need for different management strategies. Therefore, it is recommended that stricter regulations may have to be introduced if vessels are found to be fishing in these SACs.

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Chapter 4

Cold-water coral microbiome and environmental microbial communities in a remote NE Atlantic submarine canyon setting: microbial diversity and coral health

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All authors contributed to the success of the manuscript. John Appah designed the project, was also involved in the data collection at sea and performed all the data generation and data analysis for the Porcupine Bank Canyon dataset, and was the primary author who wrote most of the paper, compiled the first draft and incorporated subsequent modifications. Dr Aaron Lim was chief scientist on the cruises that collected the data set and edited the draft. Profs Wheeler and Ruth O'Riordan edited the draft and provided technical advice. Luke O'Reilly and Larissa de Oliveira were involved in data collection. Funding for this project was secured by Prof. Andy Wheeler with Dr. Aaron Lim through the SFI from MMMonKey_Pro (SFI from MMMonKey_Pro (grant number: 16/IA/4528) and forms a contribution to the European

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Abstract

In the Porcupine Bank Canyon, *Lophelia pertusa* and *Madrepora oculata* are the main framework-forming corals producing three dimensional structures which provide a habitat for a range of benthic fauna and microbial communities. To understand the roles and functions that microbes perform in coral health in the Porcupine Bank Canyon (PBC), three groups of samples (corals, sediment and water) were collected between 600 - 800 m depth. DNA was extracted from these samples and metabarcoding was performed on the V3-V4 region of the 16S RNA gene using Illumina technology. The coral samples showed greater microbial diversity followed by sediment and water samples respectively. There was no divergence observed among the different groups of samples suggesting a highly dynamic canyon system with sufficient mixing and interactions of sample materials in the canyon. Gammaproteobacteria, Actinobacteria, Firmicutes and Bacteroidetes were the dominant bacterial taxa on the corals, sediment and water samples.

Keywords: microbiome, submarine canyons, *Lophelia pertusa*, *Madrepora oculata*, bacteria, cold-water corals, Ireland.

1. Introduction

Cold-water corals (CWCs) are scleractinian corals that live in the deep-sea. They are globally distributed and occur in greater abundance in the northeast Atlantic (Roberts et al., 2009), including in submarine canyons. CWCs live permanently in the dark, do not form associations with *Symbiodinium* spp., lack a carbon source and are filter feeders. They are important

ecological engineers and over 1,300 marine species can be associated with them. CWC reefs formed by *Lophelia pertusa* and *Madrepora oculata* have been recognised as hotspots of biodiversity, comparable to tropical corals. *Lophelia pertusa* and *M. oculata* growth and survival have been described to occur at temperatures between 4 - 13 °C and salinity limits of 32 - 38.8 psu (Roberts et al., 2006).

Lophelia pertusa is the primary framework-forming coral in the Porcupine Bank Canyon (PBC) in the northeast Atlantic. The PBC supports a high biomass and CWC habitats generally occur at depths between 600 - 1,200 m. CWCs form networks of complex foodwebs and can affect sedimentary processes in the canyon. Anthropogenic activities such as sedimentation, fisheries and litter pollution have been observed in the PBC (Appah et al., 2020). These anthropogenic activities including climate change can disrupt the normal functioning of beneficial microbes (Thurber et al., 2009) by altering the microbial community during stressful conditions (McDevitt-Irwin et al., 2017).

The distribution of CWC colonies in the northeast Atlantic can be influenced by microbes that live on them (Neulinger et al., 2008). Microbes live in the mucus, the polyp tissues and on the coral skeleton as well as in the ambient environment of the corals. While there are differences in the coral-associated microbial communities of living, dead and fossilized CWCs and the ambient environment (Hansson et al., 2009; Schöttner et al., 2009), no divergence has been observed between the different colour morphotypes of *L. pertusa* (Neulinger et al., 2008). Also, species-specific distribution of CWC-associated microbes has been reported (Röthig et al., 2017; Schöttner et al., 2012), whilst it has been noted that microbial diversity is conserved across different species (Lawler et al., 2016). CWC-associated microbial communities are involved in the formation of carbonate mounds (Templer et al., 2011). Microbes bind mound

sediment together through carbonate precipitation, which eventually help preserve the mound structure (Templer et al., 2011). Microbial diversity and its interaction with the host and the environment facilitates identification of important linkages existing between the microbial communities and macroecological change (Ainsworth et al., 2010). Research on microbial community composition on and within CWCs is limited. As such, our understanding of the roles that microbes play in the ecology of CWCs are insufficient, making it imperative that we assess the essential roles that microbes play in the processes that drive changes in coral distributions in the deep-sea.

The different microbial organisms that interact symbiotically with the CWC host make up a CWC holobiont. Pathogens can cause energy loss in corals whilst beneficial microbes or mutualists favour corals health, growth and survival. Coral holobiont homeostasis is attained through the allocation of available resource and energy for the removal of infections or the corals' ability to respond to stress conditions in the environment (Palmer et al., 2010; Gavish et al., 2018). Coral stress response is associated with coral immunity through the maintenance of holobiont integrity (Palmer, 2018). A breakdown of the symbiotic interactions, which is the structural and functional engine of CWCs reef ecosystems, on the coral holobiont can lead to CWCs diseases and mortality (Bourne et al., 2009; Palmer, 2018).

The present study aims to: 1) characterise the composition and diversity of microbial community in the PBC and, 2) compares microbial communities in the corals, sediment and the water samples.

2. Methodology

2.1. Study site, sample collection and storage

Coral samples were randomly collected within a 100 m periphery of three primary locations in the upper PBC in separate areas: canyon head (52°13.6371, 14°55.5389), canyon flank (51°52.20624, 15°02.0148) and south branch (51°58.40933, 15°02.4996) as defined by Appah et al. (2020) (Figure 4.1). The PBC is tectonically controlled and terrestrially disconnected. The canyon head is sediment dominated and exhibits a gentle slope while the canyon flank reveals a steep slope with exposed bedrock. The south branch is a smaller canyon system feeding into the main canyon and contains both live and dead coral communities (Mazzini et al., 2012). Generally, particulate organic matter concentration is highest in the south branch with the canyon head and canyon flank showing similar concentrations (Appah et al., 2020). Current speed in the PBC ranges from 34.1 cm s⁻¹ to 114.2 cm s⁻¹ with max. mean flow of 31.3 cm s⁻¹ recorded in the flank, 25.4 cm s⁻¹ in the south branch and 18.2 cm s⁻¹ in the canyon head (Appah et al., 2020; Lim et al., 2020). The water flow is generally uni- and bidirectional in the canyon head and canyon flank and unidirectional in the south branch with flows showing tidal characteristics (Lim et al., 2020). The prevailing watermass in the PBC is the Eastern North Atlantic Water (ENAW; Appah et al., 2020).

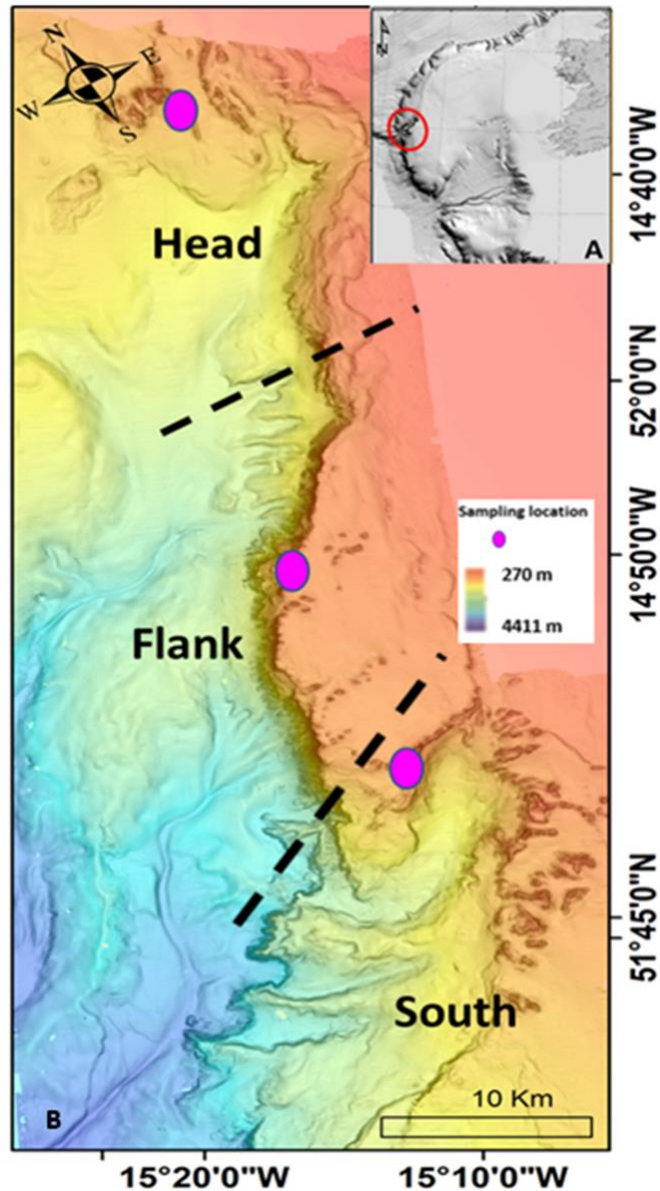


Figure 4.1. Location map showing: A) the upper Porcupine Bank Canyon (PBC) on the Irish continental margin (red ellipse), B) different areas of the upper PBC. The black broken line demarcates the canyon head, canyon flank and south branch in the upper PBC.

Coral samples were collected between 607.0 - 721.0 m depth with an average salinity and temperature of 36.3 psu and 9.3 °C, respectively (Table 4.1). Seven coral colonies (5 *Lophelia pertusa* and 2 *M. oculata*) were collected with an ROV-guided manipulator arm and stored in bio-boxes. Coral samples collected were stored in 100% ethanol at - 40 °C for the duration of the cruise. Seawater samples (one at each site location) were collected with a 5 litre (l) ROV

Niskin bottles (in the vicinity of the corals) and stored in 1 litre sterile bottles while sediment samples (one at each site location) were collected with push cores and stored in 1 litre sterile zip-lock bags. Seawater and sediment samples were stored at - 40 °C. All samples were collected between the 15 - 17/05/2019.

Table 4.1. Groups of samples, sample name, sample code, coordinates, depth (m), temperature (°C) and salinity (psu).

Group	Sample name	Sample code	Latitude	Longitude	Depth (m)	Temperature (°C)	Salinity (psu)
G1	<i>L. pertusa</i>	HF1	52°13.62980	14°55.53560	721.0	10.0	35.0
	<i>L. pertusa</i>	HF5	52°13.62616	14°55.54294	719.0	-	-
	<i>L. pertusa</i>	SF3	51°52.21990	15°01.99608	609.0	8.8	38.0
	<i>L. pertusa</i>	SC1	51°52.20370	15°01.99106	607.0	9.3	37.0
	<i>L. pertusa</i>	SF4	51°52.19837	15°02.00000	607.0	8.8	38.0
	<i>M. oculata</i>	SF2	51°52.20500	15°01.98934	608.0	8.7	37.0
	<i>M. oculata</i>	FF3	51°58.39740	15°02.52970	691.0	9.4	36.0
G2	Water	W3	52°13.62923	14°55.53959	718.0	10.0	35.0
	Water	W6	51°58.40160	15°02.51025	698.0	9.8	35.0
	Water	W9	51°52.19730	15°02.99540	607.0	8.7	38.0
G3	Sediment	CH1	52°13.62660	14°55.54270	718.0	9.8	36.0
	Sediment	SS2	51°58.40260	15°02.52119	691.0	9.8	35.0
	Sediment	SS3	51°52.19736	15°02.00890	607.0	8.7	38.0

G1 = coral samples; G2 = water samples; G3 = sediment samples

2.2. DNA extraction of coral, sediment, and seawater samples

All procedures were performed in a laminar flow hood which, along with the tools used, was decontaminated with a 10% bleach solution and DNA AWAY® (Thermo Fisher Scientific, St Leon-Rot, Germany) before and between each sample preparation and each set of extractions. Coral samples were crushed to a fine powder using liquid nitrogen and aliquots of sediment were weighed to the required amount (200 - 250 mg) for DNA extraction. Extractions were performed using the DNeasy PowerSoil Pro kit (Qiagen) following manufacturer's protocol. DNA from seawater samples was extracted using DNeasy® Blood and Tissue kit (Qiagen) following the methodology outlined in Spens et al. (2017). Specifically, seawater samples were filtered over sterile 0.22 µm Sterivex™-GP filters (Merck Millipore, Germany) using

60 ml syringes (Soft-Ject®, HSW, Tuttlingen, Germany). After filtering, one opening of the Sterivex™-GP filters was sealed with parafilm, 720 µl of ATL-buffer and 80 µl of proteinase K were added, the opening sealed, and the mixture was incubated at 56 °C for 2 h with agitation. The buffer mix was transferred with a 3 ml leuer-lock™ syringe into a 2 ml Eppendorf tube. DNA extraction was continued following the manufacturer's protocol, with buffer volumes adjusted for the amounts of lysate recovered from the sterivex filter column. Genomic DNA samples were sent to Novogene (Cambridge, UK) for microbial amplicon-based metagenomics sequencing 16S (V3-V4). The purity and concentration of genomic DNA samples were assessed on a 1% agarose gel and Qubit Fluorometer (Invitrogen, USA) respectively. The 341 F (5'-CCTAYGGGRBGCASCAG-3') and 806 R (5'-GGACTACNNGGGTATCTAAT-3') primers with barcodes were used to amplify the V3-V4 region (466 bp) of the 16S rRNA gene and sequenced using the Illumina NovaSeq 6000 SP with paired ends (2 x 250 bp) strategy (Novogene). Amplicon products at concentrations ≥ 12 ng/µL were used to prepare sequencing libraries. PCR reactions were performed in a 20 µl reaction volume using the Phusion® High-Fidelity PCR Master Mix (New England Biolabs) with ~1 - 2 ng template DNA. The final primer concentration was adjusted to 0.5 µM. Amplicons were run on a 2% agarose gel for detection, desired bands were excised and purified using Qiagen Gel Extraction Kit (Qiagen, Germany).

2.3. Bioinformatic analysis and statistics

Raw reads were quality controlled with FastQC 0.11.9 (Andrews et al., 2014), trimmed (mean quality score of 30 in a sliding window of 10 bp) with Trimmomatic 0.39 (Bolger et al., 2014) and merged into contigs using FLASH 1.2.11 (Magoč and Salzberg, 2011). Quality filtering of the sequence data to remove chimeras was performed using Dada 2 as implemented in qualitative insights into microbial ecology (QIIME 2) v2020.8 (Bolyen et al., 2019).

Sequencing data were rarefied to a sample depth of 18,000 corresponding to the least number of sequences available for all thirteen samples. Each Dada 2 amplicon sequence variant (ASV) was utilized for taxonomic classification via the QIIME 2 feature-classifier (Bokulich et al., 2018) with the sklearn technique. Diversity indices of the samples were assessed using the QIIME 2 pipeline (<https://docs.qiime2.org>). The relationship between temperature, salinity, depth and alpha diversity indices were assessed. Mitochondrial, chloroplast and unassigned ASVs were removed before the analysis. The sequences were aligned using Mafft and FastTree to construct a phylogenetic tree (Kato and Standley, 2013; Price et al., 2010). Shannon (Shannon, 1948), Pielou's evenness (Pielou, 1966) and Faith phylogenetic diversity (Faith, 1992) were assessed to determine the microbial diversity within each sample. Beta diversity based on weighted unifracs distance (UniFrac; Lozupone and Knight, 2005) was performed. Principal coordinates analysis (PCoA) plots were made in QIIME 2 and the differences in microbial composition among the different groups of samples were visualised in emperor (Vázquez-Baeza et al., 2013). Significant differences among groups of samples were evaluated using permutational multivariate analysis of variance (PERMANOVA; Tang et al., 2016). Kruskal-Wallis test was used to compare alpha diversity indices among groups of samples. Taxonomic assignment was made from the Greengenes 13_8 database (DeSantis et al., 2006; based on 99% similarity of sequence data to the Greengenes database).

3. Results

A total of 2,586,928 raw sequences yielded 529,513 effective tags for sequence analysis after processing and quality filtering of raw reads. The removal of unassigned, mitochondrial and chloroplast ASVs resulted in the least features being observed in HF5 (18,151) whilst the highest features were detected in FF3 (73,600). A total of 4,494 sequence variants with mean length of 190 were recorded, whilst a total of 522,608 features were observed in the thirteen

samples following the removal of unassigned, mitochondrial and chloroplast ASVs. Corals contained 344,782 ASVs, sediment 91,429 ASVs and water 86,397 ASVs. One feature occurred in eleven samples whilst 236 features were identified in one sample.

3.1. Alpha and beta diversity indices

Shannon's index among the groups of samples was not significantly different ($H = 2.19$, $P = 0.33$) with mean $\pm$ standard error of 7.08 ± 0.79 in corals, 6.51 ± 0.29 in sediment and 5.50 ± 0.77 in water samples (Table 4.2). Species evenness among the groups of samples was not significant ($J' = 1.66$, $P = 0.43$) and varied from 0.79 ± 0.07 in corals, 0.78 ± 0.02 in sediment and 0.72 ± 0.08 in water samples (Table 4.2). There was no significant difference (Features = 5.58 , $P = 0.06$) in the number of features for the different samples with 513.00 ± 84.28 in corals, 333.00 ± 32.50 in sediment and 191.33 ± 25.54 in water (Table 4.2). *Lophelia pertusa* generally showed high diversity compared to *M. oculata*, whilst sediment contained high microbial diversity than water samples. Depth, salinity and temperature did not correlate ($P > 0.05$; Spearman) with the observed alpha diversity measures. Species distribution curves showed that all thirteen samples were sufficient to capture the different patterns of bacterial and archaeal diversities and assigned highest features to corals and the least to water samples (Figure 4.2A).

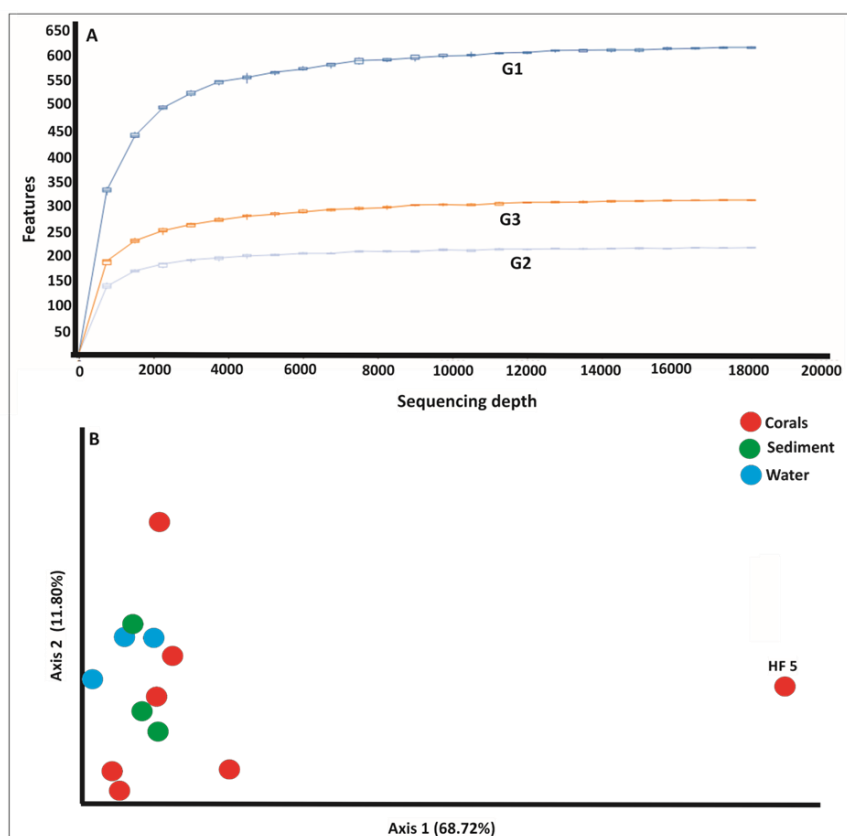


Figure 4.2. Sampling depth at 18,000 sequence variants used to make: A) Species accumulation curves across three groups, B) Principal coordinates analysis (based on weighted unifrac distance) plot of microbial composition among cold-water corals, sediment and water samples.

Table 4.2. Sample groups, names, codes, %ASVs that remained after removal of unassigned, mitochondrial and chloroplast sequences, features, Pielou's evenness (J'), Shannon's index (H) and Faith Phylogenetic diversity (Faith PD).

Group	Sample name	Sample code	%ASV remain	Features	Pielou's evenness	Faith PD	Shannon's index
G1	<i>L. pertusa</i>	HF1	0.89	817.00	0.85	67.14	8.24
	<i>L. pertusa</i>	HF5	13.43	379.00	0.67	64.27	5.75
	<i>L. pertusa</i>	SF3	0.49	652.00	0.89	37.73	8.32
	<i>L. pertusa</i>	SC1	0.37	624.00	0.93	36.52	8.67
	<i>L. pertusa</i>	SF4	1.91	604.00	0.94	43.49	8.65
	<i>M. oculata</i>	SF2	0.91	351.00	0.82	25.85	6.91
	<i>M. oculata</i>	FF3	2.54	164.00	0.41	16.61	3.04
G2	Water	W3	0.02	209.00	0.78	16.69	6.05
	Water	W6	0.02	224.00	0.83	24.53	6.46
	Water	W9	0.06	141.00	0.56	15.18	3.98
G3	Sediment	CH1	0.16	300.00	0.79	23.83	6.54
	Sediment	SS2	0.29	301.00	0.73	30.72	5.99
	Sediment	SS3	1.02	398.00	0.81	37.83	6.99

PERMANOVA revealed that microbial compositions among groups of samples were not significant (Pseudo-F = 0.70, P = 0.56). PCoA plot clustered all samples together except sample HF5, suggesting sample HF5 as an outlier in the distribution of sample frequencies based on its total frequency (Figure 4.2B). Excluding sample HF5 in a separate analysis yielded a significant difference (P = 0.04; Bray-Curtis distance) among the groups of samples.

3.2. Taxonomic classification

At the order level of classification, corals contained 212 features, sediment contained 135 features and water contained 80 features. Gammaproteobacteria dominated the bacterial and archaeal communities in corals whilst they were similar in abundance in sediment and water samples (Figure 4.3 and 4.4). Gammaproteobacteria was 3x higher in *M. oculata* compared to *L. pertusa* whilst *L. pertusa* contained many rare taxa compared to *M. oculata* (Figure 4.3). Alteromonadales were dominant in water and sediment samples while Gammaproteobacteria were abundant in corals (Figure 4.3 and 4.4). Rhodobacterales on the other hand was abundant in water and least in corals (Figure 4.3 and 4.4). At the phylum level, corals contained 38 features, sediment 32 features and water 22 features. Proteobacteria were dominant (> 60.00%) in all the samples (Table 4.3). Bacteroidetes (> 5.00%) and Firmicutes (> 5.00%) were also relatively abundant in all the samples (Table 4.3). Chloroflexi were represented in high abundance (1.83%) in sediment samples and at low abundance (< 1.00%) in corals and water samples. Verrucomicrobia were more abundant in corals (1.16%), followed by sediment (0.19%) and water (0.04%) samples. Candidate phylum TM6 were more abundant in sediment (1.31%) than in corals (0.03%) and water (0.01%) samples while candidate phylum TM7 were more abundant in corals (0.23%) than sediment (0.04%) and water (0.04%) (Table 4.3). Fusobacteria, Lentisphaerae, Elusimicrobia, Fibrobacteres and Synergistetes were observed

only in corals at < 0.10% (Table 4.3). Also, Chlorobi (0.01%) and Chlamydiae (0.08%) were present only in sediment while SAR406 (0.05%).

Table 4.3. Percentage abundance of features present in the corals, sediment and water samples in the uPBC.

Feature	FF3	SF2	HF1	HF5	SC1	SF3	SF4	mean	CH1	SS2	SS3	mean	W3	W6	W9	mean
Archaea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.04	0.00	0.00	0.00	0.00
Crenarchaeota	0.00	0.66	0.04	0.00	2.18	1.33	4.82	1.29	0.13	0.17	0.68	0.32	0.00	0.10	2.94	1.01
Euryarchaeota	0.01	0.02	0.02	0.00	0.01	0.00	0.17	0.03	0.00	0.03	0.11	0.05	0.01	0.00	0.02	0.01
Bacteria	0.21	0.26	6.33	48.55	0.58	0.19	1.41	8.22	0.17	0.57	1.70	0.81	0.09	0.26	0.78	0.38
Bacteria	0.02	0.19	1.48	0.68	0.19	0.45	1.17	0.60	0.05	0.15	0.14	0.11	0.07	0.36	0.03	0.15
AC1	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.11	0.04	0.00	0.00	0.00	0.00
Acidobacteria	0.01	0.38	1.60	0.06	0.59	0.66	2.19	0.78	0.18	0.32	0.33	0.27	0.00	0.08	0.82	0.30
Actinobacteria	0.87	1.29	10.82	1.36	3.10	5.25	4.50	3.88	1.32	2.05	2.18	1.85	0.84	1.21	0.24	0.76
Armatimonadetes	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
Bacteroidetes	0.66	8.77	5.06	2.56	20.63	12.12	13.78	9.08	7.12	7.33	7.72	7.39	19.96	5.43	5.16	10.18
CD12	0.00	0.00	0.00	0.00	0.02	0.00	0.01	0.00	0.01	0.29	0.33	0.21	0.00	0.02	0.00	0.01
Caldithrix	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.01	0.00	0.02	0.00	0.01	0.00	0.00	0.00	0.00
Chlamydiae	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.09	0.15	0.08	0.00	0.00	0.00	0.00
Chlorobi	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.03	0.01	0.00	0.00	0.00	0.00
Chloroflexi	0.02	0.07	1.91	0.20	0.46	0.32	0.49	0.50	0.38	1.69	3.43	1.83	0.00	0.06	0.08	0.05
Cyanobacteria	0.00	0.04	0.01	0.13	0.11	0.11	0.08	0.07	0.04	0.11	0.17	0.11	0.12	0.10	0.00	0.07
Elusimicrobia	0.00	0.01	0.00	0.00	0.03	0.01	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fibrobacteres	0.00	0.00	0.01	0.00	0.02	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Firmicutes	1.63	19.64	8.74	2.96	26.24	7.81	11.94	11.28	10.25	13.19	18.99	14.15	10.48	14.89	2.06	9.14

Table 4.3. Percentage abundance of features present in the corals, sediment and water samples in the uPBC.

Feature	FF3	SF2	HF1	HF5	SC1	SF3	SF4	mean	CH1	SS2	SS3	mean	W3	W6	W9	mean
Fusobacteria	0.00	0.00	0.71	0.36	0.01	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
GN02	0.00	0.00	0.02	0.02	0.00	0.03	0.07	0.02	0.00	0.00	0.02	0.01	0.01	0.00	0.02	0.01
GN04	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
GOUTA4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
Gemmatimonadetes	0.00	0.04	0.75	0.06	0.22	0.06	0.21	0.19	0.12	0.14	0.26	0.17	0.00	0.00	0.43	0.14
Lentisphaerae	0.00	0.00	0.01	0.20	0.00	0.00	0.07	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
NC10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
NKB19	0.00	0.00	0.02	0.00	0.02	0.02	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
Nitrospirae	0.00	0.53	0.01	0.03	0.59	0.27	0.81	0.32	0.00	0.11	0.13	0.08	0.05	0.09	0.05	0.06
OD1	0.00	0.00	0.03	0.00	0.01	0.07	0.03	0.02	0.00	0.00	0.02	0.01	0.00	0.00	0.00	0.00
OP8	0.00	0.00	0.00	0.00	0.08	0.07	0.00	0.02	0.00	0.40	1.10	0.50	0.00	0.06	0.00	0.02
Planctomycetes	0.08	0.00	0.10	0.00	0.02	0.06	0.22	0.07	0.00	0.00	0.07	0.02	0.00	0.00	0.00	0.00
Proteobacteria	96.22	67.42	59.99	42.50	43.70	66.98	55.85	61.81	79.82	69.82	60.99	70.21	68.14	77.06	87.13	77.44
SAR406	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.05

Table 4.3. Percentage abundance of features present in the corals, sediment and water samples in the uPBC.

Feature	FF3	SF2	HF1	HF5	SC1	SF3	SF4	mean	CH1	SS2	SS3	mean	W3	W6	W9	mean
SBR1093	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Spirochaetes	0.01	0.09	0.03	0.05	0.06	0.16	0.15	0.08	0.09	0.02	0.20	0.10	0.05	0.27	0.00	0.11
Synergistetes	0.03	0.00	0.00	0.00	0.05	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
TM6	0.00	0.03	0.02	0.00	0.08	0.04	0.06	0.03	0.02	3.31	0.59	1.31	0.04	0.00	0.00	0.01
TM7	0.00	0.01	1.58	0.00	0.02	0.02	0.01	0.23	0.00	0.07	0.06	0.04	0.12	0.00	0.00	0.04
Tenericutes	0.00	0.05	0.07	0.00	0.14	0.00	0.00	0.04	0.00	0.04	0.13	0.06	0.00	0.00	0.00	0.00
Verrucomicrobia	0.24	0.50	0.63	0.29	0.84	3.95	1.67	1.16	0.29	0.10	0.17	0.19	0.01	0.02	0.08	0.04
WS3	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.02	0.00	0.00	0.03	0.01	0.00	0.00	0.00	0.00

Generally, Gammaproteobacteria, Actinobacteria, Firmicutes and Bacteroidetes were abundant on our corals and non-coral samples. Planctomycetes, Tenericutes were observed in corals and sediment samples at < 0.10% (Table 4.3). Archaea were found in the samples in low abundances ($\leq 5.00\%$).

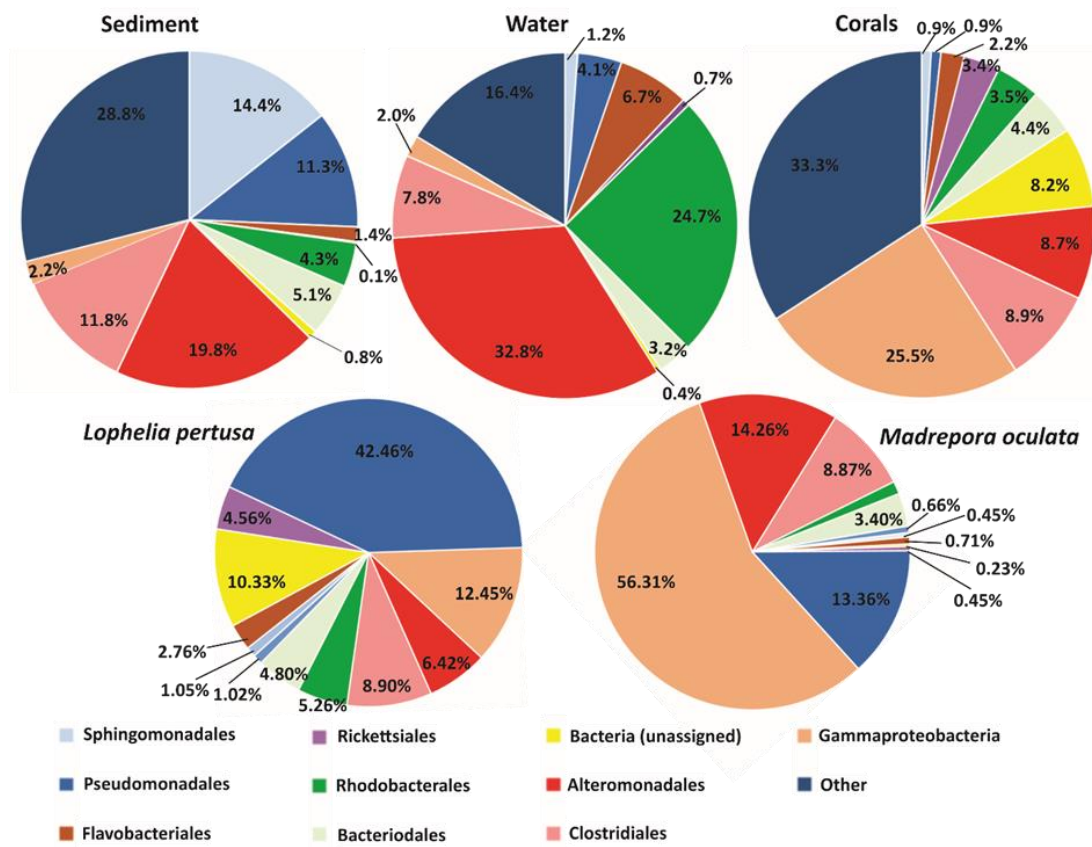


Figure 4.3. Average bacterial abundance at order-level of classification in corals (*Lophelia pertusa* and *Madrepora oculata*), water and sediment samples from the PBC.

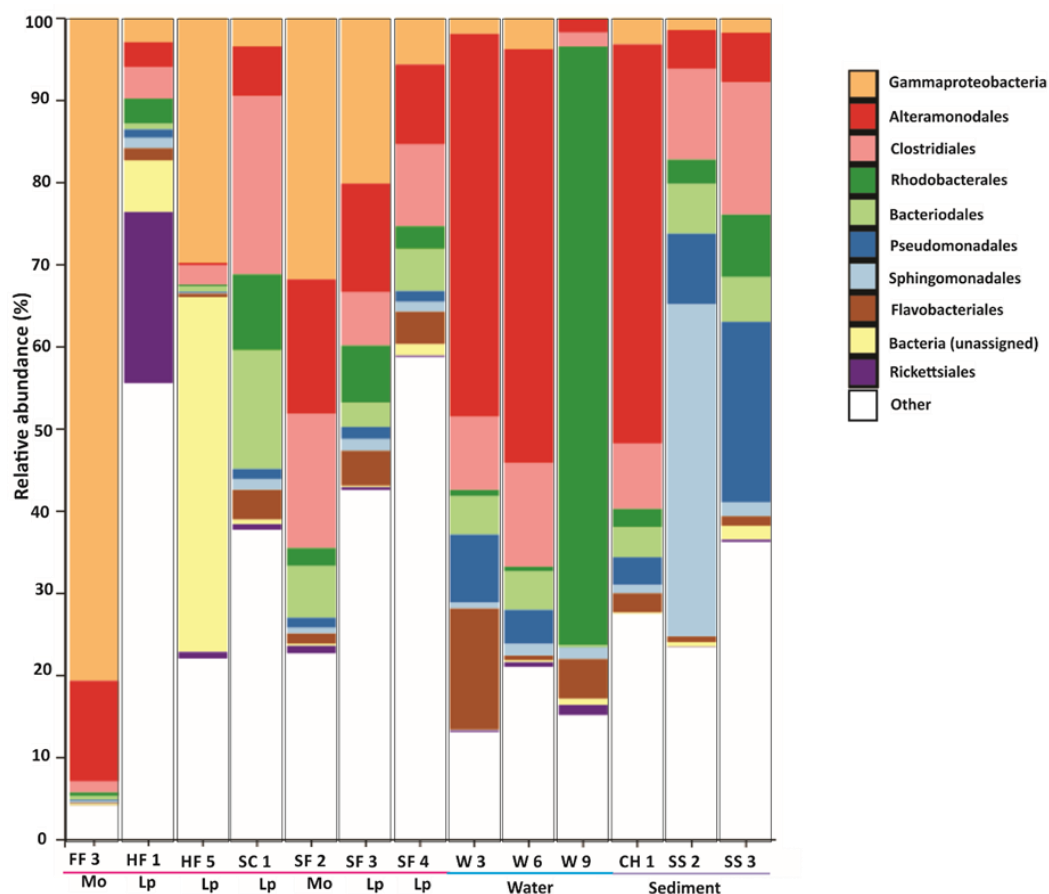


Figure 4.4. Relative abundances of archaeal and bacterial taxa at order-level of classification in cold-water corals (Lp = *Lophelia pertusa*; Mo = *Madrepora oculata*), water, and sediment samples in the upper PBC.

4. Discussion

4.1. Microbial alpha and beta diversity

Seabed morphology is known to influence the dynamics of the physical and chemical properties (e.g. dissolved and particulate organic matter and current regimes) of the deep-sea including in the upper PBC (Lim et al., 2020). These properties can potentially influence the composition of microbial communities on CWCs, sediment and the ambient water. The many rare microbial taxa in corals in the present study were reflected in the high mean observed features and Shannon's index detected in corals than the water and sediment samples. Higher Shannon's

index was observed in the corals than in the sediment and water samples in the present study and seems to be higher in these coral samples than what has been reported in other studies (Kellogg et al., 2017, 2016; Meistertzheim et al., 2016). Similarly, bacterial communities associated with coral habitats in the Langedugen fjord were more biodiverse than those associated with non-coral habitats (Schöttner et al., 2009). There was no correlation between temperature, salinity and microbial diversity in the present study. The temperature and salinity measures recorded between 607.0 - 721.0 m depth were fairly stable without much variation (Table 4.1), implying that variations in watermass do not influence the bacterial community composition in the PBC. There was no divergence in the microbial composition associated with the corals, water and sediment samples in this study. These results contrast studies from the Rockall Bank (van Bleijswijk et al., 2015) and Trondheimsfjord (Neulinger et al., 2008). It is most likely no divergence was detected as a result of sufficient interactions of coral materials (e.g. mucus) between the different samples caused by oceanographic and hydrographic processes. Also, the push cores used to collect sediment samples contained water at two of the sites, which most likely resulted in mixing of sample materials and possible exchange of microbial communities in this study. Mucus dissolves in the water and can fuel the growth of microbes (Taniguchi et al., 2015). Mucus from sponges from reef ecosystems have been found to share high operational taxonomic units (OTUs) with sediment samples (Schöttner et al., 2013). The PBC is a highly dynamic canyon environment with current speeds of up to 114 cm s^{-1} recorded (Lim et al., 2020). The high current speed can entrain large concentrations of sediment and particulates (Appah et al., 2020) into the water column resulting in sufficient mixing of coral materials and microbial communities in the water and sediment samples in the canyon. Bioturbation can also entrain sediment materials into the surrounding water and corals to ensure sufficient mixing of microbial communities.

4.2. Microbial composition in corals, water and sediment samples

Generally, Gammaproteobacteria, Actinobacteria, Firmicutes and Bacteroidetes were abundant on our corals and non-coral samples. These taxa have been described to be dominant in CWCs from the Atlantic (Kellogg et al., 2017; Penn et al., 2006; van Bleijswijk et al., 2015), the Mediterranean (Meistertzheim et al., 2016) and the Red Sea (Röthig et al., 2017). The genera *Mycoplasma* and *Endozoicomonas* were observed in coral mucus and skeleton from the Rockall Bank (van Bleijswijk et al., 2015), but were not detected in our corals or non-coral samples. This may likely be because of biogeography and regional effects. Similarly, biogeography could be attributed to why candidate phylum TM7 were observed in the Atlantic (this study; Kellogg et al., 2017; Neulinger et al., 2008; van Bleijswijk et al., 2015), but not the Mediterranean (Meistertzheim et al., 2016). However, sampling and methodological variations can also influence community composition in microbiome studies (Bailén et al., 2020; Kaszubinski et al., 2020; López-García et al., 2018; Marotz et al., 2019; Pootakham et al., 2017). Crenarchaeota were represented in high abundance in the corals than the non-coral samples. Similarly, Thaumarchaeota were represented in high abundance in the corals than the water and sediment samples. The dominance of Thaumarchaeota on the coral samples could be a selective mechanism which parallels with the feeding strategy of *Lophelia*. Thaumarchaeota were also identified as the dominant archaeal taxa of CWCs from the Rockall Bank (van Bleijswijk et al., 2015). Rhodobacterales and Rhizobiales were detected in relatively high abundances in our coral samples. These bacterial taxa have been associated with nutrition and nitrogen cycling activities in CWCs (Kellogg et al., 2016; Lawler et al., 2016; Middelburg et al., 2015). The abundance of Rhodobacterales in the water and sediment samples suggest the importance of organic matter from coral mucus to their growth (Taniguchi et al., 2015). Organic sulfur compounds (dimethyl sulfide and dimethylsulfoniopropionate) contained in coral mucus can also be utilised by Rhodobacterales for growth (Broadbent and

Jones, 2004). Conversely, coral mucus can inhibit bacterial growth in the surrounding environment through their antibacterial function. However, differences in microbial compositions between *L. pertusa* and *M. oculata* could be because of differences in their food sources and life history strategies. Thermoplasmata were the only archaea present in sample FF3 (*Madrepora* sample) from the canyon flank and highly abundant in only SS2 (sediment sample) which is also from the canyon flank but absent from SF2 (*Madrepora* coral sample) in the south branch, suggesting that Thermoplasmata could be more associated with location in the canyon rather than the corals. In the present study, Chloroflexi and Gammaproteobacteria were observed in high abundances in sediment samples. This corroborates with studies that have characterised Chloroflexi and Gammaproteobacteria as dominant bacteria of deep-sea sediments with Bacteroidetes and Planctomycetes being less abundant (Jensen et al., 2008; Parkes and Sass, 2009).

5. Conclusions

This study is the first to describe the coral-associated microbiome from the Porcupine Bank Canyon. The pattern of distribution of microbial communities associated with coral, water and sediment samples in the upper PBC was characterised. It was observed that the host-bacterial composition exhibited no divergence among the different groups of samples with coral samples showing high bacterial diversity. There was no structure in the bacterial composition associated with *L. pertusa* and *M. oculata*. Coral samples showed high features for a given sequencing depth whilst water samples contained the least features at a given sequencing depth. Generally, the results indicate a high energy canyon environment with sufficient mixing of materials and community composition among the corals, water and sediment samples.

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Additional Information

Raw sequence data used in this study can be accessed from the project link <https://www.ncbi.nlm.nih.gov/sra/PRJNA729568>

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Chapter 5

A health survey of the reef forming scleractinian cold-water corals *Lophelia pertusa* and *Madrepora oculata* in a remote submarine canyon on the European continental margin, NE Atlantic

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All authors contributed to the success of the manuscript. John Appah designed the project, was also involved in the data collection at sea and performed all the data generation and data analysis for the Porcupine Bank Canyon dataset, and was the primary author who wrote most of the paper, compiled the first draft and incorporated subsequent modifications. Dr Aaron Lim was chief scientist on the cruises that collected the data set and edited the draft. Profs Wheeler and Ruth O’Riordan edited the draft and provided technical advice. Dr Sharon Lynch provided technical advice and edited the draft whilst Luke O’Reilly and Larissa de Oliveira were involved in data collection. Funding for this project was secured by Prof. Andy Wheeler with Dr. Aaron Lim through the SFI from MMMonKey_Pro (SFI from MMMonKey_Pro (grant number: 16/IA/4528) and forms a contribution to the European Union’s Horizon 2020 Research and Innovation Program “iAtlantic” project (grant number: 818123).

Abstract:

Monitoring of cold-water corals (CWCs) for pathogens and diseases is limited due to the environment, protected nature of the corals and their habitat, as well as the challenging sampling effort required. It is recognised that environmental factors such as temperature and pH can expedite the ability of pathogens to cause diseases in cold-water corals therefore the characterisation of pathogen diversity, prevalence and associated pathologies is essential. The present study combined histology and polymerase chain reaction (PCR) diagnostic techniques to screen for two significant pathogen groups (bacteria of the genus *Vibrio* and the protozoan Haplosporidia) in the dominant NE Atlantic deep-water framework corals *Lophelia pertusa* (13 colonies) and *Madrepora oculata* (2 colonies) at three sampling locations (canyon head, south branch and the flank) in the Porcupine Bank Canyon (PBC), NE Atlantic. One *M. oculata* colony and four *L. pertusa* colonies were collected from both the canyon flank and the south branch whilst five *L. pertusa* colonies were collected from the canyon head. No pathogens were detected in the *M. oculata* samples. Neither histology nor PCR detected *Vibrio* spp. in *L. pertusa*, although Illumina technology used in this study to profile the CWCs microbiome, detected *V. shilonii* (0.03%) in a single *L. pertusa* individual, from the canyon head, that had also been screened in this study. A macroborer was observed at a prevalence of 0.07% at the canyon head only. Rickettsiales-like organisms (RLOs) were visualised with an overall prevalence of 40% and with a low intensity of 1 to 4 (RLO) colonies per individual polyp by histology. *L. pertusa* from the PBC canyon head had an RLO prevalence of 13.3% with the highest detection of 26.7% recorded in the south branch corals. Similarly, unidentified cells observed in *L. pertusa* from the south branch (20%) were more common than those observed in *L. pertusa* from the canyon head (6.7%). No RLOs or unidentified cells were observed in corals from the flank. Mean particulate organic matter concentration is highest in the south

branch ($2,612 \mu\text{g l}^{-1}$) followed by the canyon head ($1,065 \mu\text{g l}^{-1}$) and lowest at the canyon flank ($494 \mu\text{g l}^{-1}$). Although the route of pathogen entry and the impact of RLO infection on *L. pertusa* is unclear, particulate availability and the feeding strategies employed by the scleractinian corals may be influencing their exposure to pathogens. The absence of a pathogen in *M. oculata* may be attributed to the smaller number of colonies screened or the narrower diet in *M. oculata* compared to the unrestricted diet exhibited in *L. pertusa*, if ingestion is a route of entry for pathogen groups. The findings of this study also shed some light on how environmental conditions experienced by deep sea organisms and their life strategies may be limiting pathogen diversity and prevalence.

Keywords: Haplosporidia; *Vibrio*; Rickettsiales-like organisms; Histology; Pathogen; Cold-water corals

1. Introduction

Coral pathogen and disease studies allow researchers to understand the dynamics and mechanisms of infection, their interaction with the host organism and the environment. Coral diseases may cause rapid mortality and injury of cold-water and tropical corals, thereby affecting their geographic distribution (Woodley et al., 2016). Disease studies in coral species can be used as a proxy of stress conditions that the corals are exposed to in the environment (Woodley et al., 2016). Environmental stressors such as sedimentation, low salinity and high temperature can change healthy coral-associated microbes to become virulent coral-associated microbes in tropical and cold-water corals (Galloway et al., 2007; Thurber et al., 2009; Mouchka et al., 2010; Vidal-Dupiol et al., 2011; La Riviere et al., 2013; Vezzulli et al., 2013; Kvitt et al., 2015). Coral stress response is linked to coral immunity through the maintenance of coral holobiont integrity, which is the ability of a coral to accept useful microbes whilst

preventing harmful microbes/pathogens from entering it (Gavish et al., 2018; Palmer, 2018). The symbiotic interactions between the CWCs host and the array of microbes associated with the coral host is the structural and functional engine of coral reef ecosystems and health (Bourne et al., 2009). The point at which the complex symbiotic interactions between the CWCs and the associated microbes is broken and coral damage in the form of coral diseases/mortality is elicited is the damage threshold of the coral holobiont (Palmer, 2018). Coral disease studies have focused primarily on shallow water stony corals, with less of a focus on shallow water soft corals and even fewer studies on cold-water corals (Hall-Spencer et al., 2007; Rosenberg and Loya, 2013; Woodley et al., 2016). Historical monitoring of cold-water corals for pathogens and disease has been limited due to the environment, protected nature of the corals and their habitat, as well as the sampling effort required resulting in much less knowledge than for tropical coral health. It is recognised that there is a lack of a model species for the surveying of cold-water coral diseases (Work and Meteyer, 2014). Also, there remains a limitation to develop frameworks to systematically characterise cold-water and tropical coral pathologies (Galloway et al., 2007; Pollock et al., 2011).

Cold-water coral reefs formed by the dominant NE Atlantic framework corals *Lophelia pertusa* and *Madrepora oculata* have been recognised as hotspots for biodiversity (Roberts et al., 2006). *L. pertusa* and *M. oculata* show slow growth and survival at temperatures between 4 to 13 °C and salinities of 32 to 38.8 psu (Freiwald, 2002; Roberts et al., 2009). The two scleractinian corals live permanently in the dark and do not form associations with *Symbiodinium* spp., they also lack a carbon source and are filter feeders. Both coral species and the reefs that they form can have over 1,300 marine species associated with them (Roberts et al., 2009). Studies of diseases in cold-water corals are limited, despite their importance as ecological engineers (Jonsson et al., 2004). Health surveys that have been carried out on cold-

water corals include species from the southwest England (gorgonian *Eunicella verrucosa*: (Hall-Spencer et al., 2007)), and Indonesia (scleractinian *Madrepora* spp. (Grygier and Cairns, 1996)). The pathogens identified (using histological and/or molecular techniques) in those studies included bacteria of the genus *Vibrio* spp., and the petracid crustacean *Patrarca madreporae* respectively. Pathogenic *Vibrio* spp. are ubiquitous in the environment, including the deep sea, and most species are problematic for organisms. A recent study isolated *Vibrio bathopelagicus* sp. nov. (closely related to pathogenic coastal *Vibrio* strains) from a water depth of 3309 m (Lasa et al., 2021), making pathogenic *Vibrio* a potential threat to deep sea ecosystems. It is recognised that Haplosporidia and *Vibrio* spp. are problematic in a host population and are associated with mortalities when they are present at very high prevalences (Bythell et al., 2002; Hall-Spencer et al., 2007).

The Haplosporidia are a significant pathogen group globally that have been associated with mortality events in near shore marine invertebrate species (Lynch et al., 2007; Arzul and Carnegie, 2015). A Haplosporidian of the rainbow abalone *Haliotis iris*, that is closely related to *Bonamia exitiosa*, contains within its cytoplasm a Rickettsiales-like bacteria that belongs to the spotted fever group (SFG) and is pathogenic (Hine et al., 2002). Pathogenic Haplosporidia may exist as spores, plasmodia, single cell uninucleate or binucleate life stages in their hosts (Burreson and Ford, 2004; Stentiford et al., 2013; Lynch et al., 2020). The Haplosporidian species *Urosporidium crescens* and *Haplosporidium costale* have been detected in methane seeps (Takishita et al., 2007) and their presence in the deep sea poses a possible threat to deep sea anthozoans. The genera *Urosporidium* and *Haplosporidium* are spore forming Haplosporidia (Molloy et al., 2012), which may have existed as spores due to the harsh environmental conditions that exist in methane seeps. These spores can be transported from shallow waters into the deep sea (Le Moigne, 2019) and from methane seeps into the water

column. Haplosporidian spores can remain in the environment for decades, until there are favourable conditions for growth and re-emergence from this dormant life stage (Ford et al., 1999; Burreson and Ford, 2004).

The order Rickettsiales contains clinically important bacterial groups (collectively called Rickettsiales-like organisms (RLOs)) that are commonly detected in the epithelial and digestive tissues of both deep and shallow marine invertebrates (Gulka et al., 1983; Castelli et al., 2016; Getchell et al., 2016). They exist in different sizes and morphological forms (Noguchi, 1926; Humphrey, 2008). The pathogenic significance of RLOs in corals is unclear due to their high prevalence in apparently healthy and diseased corals (Casas et al., 2004; Miller et al., 2014; Godoy-Vitorino et al., 2017). Detection of novel pathogens (including Haplosporidia) in marine invertebrates has become increasingly difficult due to host selection and partitioning (Lynch et al., 2020) as well as our excessively dependent use of generic molecular markers that are unable to amplify the highly divergent genes of pathogens (Hartikainen et al., 2014).

The present study combined histology and molecular techniques (standard PCR and Illumina sequencing) to investigate: 1) the presence/absence of Haplosporidia and *Vibrio* spp. in *L. pertusa* and *M. oculata* in the Porcupine Bank Canyon (PBC), 2) describe other potential pathogens observed in the tissues of *L. pertusa* and *M. oculata*, and 3) report the distribution of these potential pathogens in the PBC. Findings from this study will build on the limited existing knowledge of pathogen diversity and prevalence in cold-water coral species.

2. Materials and Methods

2.1. Study site, sampling and storage

The Porcupine Bank Canyon is located 310 km to the southwest of Ireland. Coral colonies (n=15; 2 *M. oculata* and 13 *L. pertusa*) were collected during a cruise in May 2019 (Lim et al., 2019) within a 100 m periphery of each of three site locations: canyon head (52°13.6371, 14°55.5389), canyon flank (51°58.40933, 15°02.49959) and south branch (51°52.20624, 15°02.01476) in the PBC (Appah et al., 2020) (Figure 5.1). The canyon head was sediment dominated and exhibited a gentle slope while the flank reveals a steep slope with exposed bedrock. The south branch is a small canyon system attached to the main canyon, where the presence of cold-water coral frameworks has been noted (Mazzini et al., 2012). Current speed in the PBC ranges from 34.1 cm s⁻¹ to 114.2 cm s⁻¹ and is highest at the canyon flank (31.3 cm s⁻¹) and lowest in the canyon head (18.2 cm s⁻¹) (Appah et al., 2020; Lim et al., 2020). Also, the water flow is generally uni- and bidirectional in the canyon head and flank and unidirectional in the south branch (Lim et al., 2020). Mean particulate organic matter concentration in the south branch is 2,612 µg l⁻¹ in the canyon head 1,065 µg l⁻¹ and in the canyon flank 494 µg l⁻¹ (Appah et al., 2020).

Coral samples from the canyon head were collected from depths of between 710 to 720 m, the flank was between 688 to 693 m and the south branch were between 600 to 610 m water depth. The temperature and salinity ranges were 8.7 to 10 °C and 34.0 to 38.0 psu respectively. *L. pertusa* and *M. oculata* samples were collected with the guided manipulator arm of a remotely operated vehicle (ROV) and stored in bio boxes. For histological analysis, five colonies were collected from each of the three site locations, and a branch with five polyps was broken off from each colony resulting in twenty-five individual polyps being processed and screened per site location. One *M. oculata* colony and four *L. pertusa* colonies were collected from both the

canyon flank and the south branch respectively whilst five *L. pertusa* colonies were collected from the canyon head. Additionally, five polyp samples were collected from each colony fragment for DNA extractions and Illumina sequencing. Coral samples collected for histology were fixed in Davidson's solution for 48 hours and transferred into 70% ethanol at room temperature for the duration of the cruise. Davidson-fixed coral samples were used for formalin fixed paraffin-embedded (FFPE) tissues DNA extractions and standard PCR techniques. Also, coral samples collected for DNA extractions and Illumina technology were stored in 100% ethanol at - 40 °C (Straube and Juen, 2013). Coral samples were decalcified with TBD-2 formic acid decalcifier (Thermo Scientific). Each polyp was placed in an individual tissue embedding histocassette (n = 75 polyp samples: *L. pertusa* (n = 65 polyps) and *M. oculata* (n = 10 polyps)).

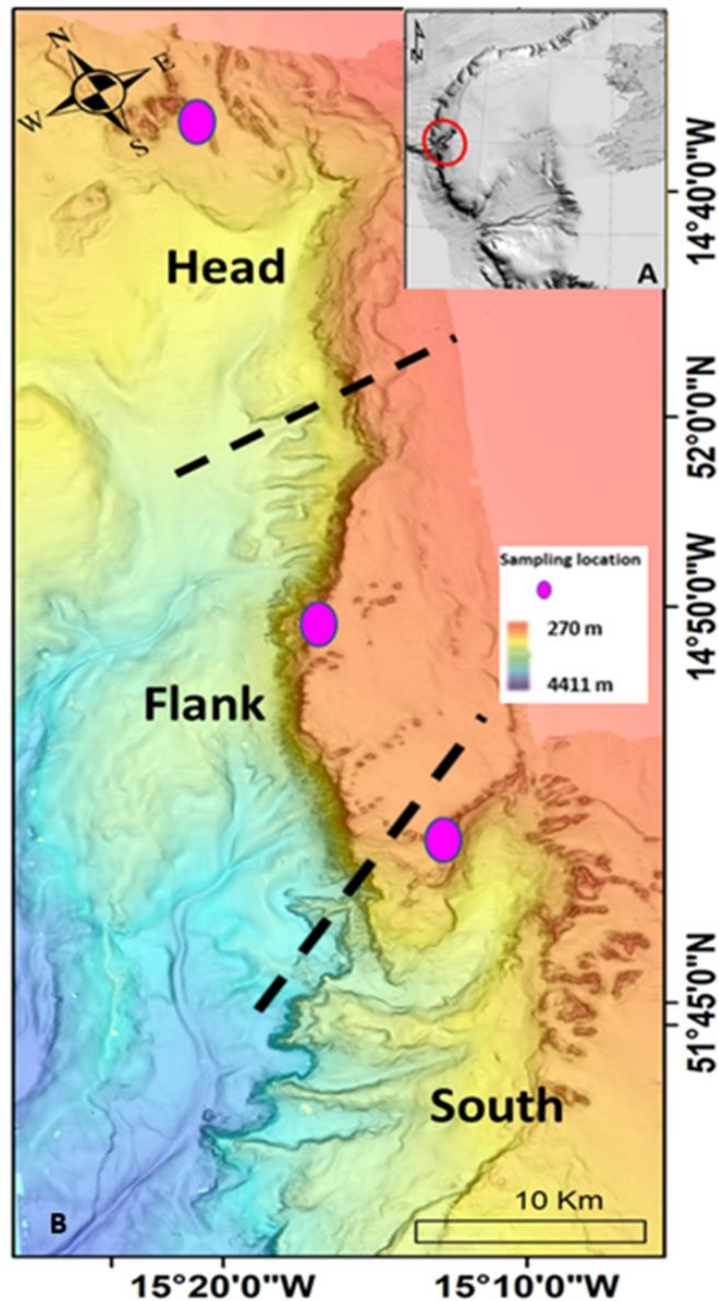


Figure 5.1. Location map showing: A) the Porcupine Bank Canyon (PBC) on the Irish continental margin (red ellipse) and the, B) different areas of the PBC. The black broken line demarcates the canyon head, canyon flank and south branch in the PBC.

2.2. Histology

Fixed samples were then prepared for embedding in wax, for histological examination, using a 20-hr dehydration cycle of graded volumes of ethanol adapted from Howard (2004). The

paraffin embedded samples were then sectioned using a Leica microtome at 5 μ m, were mounted on sterile glass slides, and air dried for 7 days prior to Haematoxylin and Eosin staining (Humason, 1962). Stained samples were cover-slipped and allowed to air-dry. Microscopic image analysis of the Haematoxylin-Eosin slides was conducted to identify the pathogen groups, including screening of the epidermal, gastrodermal and the connective tissues of the corals. Also, DNA was isolated from Davidson-fixed, formalin-fixed paraffin embedded (FFPE) tissue sections to screen *Vibrio* spp. and *Haplosporidium* spp.

2.3. DNA extraction and standard polymerase chain reaction (PCR)

DNA was extracted from 7 μ m FFPE tissue sections. Polyp tissues were deparaffinized (Shi et al., 2004) and DNA extractions were carried out using a Qiagen DNA extraction kit (QIAamp DNA FFPE Tissue Kit), following manufacturer's protocol. The quality and quantity of DNA were evaluated using a NanoDrop 1000 spectrophotometer (ThermoScientific). Good-quality DNA will have an A260/A280 ratio of 1.7 to 2.0. A reading of 1.6 does not render the DNA unsuitable for any application, but lower ratios indicate that more contaminants such as proteins are present. Routinely used generic PCR assays (Hap1/R1, Hap1/R3, ssu980/R1) for Haplosporidia and specific (MSXA/MSXB) haplosporidian primers (Table 5.1) were run on extracted DNA samples following Molloy et al. (2012) and Renault et al. (2000) while PCR for *Vibrio* spp. was performed as per Albuixech-Martí et al. (2021a), Kett et al. (in review), and Notaro et al. (2021). Positive controls (i.e. Haplosporidia genomic DNA and *Vibrio* spp. from heavily infected cockles) were included for all PCRs. A negative control consisting of double distilled water (ddH₂O) was included in each PCR. Amplifications of *Haplosporidium* spp. were carried out in a total reaction volume of 20 μ l, including approx. 1 μ l template DNA, 4 μ l of 5X green buffer, 3.2 μ l of 1.25 mM dNTPs, 0.1 μ l GoTaq DNA Polymerase (Advanced Biotechnologies™), 11.3 μ l ddH₂O and 0.2 μ l each of forward and reverse primers (Table 5.1).

The thermal profiles comprised of one cycle of denaturation at 95 °C for 180 s followed by 35 cycles at 95 °C for 30 s, 48-59 °C for 30 s, 72 °C for 30-60 s and a final extension at 72 °C for 300s. Amplifications of *Vibrio* spp. were carried out in a total reaction volume of 25 µl, including approx. 1 µl template DNA, 5 µl of 5X green buffer, 5 µl of 1.25 mM dNTPs, 0.1 µl GoTaq DNA Polymerase (Advanced Biotechnologies™), 0.5 µl of 2.5 mM MgCl₂, 12.9 µl ddH₂O and 0.25 µl each of forward and reverse primers (Table 5.1). The thermal profile for *Vibrio* spp. comprises one cycle of denaturation at 95 °C for 60 s followed by 35 cycles at 94 °C for 20 s, 56 °C for 30 s, 72 °C for 30 s and a final extension at 72 °C for 4200s. Amplicons were run on a 2% agarose gel stained with 22 µl Sybr stain (Invitrogen, Paisley, UK) and run for 35 to 45 min at 110 V for detecting DNA amplicons.

2.4. DNA extraction, Illumina sequencing technology and bioinformatics for microbiome analysis (Appah et al., unpublished)

Coral samples were crushed using liquid nitrogen and DNA extraction was performed with DNeasy PowerSoil Pro kit (Qiagen) following manufacturer's protocol. Genomic DNA samples were sent to Novogene (Cambridge, UK) for amplicon-based metagenomics sequencing to be carried out. The purity and concentration of genomic DNA samples were assessed on a 1% agarose gel and Qubit Fluorometer (Invitrogen, USA) respectively. Amplicon products of the 16S rRNA gene at the V3-V4 region were used to prepare sequencing libraries. Amplicon products at concentrations ≥ 12 ng/µl were used to prepare sequencing libraries. PCR reactions were performed in a 20 µl reaction volume using the Phusion® High-Fidelity PCR Master Mix (New England Biolabs) with approx. 1 - 2 ng template DNA. The final primer concentration was adjusted to 0.5 µM. Amplicons detections were carried out on a 2% agarose gel, desired bands were excised and purified using Qiagen Gel Extraction Kit (Qiagen, Germany). Sequencing was performed using the Illumina NovaSeq 6000 SP with

paired ends (2 x 250 bp) strategy (Novogene). Seven coral and six non-coral samples contained sufficient sequence data (BioProject Accession Number: PRJNA729568) for read processing, quality control and bioinformatic analysis.

2.4. Bioinformatic analysis and quality control

Raw reads were quality controlled with FastQC 0.11.9 (Andrews et al., 2014), trimmed (mean quality score of 30 in a sliding window of 10 bp) with Trimmomatic 0.39 (Bolger et al., 2014) and merged into contigs using FLASH 1.2.11 (Magoč and Salzberg, 2011). Quality filtering of the sequence data to remove chimeras was performed using Dada 2 as implemented in qualitative insights into microbial ecology (QIIME 2) v2020.8 (Bolyen et al., 2019). Sequencing data were rarefied to a sample depth of 18,000 corresponding to the least number of sequences. Each Dada 2 amplicon sequence variant (ASV) was utilized for taxonomic classification via the QIIME 2 feature-classifier (Bokulich et al., 2018) with the sklearn technique. Taxonomic assignment was made from the Greengenes 13_8 database (DeSantis et al., 2006; based on 99% similarity of sequence data to the Greengenes database). Mitochondrial, chloroplast and unassigned ASVs were removed before the analysis.

Table 5.1. Description of PCR primer-pairs, sequences of forward and reverse primers and expected products. T_a is annealing temperature.

Primer pair	Forward and Reverse	T _a (°C)	Size (bp)	reference
Hap F1/ Hap R1	F: GTT CTT TCW TGA TTC TAT GMA R: CTC AWK CTT CCA TCT GCT G	48	348	Renault et al. (2000); Molloy et al. (2012)
Hap F1/Hap R3	F: GTT CTT TCW TGA TTC TAT GMA R: AKR HRT TCC TWG TTC AAG AYG A	48	348	Renault et al. (2000); Molloy et al. (2012)
SSU980/Hap R1	F: CGA AGA CGA TCA GAT ACC GTC GTA R: CTC AWK CTT CCA TCT GCT G	54	348	Renault et al., (2000); Molloy et al. (2012)
MSXA/MSXB	F: CGA CTT TGG CAT TAG GTT TCA GAC C R: ATG TGT TGG TGA CGC TAA CCG	59	573	Renault et al. (2000); Molloy et al. (2012)
<i>Vibrio</i> spp. F3/R3	F: CAA CAG AAG AAG CAC CGG CT R: CAC GCT TTC GCA TCT GAG TG	56	-	Albuixech-Martí et al. (2021a); Notaro et al. (2021); Kett et al. (in review)

3. Results

3.1. DNA quality and quantity of the CWCs

DNA quantity and quality (A260/A280 ratio) for paraffin-embedded tissues ranged between 2.2 to 11.1 ng/μl and 1.50 to 1.88 respectively.

DNA quantity and quality for Illumina sequencing samples ranged between 3.6 to 65.5 ng/μl and 1.79 to 1.99 respectively.

3.2. *Haplosporidia* spp. and *Vibrio* spp. polymerase chain reaction (PCR)

Neither *Haplosporidia* nor *Vibrio* spp. were detected in the two coral species screened by PCR using multiple primer pairs (Table 5.1).

3.3. Histology

The quality of the coral polyp tissues was optimal for histological analysis. Histological analysis did not reveal any *Haplosporidia*-like life stages (spores, plasmodia, single cells) in the cells or tissues of the coral samples. Pathological conditions associated with *Vibrio* spp. infection such as haemocyte accumulation in the connective tissues (McCleary and Henshilwood, 2015) were not observed in the samples. Sloughing was observed in 13.3% (2/15) of the coral.

RLOs were detected in the epidermal 33.3% (5/15) and gastrodermal tissues 6.7% (1/15) of the *L. pertusa* samples exclusively (Figure 5.2A and B). RLOs in this study were small, ellipsoid and round with eosinophilic inclusions or granules. Overall, 40% (6/15) of RLOs were detected in the polyp tissues that were screened, 26.7% (4/15) were observed in the south branch whereas 13.3% (2/15) were observed in the canyon head (Figure 5.3A). The intensity of RLOs identified in individual polyps was low (1 to 4 colonies per individual). The percent

prevalence of the unidentified cells was 26.7% (4/15) with 20% (3/15) detected in the south branch and 6.7% (1/15) in the canyon head while none were detected in corals from the canyon flank (Figure 5.3A and B).

Generally, the size of the unidentified cells ranged between 4.06 to 19.25 μm in diameter with an average size of 7.94 μm . Both bi- and multinucleate cells with a well bounded membrane were recorded. The unidentified binucleate cell (Figure 5.2C) was slightly ellipsoid in shape. An unidentified cell (most likely a macroborer belonging to the genus *Sipunculus*), was detected in *L. pertusa* 0.07% (1/15) at the canyon head exclusively. This organism showed an irregular shape that was blunt at one end (posterior) and tapered at the other (anterior), with a slight depression on both sides of the trunk (and what seem to be a groove at the ventral side close to the anterior) (Figure 5.2D). The *L. pertusa* cells associated with the burrow and the acellular space that surrounds the unidentified macroborer suggests growth of the borer (Figure 5.2D).

3.4. *Haplosporidia* spp. and *Vibrio* spp. Illumina sequencing

The sequences obtained from the Illumina sequencing of *L. pertusa* was identified as an uncultured Rickettsiales bacterium and *Haplosporidium* sp. endosymbiont. *Vibrio shilonii* 0.03% (1/7) was detected in a single *L. pertusa* individual from the canyon head using Illumina sequencing. The uncultured Rickettsiales bacterium 0.03% (1/7) and *Haplosporidium* sp. endosymbiont 0.03% (1/7) were detected in a single *L. pertusa* individual from the canyon head.

Sequences obtained from the Illumina sequencing of *L. pertusa* had E-value of 2e-63, 100% Query Coverage and 99.29% Percent Identity to the uncultured Rickettsiales bacterium and

Haplosporidium sp. endosymbiont AbFoot 16S RNA sequences in GenBank using BLAST analysis.

A total of 2,586,928 raw sequences yielded 529,513 effective tags for sequence analysis after processing and quality filtering of raw reads. The removal of unassigned, mitochondrial and chloroplast ASVs resulted in the least microbial taxa (18,151) being observed in *L. pertusa* in the canyon head (52°13.62616, 14°55.54294) whilst the highest microbial taxa (73,600) were detected in *M. oculata* in the canyon flank (51°58.39740, 15°02.52970). A total of 4,494 sequence variants with mean length of 190 were recorded, whilst a total of 522,608 microbial taxa were observed in the coral and non-coral samples following the removal of unassigned, mitochondrial and chloroplast ASVs. Corals contained 344,782 ASVs and non-corals 177,826 ASVs.

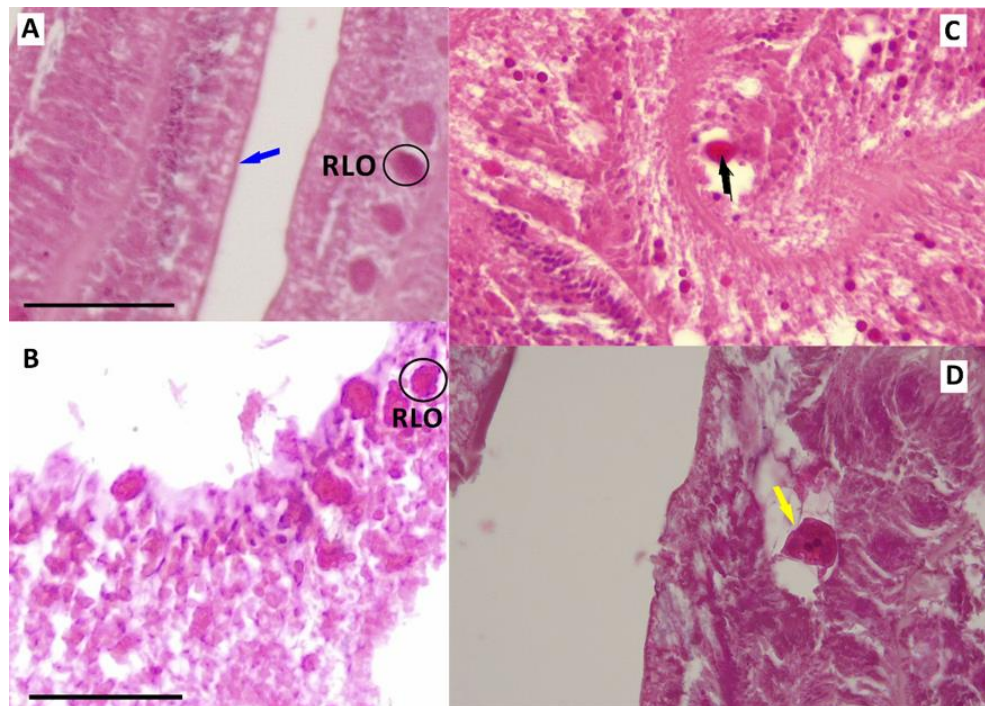


Figure 5.2. Histological observations of potentially harmful cells in *L. pertusa*. scale = 50 μ m: A) Rickettsiales-like organism in epithelial tissue, but without any visible pathology, B) Rickettsiales-like organism tissues without epithelium, C) unidentified binucleate cell, and D) unidentified macroborer. Black circle = Rickettsiales-like organism (RLOs); blue arrow = intact epithelial tissue; yellow arrow = unidentified macroborer; black arrow = unidentified binucleate cell.

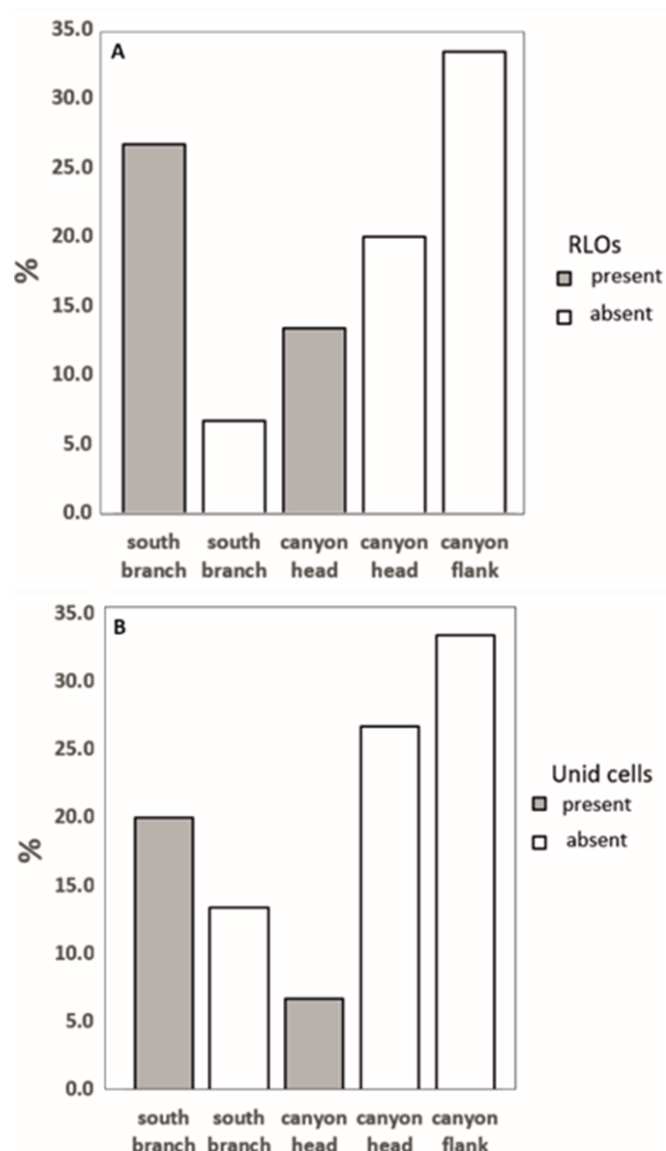


Figure 5.3. The percent prevalence of: A) Rickettsiales-like organisms, and B) unidentified cells. Unid cells = unidentified cells; RLOs = Rickettsiales-like organisms. Descriptive data analyses were used, with the percentage of absence or presence for all samples analysed in the canyon head, canyon flank and the south branch summing up to 100%. The data correspond to *Lophelia pertusa*.

4. Discussion

4.1. Tissue preservation, storage and DNA extraction

Generally, DNA extracted from Davidson-fixed paraffin embedded tissues that was used for standard PCR in this study showed DNA with low quality and quantity compared to DNA from ethanol-preserved tissues used for Illumina sequencing. As a result, the pathogen groups, RLOs and *Vibrio* spp., were not detected using DNA extracted from FFPE and standard PCR

but were detected using Illumina sequencing. DNA isolated from Davidson-fixed paraffin embedded tissues can result in failure in PCR amplification due to fragmentation of DNA for histological tissue preservation (Lynch et al., 2013; Ochoa et al., 2020). Also, the time and the conditions of tissue storage can affect DNA extraction and PCR amplification (Lynch et al., 2013). Different methods of DNA extractions can cause variations in DNA quality and quantity which in turn can greatly impact sequencing results (Mygind et al., 2003; Morgan et al., 2010).

4.2. Pathogen diversity and environmental factors

Pathogen diversity observed in this study was limited with two to three different pathogen groups (Illumina sequencing; RLOs and *Vibrio*) and (Histology and standard PCR; RLOs, macroborer and unidentified non-coral cells whose origin is unknown) being observed in *L. pertusa*, respectively. The low diversity of pathogens detected suggests that *L. pertusa* invests energy in an enhanced immune function, which is typical of slow-growing r-strategist organisms (Mydlarz et al., 2008; Palmer et al., 2010; Gavish et al., 2018), and may likely provide them with a reduced susceptibility to pathogen groups. Coral immunity is expressed when the energy allocation processes of the coral holobiont are used to expunge/fight pathogens and or parasitic associations whilst accepting useful microbes/mutualist for growth and survival (Gavish et al., 2018; Palmer, 2018). RLOs generally showed low intensity in the coral tissues and were most prevalent in the south branch of the PBC. Similarly, unidentified cells were most prevalent in the south branch whereas a single macroborer was detected in the canyon head. Although the *M. oculata* specimens were sampled near the *L. pertusa*, none of these organism groups were observed in those samples. Similarly, no Haplosporidia or *Vibrio* spp. were detected in this cold-water coral species. The two species of scleractinian corals exhibit different feeding strategies (Mortensen, 2001; Duineveld et al., 2007; Meistertzheim et

al., 2016) and this may be the reason why no potential pathogen was detected in *M. oculata*, since ingestion is a pathway for pathogen intake and subsequent infection (Lynch et al., 2007; Gavish et al., 2018). Additionally, the lack of potential pathogens in *M. oculata* can be attributed to the fewer *Madrepora* samples screened in this study because sample size is directly proportional to the probability of detecting a pathogen. *M. oculata* shows a narrower diet compared to *L. pertusa* (Mortensen, 2001; Meistertzheim et al., 2016), which may be limiting pathogen entry via ingestion.

Temperatures above 3 °C and salinities above 25 psu favour proliferation and a higher rate of infection of certain Haplosporidia respectively (Burreson and Ford, 2004; Albuixech-Martí et al., 2020). Haplosporidia were not detected in the two cold-water coral species from histological examinations and standard PCR in this study, even though the deep-sea mean temperature (9.3 °C) and salinity (36.3 psu) were optimal for the growth and infection of particular Haplosporidia species such as those belonging to the genus *Bonamia*. It is probable that local abiotic conditions on the high seas and in the deep sea such as current speed and sedimentation do not favour the development and retention of the Haplosporidia. Also, existing conditions may not have supported the growth and survival of a Haplosporidia intermediate host or vector that completes the life cycle of the pathogen. However, a negative histology or PCR result may not necessarily indicate the absence of Haplosporidia in the two deep sea coral species examined in this study. Screening for pathogens that are present at a low prevalence has been described as “looking for a needle in a haystack” even in near shore environments that are considered hot spots of infection. The probability of pathogen detection increases with the number of host specimens that are screened (Lynch et al., 2007; Albuixech-Martí et al., 2021b). Additionally, different diagnostic methods may yield different results (Lynch et al., 2013; Flannery et al., 2014) and although the extraction of DNA from FFPE samples can result

in fragmented DNA being screened, the expected product size for both PCRs used in this study were small enough to be amplified (Renault et al., 2000; Lynch et al., 2013). A recent study to detect an RNA virus infecting marine shrimp using DNA from Davidson-fixed paraffin embedded tissue showed that amplicon size of approx. 230 bp detected the virus in only 4/29 samples (Ochoa et al., 2020). However, at a reduced amplicon size of approx. 150 bp, most samples were successfully amplified (Ochoa et al., 2020), suggesting that reducing amplicon size of the *Haplosporidium* from approx. 350 bp in the present study to approx. 150 bp in the future may eliminate the possibility of failure in PCR amplification of DNA from FFPE samples due to DNA fragmentation. There is generally an inherent bias towards shorter amplicons in PCR reactions. In addition, latent, early or light Haplosporidia infections may be overlooked using both methods, as has been observed in other studies (Lynch et al., 2013; Flannery et al., 2014) i.e. the part of the tissue block that was sectioned and used for histology and subsequent PCR may not have been where the pathogen was localised in the tissues of the coral species, thus highlighting the need for more individuals from a colony to be screened. Also, it is important to note that older individuals with longer exposure to pathogen groups build up resilience/resistance over time (Albuixech-Martí et al., 2020). In the present study however, sequences obtained from the Illumina sequencing of *L. pertusa* was identified as a *Haplosporidium* sp. endosymbiont that is associated with the abalone *Haliotis iris*. Of importance, their presence in cold-water corals suggests that Haplosporidia can be transported from surface waters into deep seas.

Vibrio spp. are closely associated with chitin-containing organisms (e.g. copepods), which represent one of the most important environmental reservoirs of these bacteria. Copepods have been described from different deep-sea environments (Auel, 1999; Humes, 1987; Thistle and Eckman, 1990; Bode et al., 2017) and are a known food source for *L. pertusa* (Dodds et al.,

2009). *Vibrio* are associated with phytoplankton as well as aquatic plants and can also infect oysters at temperature ranges of 9 to 13°C and 19 to 20°C (Health and Welfare (AHAW), 2010; Vezzulli et al., 2016). No visible *Vibrio*-associated pathologies were observed nor were they amplified in the standard PCR. This might be due to the *Vibrio* spp. being present at a low prevalence and intensity or they may simply be absent in the coral tissues. More importantly, the mean temperatures and salinities in the PBC generally are unfavourable for *Vibrio* spp. growth (Banin et al., 2003).

Recent histopathological studies have described pathogenic RLOs in scleractinian corals (Klinges et al., 2019), which have been associated with oil contamination in deep sea waters (Simister et al., 2016). Sequences obtained from the Illumina sequencing of *L. pertusa* in this study was identified as an uncultured Rickettsiales bacterium and a Rickettsiae (an endosymbiont of *Haplosporidium* sp.) contained within the cytoplasm of Haplosporidia closely related to *Bonamia exitiosa*. This uncultured Rickettsiales bacterium has been associated with the Japanese spiky sea cucumber *Apostichopus japonicus*. These RLOs are thought to possess parasitic capabilities. RLOs are obligate pathogens that can infect many marine organisms and cause various degrees of pathologies in the tissues of infected species (Miller et al., 2014). The intensity of RLOs detected in this study was similar to infection intensities described in tropical corals from the Caribbean (Miller et al., 2014; Peters, 2014). In the present study, gastrodermal epithelial tissues appeared sloughed and lysed with vacuolations similar to observations that were made in RLOs associated infections of the staghorn coral *Acropora cervicornis* tissues (Miller et al., 2014). Sloughing is characterised by lost or loose epithelial cells while necrosis is characterised by vacuolisation and cell rupture (Quéré et al., 2015), and these pathologies can cause the death of the coral organism. However, not all the RLOs infected tissues showed such pathologies in this study.

The unidentified borer (most likely of the genus *Sipunculus*) in the present study can be an opportunistic coloniser and not necessarily a pathogen. Sipunculids are generally peanut-shaped, marine and have a wide range of habitats including the soft tissues of cold-water and tropical corals (Pancucci-Papadopoulou et al., 2014; Schulze and Kawauchi, 2021). Diseased, weakened tissues and/or acidified environment become vulnerable to invasion by borers (Quéré et al., 2015). Also, microborers are recognised agents of bioerosion in living tissues and can be the cause of diseases (Quéré et al., 2015). The acellular space detected around the borer in this study can be the result of chemical secretions of the borer on the surrounding *Lophelia* cells (Quéré et al., 2015).

The importance of the unidentified cells in the coral tissues were not determined as it was beyond the scope of the present studies. However, some organisms such as coccidia, ciliates and algae (although the cells detected in this study do not look similar) have been observed associated with diseased coral tissues and have been recognised to have capabilities that drive virulence or causes disease in the host (Galloway et al., 2007; Schulze and Kawauchi, 2021).

The disproportionate distribution of RLOs and unidentified cells in the coral samples is consistent with the amount of particulate organic matter (POM) concentration throughout the PBC. The concentration of particulates measured in the PBC was highest in the south branch and least in the canyon flank (Appah et al., 2020), making POM readily available for *Lophelia* in the south branch, which can be indicative of high particulate ingestion and subsequently high infection in the south branch (Bythell et al., 2002). Pathogens are borne on and transported by particulates to the deep sea (Simister et al., 2016), so it is probable that the observed particulates disproportionately transported RLOs and unidentified cells to the corals. However, the results

must be interpreted with caution as the total number of coral samples screened was constrained by the fragile and protected nature of these deep-water corals. Additionally, this survey was based on a once off sample, which may not have coincided with a high pathogen prevalence in the PBC. Certain near shore Haplosporidia species that infect other invertebrate species such as bivalves can be present year-round but do peak in particular months, which might be the cause for the lack of detection in the corals. Thus, future sampling to represent all seasons would be required to confirm this. Also, sampling and screening for pathogens in late spring (May) would be routinely used in the health surveys of marine invertebrates in near shore environments, however, this may not be the case for deep sea surveys and pathogen prevalence patterns may differ in this environment. For instance, deep-sea surveys for coral health studies by Hall-Spencer et al. (2007) were carried out in August 2003. As such it is important that these cold-water corals are continuously monitored with the aim of evaluating their health, pathogen diversity and prevalence, as well as growth and development. Additionally, further analysis of their immune function warrants investigation to provide more knowledge on slow-growing, long-lived organisms and their susceptibility, or lack of, to pathogen groups.

5. Conclusion

Despite the presence of RLOs and the low detection of *Vibrio* spp., Haplosporidia were not detected. *L. pertusa* and *M. oculata* in this isolated canyon, remote from direct terrestrial and anthropogenic influences, appeared healthy although slightly less so in the south branch where environmental stressors such as sedimentation may be higher. The overall health of these reef-forming cold-water corals is encouraging and suggests that under current environmental conditions these corals experience low pathogen diversity.

This study not only adds to the limited knowledge that is known on the pathogens of cold-water corals, but it also provides a baseline for future studies carried out at the PBC. This will be valuable as monitoring continues moving into the future in a changing marine environment.

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Additional Information

Raw sequence data used in this study can be accessed from the project link <https://www.ncbi.nlm.nih.gov/sra/PRJNA729568>

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Chapter 6

Conclusions, challenges and recommendations following investigations of the cold-water coral habitats (uPBC and wBMP) on the Irish Continental Shelf, NE Atlantic

1. Conclusions, challenges and recommendations

1.1. Conclusions

This thesis advances our knowledge and understanding of the dynamic interactive processes fundamental to geology, biology and/or ecology, hydrology and human activities that exist within cold-water coral habitats (uPBC and wBMP, designated as SACs) along the Irish continental margin in the northeast Atlantic, including submarine canyons. Since submarine canyons are features on the seafloor and are not isolated systems within the deep oceans, activities in and around the canyon affect processes in the canyon. The uPBC is a cold-water coral rich ecosystem with *L. pertusa* being the main framework-forming coral that can support high abundance of marine species and as a result, has been designated as a Special Area of Conservation (SAC) under the EU Habitat Directive (92/43/EEC). The slow growth rate of *L. pertusa* means that the ecosystems in canyons be managed and protected. Although deep-sea research is very expensive, the data collected for this study add to our limited knowledge and broadens our understanding of how natural and human-induced processes in the deep-sea ecosystem shape and organise benthic life, including providing baseline data for future studies that will be carried out in the PBC. Furthermore, the data collected, and analysis thereof is critical for the effective management and conservation of the cold-water coral habitats along the Irish margin.

The upper canyon-wide data collection provided sufficient data for the effective characterisation of benthic megafauna distribution and biodiversity in the uPBC. A high biodiversity was detected in the uPBC due to the presence of heterogeneous habitats. The substrates sediment, sediment & dropstone and bedrock, on the seafloor, constitutes non-reef habitats whereas the substrates live/dead coral and coral rubble comprises reef and rubble habitats. The prevailing water mass in the uPBC, the Eastern North Atlantic Water (ENAW), completely immerses the cold-water corals from about 500 – 1200 m water depth in the canyon. Terrain features (especially slope and depth) in the canyon and current velocities, ranging from a mean of 18.2 - 31.3 cm s⁻¹ in the head and the south branch respectively, also contribute to the high benthic diversity observed in the canyon. Benthic megafaunal distribution in the uPBC shows significant differences among the different site-locations namely canyon head, canyon flank and south branch. A total of 50.8% of the benthos were Cnidaria, 23.7% Echinodermata, 15.3% were Porifera with the remaining 10.2% belonging to the phylum Mollusca, with *Leiopathes glaberrima*, *Hexadella dedritifera*, *Cidaris cidaris* being the three most important species responsible for the compositional differences observed between habitats and site locations in the uPBC. Additionally, it was noted that non-reef habitats in submarine canyons are as important to biodiversity as are reef habitats, because of the high Shannon's diversity detected in non-reef habitats compared to coral reef and rubble habitats, although this observed difference was not significant. Percentage estimates of Shannon's diversity for non-coral and reef and rubble habitats were ($H'_{\text{non-reef}}=2.38$; $H'_{\text{reef and rubble}}=2.16$) and Pielou's evenness ($J'_{\text{non-reef}}=0.71$; $J'_{\text{reef and rubble}}=0.65$), respectively, whilst density estimates of Shannon's diversity for non-coral and reef and rubble habitats were ($H'_{\text{non-reef}}=1.72$; $H'_{\text{reef and rubble}}=1.14$) and Pielou's evenness ($J'_{\text{non-reef}}=0.54$; $J'_{\text{reef and rubble}}=0.43$), respectively. Usually, reef and rubble habitats are known to support high biodiversity. Here, non-reef habitats are observed to support high biodiversity because we are in a submarine canyon, which generally is a highly productive

system. The life strategies (e.g. feeding behaviour) of the benthic megafauna also contribute to the pattern of distribution that were seen in the uPBC.

Despite the high diversity of marine species associated with *L. pertusa* (ecological engineer) in the uPBC in this study, high current speeds affect high biodiversity as high flow speeds can bend *L. pertusa* backwards and alter food supply to the coral, inhibiting its growth as well as reducing/destroying *L. pertusa*'s capacity to form 3D structures that provide habitats for marine species. Environmental variables may be changing with climate change. In addition, anthropogenic stresses such as trawl fishing and marine litter threaten this important ecosystem. The composition of litter detected in these CWC-rich habitats suggests the expansion of anthropogenic activities into the CWCs' ecosystem, although the uPBC and the wBMP are SACs. Trawl fishing can remove the live coral reef structure and inadvertently end the engine of CWCs' reef growth and the biogenic reef cycle. Additionally, habitat use for megafauna (notably including fish spawning sites) become massively degraded. Marine litter carrying harmful microbes and pathogens can be transported to the CWCs' habitats and significantly impact the health, growth and survival of these corals, with plastics increasing the risk of coral diseases. Furthermore, macro and microplastics affect the ability of corals to capture food materials as they act as barriers to food supply with possible energy storage alteration that can reduce coral calcification as well as compromise CWCs reefs resilience and biodiversity.

Consequently, this study mapped the distribution and sources of marine litter in CWCs' habitats in the uPBC and wBMP as additional anthropogenic impacts. In the uPBC, a total of 62 litter items with 40%, 37% and 23% litter in the canyon flank, head and south branch, respectively, were identified whilst 49 (100%) were found in the northwest of the wBMP. The mean density of litter in the canyon head was 0.08 litter 100 m⁻¹, in the canyon flank was 0.45

litter 100 m^{-1} and in the south branch was $0.06\text{ litter } 100\text{ m}^{-1}$. Litter was unevenly distributed in the uPBC (80.7% fishing gear and 11.3% plastics) and the wBMP (55.1% plastics and 14.3% buoys), with fishing gear being the majority in the uPBC while plastic is most common litter in the wBMP. Large amount of energy is required to move litter on a relatively flat surface ($0 - 5^\circ$) compared to a steep slope ($>5^\circ$), given the large number of litter items that were observed between 600 - 800 m on gentle slopes than on steep slopes in the uPBC. The total distance of video transects where litter was observed in the uPBC was 52.96 km whilst the total distance of video transects that contained litter in the wBMP was 5.91 km. The sources of the litter items detected in the uPBC and the wBMP are most likely marine-based and land-based, respectively, due to the distance of both SACs from land. It is unclear if the observed fishing gear in the uPBC and wBMP may have drifted into them by deep-sea currents or were dumped before they were designated an SAC, as the SACs are closed to fishing. Additionally, the high percentage ($>60\%$) of vessels that are fishing while inside the SACs and the differences in the composition and abundance of litter between the SACs are concerning, as the SACs appear to offer limited protection to the coral habitats. Even more concerning is that more than 16% of vessels fishing while within the SACs are engaged in bottom trawling or destructive fishing activities. This suggests that the authorities involved in the management of the SACs may be under resourced or simply lack the motivation to carry out monitoring campaigns on the High Seas as it is capital intensive and difficult to undertake. It is also possible that fishermen simply flout the no fishing policy in these areas of conservation. To this effect, regular monitoring campaigns are advocated for and harsher punishment to vessels that are found fishing while inside the SACs. Interestingly, litter introduced into the CWCs' habitats in the uPBC and the wBMP provided surfaces for attachment for the scleractinian coral *Lophelia* and crinoids.

As marine litter can transport harmful microbes and or pathogenic spores (e.g. Haplosporidian spores) to the CWCs' habitats and significantly impacting their health, growth and survival, including increasing the risk of coral diseases, the present study characterised CWCs' microbiome to determine how it affects the general health of the CWCs. The different microbial organisms that symbiotically interact with the CWCs host constitute a coral holobiont, with the holobiont working together to maintain the normal functioning and health as well as the growth and survival of the CWCs. Biotic factors and abiotic conditions can stress the CWC holobiont, compromising the CWCs functioning and physiology, leading to coral diseases and or mortality. As such, this study, to characterise the microbial composition of the CWCs holobiont.

The analysis showed that the taxa Thaumarchaeota, Rhodobacterales and Rhizobiales which forms part of the CWCs holobiont and identified to be associated with nutrition and nitrogen cycling activities in CWCs were observed in relatively high abundances. Furthermore, it was realised that microbes (mean $\pm$ standard error) that are associated with the cold-water corals (7.08 ± 0.79) are more diverse than those residing in the sediment (6.51 ± 0.29) and ambient water (5.50 ± 0.77), although no divergence ($H = 2.19$, $P = 0.33$) in the bacterial and archaeal composition was observed among the corals, sediment and the water samples. Additionally, the relative proportion of bacteria among the groups of samples was not significant ($J' = 1.66$, $P = 0.43$) and varied from 0.79 ± 0.07 in corals, 0.78 ± 0.02 in sediment and 0.72 ± 0.08 in water samples. Furthermore, between the two CWC species, *L. pertusa* generally showed high diversity compared to *M. oculata*. The results highlight the importance of a high energy environment in the distribution and composition of microbial diversity among corals, water and sediment samples. This is particularly true for the uPBC where current speeds of up to 114 cm s^{-1} have been recorded.

Additionally, screening for potential coral pathogens such as Haplosporidia, *Vibrio* spp. and RLOs as part of the coral holobiont to determine the health status of the CWCs revealed that the corals in the uPBC appear to be in good health, with low Haplosporidia, RLOs and *Vibrio* sp. infections. The low diversity of pathogens detected suggest that *L. pertusa* invests energy in an enhanced immune function, which is typical of slow growing organisms, and thus provides them with a reduced susceptibility to pathogen groups. It is noted that food availability and the feeding strategies employed by the scleractinian corals can influence their exposure to pathogens. In the south branch of the uPBC high concentrations of POM ($2,612 \mu\text{g l}^{-1}$) corresponded with high pathogen infections in *L. pertusa* (unidentified cells = 20%, RLOs = 26.7%) whilst relatively low concentrations of POM ($1,065 \mu\text{g l}^{-1}$) in the canyon head corresponded with low pathogen infection (unidentified cells = 6.7%, RLOs = 13.3%) in *L. pertusa*. Moreover, the number of colonies screened is directly proportional to the detection of a pathogen group in a coral sample, suggesting the importance of large samples in health surveys. Extreme conditions exist in the deep ocean and because few studies have looked at deep-sea species, there is a greater chance of finding novel pathogens. Combining methods is important to yield results in CWCs' health screening. For instance, applying molecular techniques alone (standard PCR and Illumina sequencing) did not reveal any pathologies associated with the infected pathogens on the CWCs tissues but histology could be used to determine both the infected pathogens and their associated pathologies. Using Illumina sequencing, *Vibrio shilonii* 0.03% was detected in a single *L. pertusa* individual from the canyon head whilst uncultured rickettsiales bacterium 0.03% and *Haplosporidium* sp. endosymbiont 0.03% were detected in a single *L. pertusa* individual from the canyon head. Histology techniques were used to detect in total 40% of RLOs in the CWCs tissues with 26.7% observed in the south branch and 13.3% observed in the canyon head, including pathologies

such as sloughing that was observed in 13.3% of the coral. The findings of this research also highlight how environmental conditions experienced by deep sea organisms and their ecology may be limiting pathogen diversity and prevalence.

1.2. Challenges and recommendations

In this thesis, I show that, despite the many threats and pressures such as marine litter pollution, sedimentation and bottom trawling, the CWCs on the Irish margin, at present, appear to be resilient, well adapted to the deep sea environment and show a high biodiversity. However, there is the need for continued monitoring due to global warming and increasing anthropogenic pressures in these CWC ecosystems because the continuous trend of climate change and human pressures such as marine litter and fisheries as well as pathogen infections/coral diseases can compromise CWCs reefs resilience and biodiversity in the future.

- A. The CWCs' health status must further be researched into because certain shallow water pathogens that affect anthozoans and other marine invertebrates are being detected in the deep ocean. There is the need for preparation for any outbreak of rare diseases and novel pathogens in the CWCs in the future to facilitate proper management and conservation of the corals. The thesis provides background data on CWCs' health and sets the stage for further research to be conducted on CWCs' health and pathogen screening in relation to habitat mapping in the Porcupine Bank Canyon and probably the Belgica Mound Province.
- B. In this study, ~350 bp primers designed to amplify Haplosporidia DNA in the tissue samples failed due to the difficulty in amplifying fragmented DNA preserved in

paraffin embedded tissues, suggesting that designing smaller size primers of ~150 bp can yield result.

- C. Research surveys will have to be carried out to represent all seasons and areas if possible and must involve screening of large coral colonies as pathogen studies generally require a large sample size to increase the probability of identifying novel pathogens, if there are any.
- D. Research to monitor the changing pH of the seawater in the CWC habitats on the Irish margin is important as the detection of a macroborer may indicate a slightly acidic environment facilitating dissolution of coral skeletons. *Lophelia pertusa* and *Madrepora oculata*, the two dominant scleractinian CWCs on the Irish-Atlantic margin, incorporate aragonitic calcium carbonate into their skeletal framework, making them vulnerable to ocean acidification due to climate change.
- E. The fragmentation of plastic litter to various degrees was observed in this study. Micro or nanoplastics can be produced because of fragmentation/biodegradation. CWCs are filter feeders and cannot discriminate food materials from microplastics, which can interfere with the reproductive and feeding processes of the corals when ingested. Hence, future research on microplastics in the reef environment is suggested.
- F. It is unclear whether the finding that biodiversity was higher in non-reef habitat than reef and rubble habitat would hold true if all size classes (e.g. meiofauna, zoo/phytoplanktons, etc.) in the uPBC, and not just megafauna, were characterised. As such, it is suggested that a study involving characterising all size classes, including

megafauna be carried out in the future to get a holistic and a true understanding of the biodiversity associated with CWCs in the PBC.

Appendices

Appendix 1

Research cruises embarked on during PhD

CE19014 – Monitoring Changes in Submarine Canyon Coral Habitats II

CE19008 – Monitoring Changes in Submarine Canyon Coral Habitats I

CE18011 – Controls of Cold-Water Coral Habitat in Submarine Canyons II

Appendix 2

Travel grants

Appah, J.K.M was awarded a travel grant from the Marine Institute in October 2019

Appah, J.K.M was awarded a travel grant from the Marine Institute in November 2018

Appendix 3

Publications

Appah, J.K.M., Kileen, O., Lim, A., O’Riordan, R., O’Reilly, L. & Wheeler, A .J. (2022). Accumulation of marine litter in cold-water coral habitats: a comparative study of two Irish Special Areas of Conservation, NE Atlantic. *Marine Pollution Bulletin* 180, p.113764. <https://doi.org/10.1016/j.marpolbul.2022.113764>

Appah, J.K.M., Lynch, S.A., Lim, A., O Riordan, R., O’Reilly, L., de Oliviera, L. & Wheeler, A.J. (2022). A health survey of the reef forming scleractinian cold-water corals *Lophelia pertusa* and *Madrepora oculata* in a remote submarine canyon on the European continental margin, NE Atlantic. *Journal of Invertebrate Pathology* 192, p.107782. <https://doi.org/10.1016/j.jip.2022.107782>

Appah, J.K.M., Lim, A., Harris, K., O’Riordan, R., O’Reilly, L. & Wheeler, A.J. (2020). Are non-coral reef habitats as important to benthic diversity and composition as coral reef habitats in submarine canyons? A rich analysis of organismal distribution controls in the upper Porcupine Bank Canyon, NE Atlantic. *Frontiers in Marine Science* 7, 571820. <https://doi.org/10.3389/fmars.2020.571820>.

O'Reilly, L., Lim, A., Titschack, J., Moore, N., O'Connor, O.J., Appah, J., Fentimen, R., Butschek, F., Harris, K., Vennemann, T., Wheeler, A.J. (2022). Using novel methods to track British and Irish Ice Sheet dynamics since Late Pleistocene, along the west Porcupine Bank, NE Atlantic. *Quaternary Science Reviews* 284, p.107463. <https://doi.org/10.1016/j.quascirev.2022.107463>

Appendix 4

Conferences/workshops/seminars attended during the PhD

Appah J. K. M., Lim, A., Harris K., O'Riordan R., O'Reilly L., Wheeler A. J. 2018. Environmental controls of benthic megafauna distributions in the cold-water coral-rich habitat of the upper Porcupine Bank Canyon, NE Atlantic. INCISE Shenzhen, China.

Appah J. K. M., Lim, A., Harris K., O'Riordan R., O'Reilly L., Wheeler A. J. 2020. Environmental controls of benthic megafauna distributions in the cold-water coral-rich habitat of the upper Porcupine Bank Canyon, NE Atlantic. Irish Geosciences Early Career Symposium (iGEO, Online).

Appah J. K. M., Lim, A., Harris K., O'Riordan R., O'Reilly L., Wheeler A. J. 2020. Environmental controls of benthic megafauna distributions in the cold-water coral-rich habitat of the upper Porcupine Bank Canyon, NE Atlantic. Marine Geological & Biological Mapping (GeoHab, Online).

Appah J. K. M., Lim, A., Harris K., O'Riordan R., O'Reilly L., Wheeler A. J. 2020. Environmental controls of benthic megafauna distributions in the cold-water coral-rich habitat of the upper Porcupine Bank Canyon, NE Atlantic. International Coral Reef Symposium (ICRS, Online).

Appah J. K. M. 2021-ZY4020 Millport Online: Temperate Marine Biology (Field Course, Online).

Appah J. K. M., Kileen, O., Lim, A., O'Riordan R., O'Reilly L., Wheeler A. J. 2021. Marine litter accumulation in cold-water coral habitats: a comparative study of two Irish Special Areas of Conservation, NE Atlantic. Irish Geological Research Meeting (IGRM, Online).

INCISE Working Groups 2021. Litter in submarine canyons. International Network for Submarine Canyon Investigation and Scientific Exchange (INCISE, Online).

Appah J. K. M., Lynch, S. A., Lim, A., O’Riordan R., O’Reilly L., de Oliveira L., Wheeler A. J. 2021. Health screening of the reef forming scleractinian cold-water corals *Lophelia pertusa* and *Madrepora oculata* in a remote submarine canyon on the European continental margin, NE Atlantic (INCISE, Online).

Appah J. K. M., Lynch, S. A., Lim, A., O’Riordan R., O’Reilly L., de Oliveira L., Wheeler A. J. 2021. Health screening of the reef forming scleractinian cold-water corals *Lophelia pertusa* and *Madrepora oculata* in a remote submarine canyon on the European continental margin, NE Atlantic. Deep Sea Biology Society (DSBS, Online).

Appendix 5

Conferences/workshops/seminars presentation contributions made during the PhD

Lim, A., Conti, L., Appah, J., Harris, K., O’Reilly, L., Wheeler, A.J. 2018. Multiscale mapping and monitoring to understand habitat drivers and variability within the Porcupine Bank Canyon, NE Atlantic [Poster Presentation]. 4th International Submarine Canyon Symposium (INCISE2018), Shenzhen, China, 5-7th November, 2018.

Lim, A., Conti, L., O’Reilly, L., Appah, J. K. M., Harris, K., Wheeler, A.J. 2018. Mapping, modelling and monitoring key processes and controls on cold-water coral habitats in submarine canyons (MMMonKey_Pro) [Oral Presentation]. IGRM. Dublin, 1st March, 2019.

Lim, A., Conti, L., O’Reilly, L., Appah, J. K. M., Harris, K., Wheeler, A.J. 2018. Mapping, modelling and monitoring key processes and controls on cold-water coral habitats in submarine canyons [Poster Presentation]. Geoscience 2018. Dublin 6th November, 2018.

Lim, A., Conti, L., O’Reilly, L., Appah, J. K. M., Harris, K., Wheeler, A.J. 2018. Mapping, modelling and monitoring key processes and controls on cold-water coral habitats in submarine canyons [Poster Presentation]. Atlantic Ireland 2018. Dublin 6th November, 2018.

Lim, A., O’Reilly, L., Harris, K., Appah, J., Price, D., Titschack, J., O’Connor, O.J., Macedo, L., Summers, G., Conti, L., Wheeler, A. 2019. A health-check of Irish cold-water coral habitats: insights from an integrated study of the Porcupine Bank Canyon, Offshore Ireland. Atlantic Ireland, Dublin, October 2019.

O’Reilly, L., Lim, A., Titschack, J., Moore, N., O’Connor, O.J., Harris, K., Appah, J., Venneman, Wheeler, A.J. 2021. Temporal variability of cold-water coral habitats from the Porcupine Bank Canyon, NE Atlantic, INCISE, Gibraltar, On-line talk.

O’Reilly, L., Lim, A., Titschack, J., O’Connor, O.J., Harris, K., Appah, J., Wheeler, A. J. 2019. Temporal variability of cold-water coral habitats from the Porcupine Bank Canyon NE Atlantic. 34th IAS Meeting of Sedimentology, Rome, September 2019.

O'Reilly, L., Lim, A., Titschack, J., O'Connor, O.J., Harris, Kim, Appah, J., Wheeler, A. 2018. Temporal variability of cold-water coral habitats from the Porcupine Bank Canyon, NE Atlantic, using ROV-vibrocoring, CT-scanning and PSA: preliminary results. [Poster Presentation]. IGRM. Dublin, 1st March, 2018.

O'Reilly, L., Lim, A., Titschack, J., O'Connor, O.J., Harris, Kim, Appah, J., Wheeler, A. 2018. Temporal variability of cold water coral habitats from the Porcupine Bank Canyon, NE Atlantic, using ROV-vibrocoring, CT-scanning and PSA: preliminary results [Poster Presentation]. 4th International Submarine Canyon Symposium (INCISE2018). Shenzhen, China, 5-7th November, 2018.

Wheeler, A.J., Lim, A., Appah, J., Harrison, K., O'Connor O.J., O'Reilly, L. 2018. Mapping, modelling and monitoring key processes and controls on cold-water coral habitats in submarine canyons (MMMonKey_Pro) [Oral Presentation]. 4th International Submarine Canyon Symposium (INCISE2018). Shenzhen, China, 5-7th November, 2018.

Wheeler, A.J., O'Reilly, L., Lim, A., Appah, J., Oliveira, L.M, Conti, L., O'Connor 2020. Mapping, modelling and monitoring key processes and controls on cold-water coral habitats in submarine canyons (MMMonKey_Pro). Geoscience 2020. 20th November. On-line.

Appendix 6

Courses completed, research training undertaken and supplemental data on quadrat number, seabed terrain features, substrate type, habitats and site locations

Table A.1. Courses completed during the PhD

Courses Completed	Course Code
Research integrity	PG6015
Geographic Information System	GL6025
Project management course	FS6635
R for biologists	BL6024
Gave lectures for Temperate Marine Biology (Field Course, Online)	ZY4020

Table A.2 . Research training undertaken during PhD

Research Training	Date
Sediment trap training	20/08/2018
Malvern mastersizer training	21/08/2018
ADCP training	05/09/2018
MBES training survey	26-27/11/2018

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-1000	42.6100	323.3519	-0.8146	-978.7700	B	non-coral	flank
QUAD-1001	43.4342	320.0058	-0.6994	-978.7700	B	non-coral	flank
QUAD-1002	43.4342	320.0058	-0.6994	-978.7700	B	non-coral	flank
QUAD-1008	42.8609	303.9597	2.2907	-978.7700	B	non-coral	flank
QUAD-1010	37.9923	301.7541	2.9734	-919.1625	B	non-coral	flank
QUAD-1021	59.0176	278.6333	1.6232	-745.7606	B	non-coral	flank
QUAD-1022	60.4629	282.8117	-2.2583	-745.7606	B	non-coral	flank
QUAD-1023	60.5008	285.4223	-1.3745	-745.7606	B	non-coral	flank
QUAD-1024	61.6641	287.0815	1.7883	-745.7606	B	non-coral	flank
QUAD-1025	59.2343	289.8997	4.4161	-745.7606	B	non-coral	flank
QUAD-1026	59.2343	289.8997	4.4161	-745.7606	B	non-coral	flank
QUAD-1027	59.2343	289.8997	4.4161	-745.7606	B	non-coral	flank
QUAD-1028	59.2343	289.8997	4.4161	-745.7606	B	non-coral	flank
QUAD-1042	50.1809	281.1566	-3.6973	-966.9012	B	non-coral	flank
QUAD-1043	50.1809	281.1566	-3.6973	-966.9012	B	non-coral	flank
QUAD-1044	50.1809	281.1566	-3.6973	-966.9012	B	non-coral	flank
QUAD-1045	50.1809	281.1566	-3.6973	-966.9012	B	non-coral	flank
QUAD-1046	50.1809	281.1566	-3.6973	-966.9012	B	non-coral	flank
QUAD-1047	50.1809	281.1566	-3.6973	-966.9012	B	non-coral	flank
QUAD-1049	50.1809	281.1566	-3.6973	-966.9012	B	non-coral	flank
QUAD-1050	50.1809	281.1566	-3.6973	-966.9012	B	non-coral	flank
QUAD-1051	50.1809	281.1566	-3.6973	-966.9012	B	non-coral	flank
QUAD-1052	50.1809	281.1566	-3.6973	-966.9012	B	non-coral	flank
QUAD-1053	50.1809	281.1566	-3.6973	-966.9012	B	non-coral	flank
QUAD-1054	50.1809	281.1566	-3.6973	-966.9012	B	non-coral	flank
QUAD-1055	50.1809	281.1566	-3.6973	-966.9012	B	non-coral	flank
QUAD-1056	50.1809	281.1566	-3.6973	-966.9012	B	non-coral	flank
QUAD-1057	50.1809	281.1566	-3.6973	-966.9012	B	non-coral	flank
QUAD-1058	50.1809	281.1566	-3.6973	-966.9012	B	non-coral	flank
QUAD-1060	50.1809	281.1566	-3.6973	-966.9012	B	non-coral	flank
QUAD-1091	32.3757	321.5204	-0.1168	-934.5756	B	non-coral	flank
QUAD-1092	35.1984	328.3582	-0.1495	-934.5756	B	non-coral	flank
QUAD-1093	36.9729	325.6086	1.8822	-934.5756	B	non-coral	flank
QUAD-1094	34.8443	328.3894	2.6227	-814.9813	B	non-coral	flank
QUAD-1095	32.5223	321.7971	1.5340	-814.9813	B	non-coral	flank
QUAD-1096	24.5969	334.4269	0.0756	-814.9813	B	non-coral	flank
QUAD-1097	30.6113	345.8564	-5.6989	-814.9813	B	non-coral	flank
QUAD-1098	38.6981	345.2842	0.4272	-814.9813	B	non-coral	flank
QUAD-1099	38.6981	345.2842	0.4272	-814.9813	B	non-coral	flank
QUAD-1100	37.9747	349.0419	-0.6577	-814.9813	B	non-coral	flank
QUAD-1101	38.6981	345.2842	0.4272	-814.9813	B	non-coral	flank
QUAD-1102	37.9313	342.7389	2.0499	-814.9813	B	non-coral	flank
QUAD-1103	34.1102	337.9141	1.1262	-814.9813	B	non-coral	flank
QUAD-1104	31.9759	341.7852	1.5339	-799.3481	B	non-coral	flank
QUAD-1105	30.8852	349.9457	1.2294	-761.7075	B	non-coral	flank
QUAD-1106	30.2752	346.1635	1.1873	-761.7075	B	non-coral	flank
QUAD-1107	32.4073	352.3296	1.7027	-799.3481	B	non-coral	flank
QUAD-1108	35.0257	348.4457	1.4917	-799.3481	B	non-coral	flank
QUAD-1109	32.9908	334.4308	1.3795	-799.3481	B	non-coral	flank
QUAD-1110	32.9908	334.4308	1.3795	-799.3481	B	non-coral	flank
QUAD-1111	32.9908	334.4308	1.3795	-799.3481	B	non-coral	flank
QUAD-1112	32.9908	334.4308	1.3795	-799.3481	B	non-coral	flank
QUAD-1113	32.9908	334.4308	1.3795	-799.3481	B	non-coral	flank
QUAD-1114	32.4938	347.3558	-0.6106	-921.8431	B	non-coral	flank
QUAD-1115	34.9990	349.3606	-1.0300	-921.8431	B	non-coral	flank
QUAD-1116	34.9990	349.3606	-1.0300	-921.8431	B	non-coral	flank
QUAD-1117	34.9990	349.3606	-1.0300	-799.3481	B	non-coral	flank
QUAD-1120	31.9147	357.4410	-0.0873	-799.3481	B	non-coral	flank
QUAD-1121	31.0389	1.2007	-2.2861	-799.3481	B	non-coral	flank
QUAD-1122	35.9175	7.8998	-2.1105	-799.3481	B	non-coral	flank

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-1123	32.0148	355.6189	-2.7338	-799.3481	B	non-coral	flank
QUAD-1133	37.7056	307.2064	3.7328	-1026.2262	B	non-coral	flank
QUAD-1139	31.6113	292.8021	3.1877	-975.0831	B	non-coral	flank
QUAD-1149	46.0722	287.6937	-1.4377	-771.0963	B	non-coral	flank
QUAD-1151	48.4946	281.9803	-0.1498	-771.0963	B	non-coral	flank
QUAD-1152	48.5872	282.5700	-0.1673	-771.0963	B	non-coral	flank
QUAD-1154	49.8530	285.9186	-0.6422	-771.0963	B	non-coral	flank
QUAD-1155	49.8530	285.9186	-0.6422	-771.0963	B	non-coral	flank
QUAD-1156	49.5767	290.5868	0.0728	-771.0963	B	non-coral	flank
QUAD-1157	49.7042	297.6430	0.0562	-771.0963	B	non-coral	flank
QUAD-1158	49.7042	297.6430	0.0562	-771.0963	B	non-coral	flank
QUAD-1159	54.4460	306.0280	0.1482	-741.4037	B	non-coral	flank
QUAD-1160	54.4460	306.0280	0.1482	-741.4037	B	non-coral	flank
QUAD-1161	56.5224	304.7397	2.8234	-741.4037	B	non-coral	flank
QUAD-1162	54.1030	310.5555	2.4822	-741.4037	B	non-coral	flank
QUAD-1163	54.1030	310.5555	2.4822	-741.4037	B	non-coral	flank
QUAD-1164	54.1030	310.5555	2.4822	-741.4037	B	non-coral	flank
QUAD-1165	49.2933	318.7376	6.3395	-741.4037	B	non-coral	flank
QUAD-1167	43.1931	328.7267	3.2783	-741.4037	B	non-coral	flank
QUAD-336	1.5881	151.4207	-0.1021	-786.8438	B	non-coral	head
QUAD-596	32.0198	337.8999	-2.3146	-687.4257	B	non-coral	head
QUAD-597	40.4528	328.7032	12.2537	-687.4257	B	non-coral	head
QUAD-598	18.3952	330.3830	1.0359	-687.4257	B	non-coral	head
QUAD-742	29.2728	332.9915	-1.0092	-1168.0475	B	non-coral	flank
QUAD-750	30.8349	334.0219	0.1504	-1093.6606	B	non-coral	flank
QUAD-754	32.8602	332.7759	-0.7999	-1073.1312	B	non-coral	flank
QUAD-763	23.7842	336.8431	1.9740	-1006.6256	B	non-coral	flank
QUAD-764	22.8253	341.0707	0.6671	-992.2650	B	non-coral	flank
QUAD-771	30.7748	328.3729	-0.4205	-944.8269	B	non-coral	flank
QUAD-773	31.4825	327.3053	-0.6110	-932.3019	B	non-coral	flank
QUAD-774	31.2598	331.3672	0.7401	-932.3019	B	non-coral	flank
QUAD-775	29.7803	336.7556	-0.8782	-932.3019	B	non-coral	flank
QUAD-776	31.0540	338.5447	0.0372	-932.3019	B	non-coral	flank
QUAD-777	31.7524	336.6716	-0.8495	-932.3019	B	non-coral	flank
QUAD-778	30.5881	337.3880	1.2300	-932.3019	B	non-coral	flank
QUAD-779	26.3692	339.8789	0.3683	-932.3019	B	non-coral	flank
QUAD-780	25.7923	338.9031	-0.1590	-932.3019	B	non-coral	flank
QUAD-787	31.1901	351.7174	-0.8950	-856.4131	B	non-coral	flank
QUAD-789	31.1327	349.8527	0.1288	-856.4131	B	non-coral	flank
QUAD-790	29.1106	357.3574	0.5038	-856.4131	B	non-coral	flank
QUAD-791	29.1106	357.3574	0.5038	-856.4131	B	non-coral	flank
QUAD-792	28.3573	5.2502	0.1511	-856.4131	B	non-coral	flank
QUAD-793	28.3573	5.2502	0.1511	-856.4131	B	non-coral	flank
QUAD-794	28.8828	3.9102	0.5146	-858.4431	B	non-coral	flank
QUAD-795	28.8565	1.1453	-0.8085	-858.4431	B	non-coral	flank
QUAD-796	30.2207	4.7878	-0.2628	-858.4431	B	non-coral	flank
QUAD-797	31.2492	1.4906	0.6982	-858.4431	B	non-coral	flank
QUAD-799	31.8805	3.6154	-0.1185	-858.4431	B	non-coral	flank
QUAD-800	31.3818	5.7911	1.7884	-858.4431	B	non-coral	flank
QUAD-801	30.2493	9.6729	0.2684	-858.4431	B	non-coral	flank
QUAD-802	30.3823	11.8573	-0.2644	-797.2087	B	non-coral	flank
QUAD-805	32.2570	9.8354	-1.4406	-797.2087	B	non-coral	flank
QUAD-808	28.0116	13.4902	-0.6522	-797.2087	B	non-coral	flank
QUAD-810	26.8309	11.5357	-0.2950	-797.2087	B	non-coral	flank
QUAD-811	27.3218	14.3475	-0.4539	-795.3850	B	non-coral	flank
QUAD-815	30.6431	359.6440	-0.6544	-795.3850	B	non-coral	flank
QUAD-816	30.8288	0.4367	0.2100	-795.3850	B	non-coral	flank
QUAD-817	27.3474	2.6205	1.4350	-795.3850	B	non-coral	flank
QUAD-818	26.6664	4.3848	1.4194	-795.3850	B	non-coral	flank
QUAD-819	23.0094	357.8728	0.1605	-758.0750	B	non-coral	flank

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-820	23.0094	357.8728	0.1605	-758.0750	B	non-coral	flank
QUAD-821	20.0468	345.0279	0.0495	-758.0750	B	non-coral	flank
QUAD-822	21.1531	344.6589	-0.0778	-758.0750	B	non-coral	flank
QUAD-823	22.9095	339.0344	-0.3128	-754.0200	B	non-coral	flank
QUAD-825	21.6877	340.2860	-0.2756	-754.0200	B	non-coral	flank
QUAD-826	22.6990	344.3377	-0.7783	-754.0200	B	non-coral	flank
QUAD-827	22.1819	343.1681	0.0133	-754.0200	B	non-coral	flank
QUAD-828	18.3045	344.0541	0.6771	-754.0200	B	non-coral	flank
QUAD-830	14.3406	348.4085	0.6006	-754.0200	B	non-coral	flank
QUAD-831	11.4409	359.0895	0.6790	-749.2475	B	non-coral	flank
QUAD-832	4.0853	4.1593	1.0234	-749.2475	B	non-coral	flank
QUAD-833	2.0519	33.9053	0.5283	-735.3868	B	non-coral	flank
QUAD-854	37.4691	301.2531	0.8045	-974.6287	B	non-coral	flank
QUAD-862	41.4269	282.2676	2.8704	-928.6212	B	non-coral	flank
QUAD-869	43.4826	300.3975	2.7310	-776.6256	B	non-coral	flank
QUAD-871	40.7057	301.1700	4.0238	-776.6256	B	non-coral	flank
QUAD-908	34.6649	308.6671	0.6578	-836.6244	B	non-coral	flank
QUAD-920	45.7786	308.9124	0.3356	-727.5988	B	non-coral	flank
QUAD-921	44.9094	310.2880	-0.0250	-727.5988	B	non-coral	flank
QUAD-985	34.8954	323.3887	-1.4884	-772.7225	B	non-coral	flank
QUAD-996	40.5814	316.7511	0.4041	-1020.0956	B	non-coral	flank
QUAD-048	4.1860	126.2782	-1.0323	-939.3325	DL	coral	head
QUAD-051	3.6398	162.3313	0.0789	-926.4288	DL	coral	head
QUAD-068	22.9880	272.4224	-1.5867	-879.9375	DL	coral	head
QUAD-071	27.5385	272.5189	-0.5555	-879.9375	DL	coral	head
QUAD-073	17.0206	267.5636	2.9455	-860.5081	DL	coral	head
QUAD-074	10.1121	138.9783	-0.5623	-876.4156	DL	coral	head
QUAD-1039	21.7272	331.8756	6.8994	-703.6687	DL	coral	flank
QUAD-1040	24.8364	359.3466	3.7927	-703.6687	DL	coral	flank
QUAD-1041	6.0929	271.1705	7.0434	-703.6687	DL	coral	flank
QUAD-1144	46.0079	285.8620	-1.8907	-923.0400	DL	coral	flank
QUAD-1150	47.2965	283.7234	-2.1411	-771.0963	DL	coral	flank
QUAD-1153	48.5872	282.5700	-0.1673	-771.0963	DL	coral	flank
QUAD-1166	49.2933	318.7376	6.3395	-741.4037	DL	coral	flank
QUAD-1539	38.1020	274.5674	3.4744	-709.1325	DL	coral	south
QUAD-1542	30.9650	302.6974	1.1366	-709.1325	DL	coral	south
QUAD-1546	47.7961	347.8103	0.2123	-699.9163	DL	coral	south
QUAD-1625	23.0398	213.6913	1.6622	-936.1006	DL	coral	south
QUAD-1639	28.6267	243.7477	-0.9468	-807.1144	DL	coral	south
QUAD-1640	31.2867	245.2354	0.0323	-807.1144	DL	coral	south
QUAD-1641	31.7416	247.3591	-0.0787	-807.1144	DL	coral	south
QUAD-1642	34.7592	243.3466	0.0000	-793.6182	DL	coral	south
QUAD-1643	34.7592	243.3466	0.0000	-793.6182	DL	coral	south
QUAD-1644	36.3524	237.4280	-0.0001	-793.6182	DL	coral	south
QUAD-1645	31.1680	229.0449	3.9060	-793.6182	DL	coral	south
QUAD-1646	31.1680	229.0449	3.9060	-793.6182	DL	coral	south
QUAD-1647	27.8849	52.3794	1.9844	-797.2800	DL	coral	south
QUAD-1648	33.5799	48.8663	-2.1822	-815.4138	DL	coral	south
QUAD-1649	29.5147	91.7502	0.8567	-792.7750	DL	coral	south
QUAD-1650	28.5133	70.1698	0.7854	-814.7957	DL	coral	south
QUAD-1680	28.6607	239.2920	-3.7488	-755.6707	DL	coral	south
QUAD-1681	24.1137	235.6106	1.5043	-755.6707	DL	coral	south
QUAD-1682	28.8134	238.9284	0.2845	-726.0956	DL	coral	south
QUAD-1683	26.6308	233.2608	3.2012	-726.0956	DL	coral	south
QUAD-1684	20.9980	218.7012	-1.1354	-726.0956	DL	coral	south
QUAD-1685	9.1105	129.7436	6.5878	-726.0956	DL	coral	south
QUAD-1699	3.9504	54.6448	-1.0645	-800.0475	DL	coral	south
QUAD-1701	1.7166	229.5490	0.5356	-800.0475	DL	coral	south
QUAD-1702	1.3140	239.6311	2.3721	-796.8638	DL	coral	south
QUAD-1712	4.8172	332.4544	0.1567	-785.1887	DL	coral	south

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-1718	27.4655	260.4955	-0.2901	-732.7850	DL	coral	south
QUAD-1722	26.9696	259.3293	-0.0010	-705.8538	DL	coral	south
QUAD-1723	27.6350	258.7474	-0.2622	-705.8538	DL	coral	south
QUAD-1727	15.2838	196.5910	3.8999	-696.0325	DL	coral	south
QUAD-1728	19.7030	161.1421	1.1312	-696.0325	DL	coral	south
QUAD-1730	35.3992	177.3585	1.1823	-695.1487	DL	coral	south
QUAD-1731	33.5410	184.4535	-0.2823	-695.1487	DL	coral	south
QUAD-1733	34.7001	202.2912	-0.8729	-670.5950	DL	coral	south
QUAD-1740	34.6698	203.5046	-2.2789	-652.7100	DL	coral	south
QUAD-1741	33.4671	201.1844	1.1479	-652.7100	DL	coral	south
QUAD-1744	14.6708	70.5133	-0.0178	-706.0944	DL	coral	south
QUAD-1767	25.2034	317.7199	5.4568	-667.9637	DL	coral	south
QUAD-1768	18.9168	355.9143	4.2300	-667.9637	DL	coral	south
QUAD-1769	18.6287	1.7874	3.4178	-655.7581	DL	coral	south
QUAD-1770	16.3158	17.8348	1.4677	-655.7581	DL	coral	south
QUAD-1774	5.8154	315.5633	-0.2166	-655.7313	DL	coral	south
QUAD-248	29.9807	276.0827	0.3200	-1053.9325	DL	coral	head
QUAD-249	29.8370	269.6092	-0.0899	-1053.9325	DL	coral	head
QUAD-250	30.8243	274.4530	1.7532	-1053.9325	DL	coral	head
QUAD-252	31.0638	272.1913	-0.0001	-1053.9325	DL	coral	head
QUAD-727	24.9371	299.5910	0.7194	-694.7238	DL	coral	flank
QUAD-729	17.0262	268.4095	3.3005	-692.9500	DL	coral	flank
QUAD-730	17.3565	314.4258	2.9385	-689.0669	DL	coral	flank
QUAD-731	4.6931	34.4950	2.4512	-680.8444	DL	coral	flank
QUAD-957	23.0079	313.3937	-0.4124	-957.2687	DL	coral	flank
QUAD-970	19.2209	325.7094	-1.0356	-917.9419	DL	coral	flank
QUAD-022	7.2852	231.3565	0.3239	-991.5875	R	coral	head
QUAD-023	17.1955	231.0240	-1.6611	-991.5875	R	coral	head
QUAD-024	20.9723	232.5778	-0.1744	-976.9069	R	coral	head
QUAD-025	20.8648	228.6756	1.7534	-976.9069	R	coral	head
QUAD-026	25.7588	222.8000	0.1561	-976.9069	R	coral	head
QUAD-027	25.7588	222.8000	0.1561	-976.9069	R	coral	head
QUAD-028	26.2571	224.5733	0.9056	-976.9069	R	coral	head
QUAD-029	27.4599	227.4262	0.2007	-942.1488	R	coral	head
QUAD-030	26.1017	220.6095	-0.8855	-942.1488	R	coral	head
QUAD-031	30.6812	222.3389	-0.6149	-942.1488	R	coral	head
QUAD-032	31.0140	217.8013	-0.1766	-918.8181	R	coral	head
QUAD-033	32.0063	220.7269	1.9455	-904.7813	R	coral	head
QUAD-034	30.0092	212.0424	2.3066	-904.7813	R	coral	head
QUAD-035	22.4528	226.9135	0.8978	-904.7813	R	coral	head
QUAD-036	25.1863	229.6501	0.0826	-880.7575	R	coral	head
QUAD-037	25.2500	241.5147	0.9778	-880.7575	R	coral	head
QUAD-038	28.0219	242.1605	-0.1089	-880.7575	R	coral	head
QUAD-039	30.9053	243.2378	-0.2445	-880.7575	R	coral	head
QUAD-040	28.4113	250.2936	2.1949	-880.7575	R	coral	head
QUAD-041	20.0308	253.3378	1.7405	-856.8387	R	coral	head
QUAD-042	19.8964	250.0867	1.0528	-856.8387	R	coral	head
QUAD-043	15.5733	276.6158	2.0644	-856.8387	R	coral	head
QUAD-044	12.8287	281.4524	3.1251	-856.8387	R	coral	head
QUAD-045	8.8760	98.2329	-0.1511	-925.6269	R	coral	head
QUAD-046	7.1527	107.4411	-0.2390	-843.4898	R	coral	head
QUAD-047	5.9155	108.9937	-0.0255	-837.3554	R	coral	head
QUAD-049	2.9254	168.0814	0.0000	-939.3325	R	coral	head
QUAD-050	3.2877	165.3805	0.0790	-926.2744	R	coral	head
QUAD-052	3.8346	182.8499	-0.5023	-926.4288	R	coral	head
QUAD-053	5.7120	204.0601	-0.0001	-926.4288	R	coral	head
QUAD-063	17.0797	273.5350	-0.0212	-891.0294	R	coral	head
QUAD-065	18.3524	291.7017	0.0001	-899.1944	R	coral	head
QUAD-066	20.6489	291.6446	-0.8411	-899.1944	R	coral	head
QUAD-067	22.0676	282.9879	-1.0089	-879.9375	R	coral	head

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-069	24.9150	271.9877	0.0001	-879.9375	R	coral	head
QUAD-070	25.2385	273.8316	-0.1222	-879.9375	R	coral	head
QUAD-072	25.4335	268.9489	1.4222	-860.5081	R	coral	head
QUAD-1003	43.4950	314.3043	-0.0100	-978.7700	R	coral	flank
QUAD-1004	44.8213	305.5507	-0.3289	-978.7700	R	coral	flank
QUAD-1005	44.8213	305.5507	-0.3289	-978.7700	R	coral	flank
QUAD-1006	45.9232	306.0003	1.7155	-978.7700	R	coral	flank
QUAD-1007	42.8609	303.9597	2.2907	-978.7700	R	coral	flank
QUAD-1009	39.9309	309.9200	2.0305	-978.7700	R	coral	flank
QUAD-1011	36.8410	305.5869	2.3556	-803.1150	R	coral	flank
QUAD-1012	38.5496	294.8833	-1.9006	-803.1150	R	coral	flank
QUAD-1013	38.4161	291.4994	-1.1661	-803.1150	R	coral	flank
QUAD-1014	43.7154	287.7653	-1.2711	-803.1150	R	coral	flank
QUAD-1015	46.8493	283.8234	-0.1028	-803.1150	R	coral	flank
QUAD-1016	46.8493	283.8234	-0.1028	-803.1150	R	coral	flank
QUAD-1017	49.0907	279.9403	-6.4744	-803.1150	R	coral	flank
QUAD-1018	53.2671	277.2733	-0.2194	-803.1150	R	coral	flank
QUAD-1019	55.4928	275.8675	0.7461	-803.1150	R	coral	flank
QUAD-1020	56.7736	277.7072	-0.2094	-803.1150	R	coral	flank
QUAD-1029	59.2343	289.8997	4.4161	-745.7606	R	coral	flank
QUAD-1030	53.1258	290.2960	7.1282	-745.7606	R	coral	flank
QUAD-1031	50.3434	292.0641	2.6727	-745.7606	R	coral	flank
QUAD-1032	46.0376	290.5215	5.7927	-755.3050	R	coral	flank
QUAD-1033	38.4688	295.4550	2.5861	-716.2382	R	coral	flank
QUAD-1034	32.2279	286.6200	1.7660	-716.2382	R	coral	flank
QUAD-1035	33.5249	289.7368	2.3812	-716.2382	R	coral	flank
QUAD-1036	31.2959	285.7100	2.1777	-716.2382	R	coral	flank
QUAD-1037	33.3069	287.5582	0.5679	-716.2382	R	coral	flank
QUAD-1038	33.8774	303.4125	1.4266	-716.2382	R	coral	flank
QUAD-1048	50.1809	281.1566	-3.6973	-966.9012	R	coral	flank
QUAD-1059	50.1809	281.1566	-3.6973	-966.9012	R	coral	flank
QUAD-1061	50.1809	281.1566	-3.6973	-966.9012	R	coral	flank
QUAD-1062	54.2379	280.2577	-2.8943	-966.9012	R	coral	flank
QUAD-1063	57.1425	281.3520	-6.3356	-966.9012	R	coral	flank
QUAD-1064	57.1425	281.3520	-6.3356	-895.2888	R	coral	flank
QUAD-1065	60.9562	284.4732	-5.9099	-895.2888	R	coral	flank
QUAD-1066	63.0598	290.1782	-1.8907	-895.2888	R	coral	flank
QUAD-1067	63.4403	297.7479	1.7511	-895.2888	R	coral	flank
QUAD-1068	60.3777	314.7619	1.7012	-895.2888	R	coral	flank
QUAD-1069	60.5156	316.0398	2.4262	-895.2888	R	coral	flank
QUAD-1070	60.3971	314.3750	4.2610	-853.6569	R	coral	flank
QUAD-1071	55.4546	306.1750	2.9183	-853.6569	R	coral	flank
QUAD-1072	48.6862	301.3966	3.2605	-853.6569	R	coral	flank
QUAD-1073	34.5746	295.3338	0.5599	-853.6569	R	coral	flank
QUAD-1074	32.5941	285.8781	-0.2983	-853.6569	R	coral	flank
QUAD-1075	34.4037	286.6506	-1.3090	-853.6569	R	coral	flank
QUAD-1076	35.3826	288.6143	-0.4260	-853.6569	R	coral	flank
QUAD-1077	34.3933	291.0238	1.3533	-793.1006	R	coral	flank
QUAD-1078	32.4694	289.1317	0.0590	-793.1006	R	coral	flank
QUAD-1079	32.3987	289.0174	0.0349	-793.1006	R	coral	flank
QUAD-1080	22.3364	319.5570	-0.3901	-995.0244	R	coral	flank
QUAD-1081	22.5847	320.6517	-0.2188	-995.0244	R	coral	flank
QUAD-1082	22.5847	320.6517	-0.2188	-995.0244	R	coral	flank
QUAD-1083	22.5847	320.6517	-0.2188	-995.0244	R	coral	flank
QUAD-1084	22.3364	319.5570	-0.3901	-995.0244	R	coral	flank
QUAD-1085	22.3364	319.5570	-0.3901	-995.0244	R	coral	flank
QUAD-1088	27.1466	324.5542	-0.6517	-939.5656	R	coral	flank
QUAD-1089	30.2891	315.7361	1.7406	-939.5656	R	coral	flank
QUAD-1090	33.0032	313.0304	2.2811	-939.5656	R	coral	flank
QUAD-1124	36.5117	358.8622	-3.8956	-792.8869	R	coral	flank

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-1127	30.2686	345.9398	-2.0712	-792.8869	R	coral	flank
QUAD-1129	30.8266	334.5079	-2.8516	-754.1650	R	coral	flank
QUAD-1132	32.2202	329.9217	0.2911	-745.3775	R	coral	flank
QUAD-1134	34.8804	294.3096	2.5682	-1026.2262	R	coral	flank
QUAD-1135	32.6358	301.4301	1.7296	-984.4763	R	coral	flank
QUAD-1136	34.6033	268.7647	1.5483	-975.0831	R	coral	flank
QUAD-1137	33.5039	274.8239	2.5333	-975.0831	R	coral	flank
QUAD-1138	31.7571	283.6032	3.5990	-975.0831	R	coral	flank
QUAD-1140	34.6827	289.0995	0.8079	-975.0831	R	coral	flank
QUAD-1141	37.7955	292.9958	3.0494	-923.0400	R	coral	flank
QUAD-1142	40.1638	293.2727	-0.7851	-923.0400	R	coral	flank
QUAD-1143	42.9042	290.7473	-2.7231	-923.0400	R	coral	flank
QUAD-1145	45.1725	290.8968	-2.0071	-923.0400	R	coral	flank
QUAD-1146	46.5265	286.6591	-0.8334	-923.0400	R	coral	flank
QUAD-1251	14.4348	235.1438	0.0001	-875.6887	R	coral	south
QUAD-129	6.5416	249.8882	-1.0011	-1053.9325	R	coral	head
QUAD-1293	12.5139	278.1740	1.1355	-793.0044	R	coral	south
QUAD-1294	16.4614	293.7225	-0.8678	-780.2037	R	coral	south
QUAD-1295	18.8554	286.6958	0.0001	-780.2037	R	coral	south
QUAD-1296	17.8976	295.2755	-0.7089	-761.3868	R	coral	south
QUAD-1297	18.6386	285.1925	-0.8145	-760.8488	R	coral	south
QUAD-1298	16.2651	290.9141	0.2266	-760.8488	R	coral	south
QUAD-1299	16.0591	311.0850	1.1974	-760.8488	R	coral	south
QUAD-130	7.1909	249.5031	-1.8024	-1053.9325	R	coral	head
QUAD-1300	20.6300	318.8784	-0.8825	-738.5356	R	coral	south
QUAD-1301	15.7139	307.8700	-0.4489	-738.5356	R	coral	south
QUAD-1302	21.0458	287.2180	0.2219	-738.5356	R	coral	south
QUAD-1303	22.3111	304.4085	-0.0956	-698.9894	R	coral	south
QUAD-1306	24.9025	318.6169	0.5944	-698.9894	R	coral	south
QUAD-1307	21.1276	326.7668	0.0001	-692.5375	R	coral	south
QUAD-1308	17.7497	336.6330	1.5273	-692.5375	R	coral	south
QUAD-131	9.5999	243.4345	-0.0831	-1053.9325	R	coral	head
QUAD-132	9.9062	254.9364	0.9764	-1053.9325	R	coral	head
QUAD-133	6.4783	334.1570	0.6145	-1053.9325	R	coral	head
QUAD-134	3.2839	321.5629	-1.6658	-1053.9325	R	coral	head
QUAD-135	10.0806	231.7548	-1.3470	-1053.9325	R	coral	head
QUAD-136	10.0806	231.7548	-1.3470	-1053.9325	R	coral	head
QUAD-138	6.7254	250.9142	0.0000	-1053.9325	R	coral	head
QUAD-139	6.7973	300.3768	1.5121	-1053.9325	R	coral	head
QUAD-140	8.2816	266.5370	-1.0513	-1053.9325	R	coral	head
QUAD-141	7.8196	244.7616	-0.0001	-1053.9325	R	coral	head
QUAD-142	6.2446	243.9166	0.5190	-1053.9325	R	coral	head
QUAD-143	8.2258	201.2520	-1.3603	-1053.9325	R	coral	head
QUAD-144	8.9556	217.4515	0.5415	-1053.9325	R	coral	head
QUAD-145	3.8071	233.6586	-0.3833	-1053.9325	R	coral	head
QUAD-1455	7.4332	302.3027	0.7233	-1034.2737	R	coral	south
QUAD-146	8.1299	253.1420	-0.7408	-1053.9325	R	coral	head
QUAD-147	4.8784	238.6292	1.7612	-1053.9325	R	coral	head
QUAD-1476	10.1151	294.2763	-0.6667	-965.7081	R	coral	south
QUAD-1477	11.9378	291.1810	-0.5244	-965.7081	R	coral	south
QUAD-1478	10.9149	300.0850	-0.1400	-965.7081	R	coral	south
QUAD-1479	11.0529	293.0648	0.2300	-965.7081	R	coral	south
QUAD-1480	9.3430	285.4668	-0.6699	-956.0925	R	coral	south
QUAD-1481	10.1138	272.0482	1.4501	-956.0925	R	coral	south
QUAD-1482	6.8224	298.9983	0.6022	-956.0925	R	coral	south
QUAD-1483	7.4375	298.0678	-0.8167	-946.9269	R	coral	south
QUAD-1484	10.8000	297.6945	0.4576	-946.9269	R	coral	south
QUAD-1485	7.5691	302.1417	-0.4905	-946.9269	R	coral	south
QUAD-1486	9.2141	293.6102	-0.9023	-937.3057	R	coral	south
QUAD-1487	9.0393	289.8236	0.0527	-937.3057	R	coral	south

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-1488	8.3653	299.1796	0.7429	-937.3057	R	coral	south
QUAD-1489	12.5601	296.3872	-1.5516	-937.3057	R	coral	south
QUAD-149	1.8809	254.4969	0.3026	-1053.9325	R	coral	head
QUAD-1490	19.6721	256.4226	0.3063	-925.8794	R	coral	south
QUAD-1491	30.3223	276.4204	0.8674	-925.8794	R	coral	south
QUAD-1492	24.1861	280.5126	-0.9802	-925.8794	R	coral	south
QUAD-1493	27.4145	273.7387	-2.6943	-925.8794	R	coral	south
QUAD-1494	27.4145	273.7387	-2.6943	-925.8794	R	coral	south
QUAD-1495	30.6069	264.9651	0.4510	-925.8794	R	coral	south
QUAD-1496	30.5291	255.7609	0.3057	-884.4594	R	coral	south
QUAD-1497	31.1590	250.0850	0.5245	-884.4594	R	coral	south
QUAD-1498	29.4293	249.1200	2.4698	-884.4594	R	coral	south
QUAD-1499	27.1074	252.7392	2.0779	-884.4594	R	coral	south
QUAD-150	9.7820	211.0061	-0.7922	-1053.9325	R	coral	head
QUAD-1500	25.0107	255.7015	3.6456	-884.4594	R	coral	south
QUAD-1501	24.9427	255.2567	0.8990	-884.4594	R	coral	south
QUAD-1502	26.7605	253.7893	1.2400	-884.4594	R	coral	south
QUAD-1503	25.3578	252.3944	1.2756	-884.4594	R	coral	south
QUAD-1504	21.4981	255.4155	1.5555	-862.4056	R	coral	south
QUAD-1505	19.2352	307.3917	2.7379	-862.4056	R	coral	south
QUAD-1506	20.0039	314.3107	1.1022	-862.4056	R	coral	south
QUAD-1507	21.4333	315.8600	-0.8178	-862.4056	R	coral	south
QUAD-1508	22.6046	313.3022	-0.1954	-862.4056	R	coral	south
QUAD-1509	20.6995	301.4384	1.7878	-862.4056	R	coral	south
QUAD-1510	25.3882	282.5004	-1.9667	-839.6669	R	coral	south
QUAD-1511	29.3297	271.4845	0.0001	-839.6669	R	coral	south
QUAD-1512	18.9974	247.8345	2.8522	-839.6669	R	coral	south
QUAD-1513	17.3278	267.8469	-0.1789	-839.6669	R	coral	south
QUAD-1514	19.2073	283.1558	0.8043	-839.6669	R	coral	south
QUAD-1515	21.7238	292.1867	1.9767	-839.6669	R	coral	south
QUAD-1516	23.1895	299.9531	1.6843	-809.7781	R	coral	south
QUAD-1517	20.5644	286.6089	3.4011	-809.7781	R	coral	south
QUAD-1518	16.0524	309.0439	3.9301	-809.7781	R	coral	south
QUAD-1519	22.7916	348.2905	0.6179	-809.7781	R	coral	south
QUAD-152	4.4346	244.9239	0.6367	-1053.9325	R	coral	head
QUAD-1520	25.8698	343.8407	-0.7345	-809.7781	R	coral	south
QUAD-1521	28.2659	345.2612	1.9667	-785.9163	R	coral	south
QUAD-1522	27.7530	334.8852	0.0000	-818.5287	R	coral	south
QUAD-1523	25.6244	325.5833	-0.9921	-818.5287	R	coral	south
QUAD-1524	24.7720	322.9492	-1.1404	-818.5287	R	coral	south
QUAD-1525	23.2027	309.0142	2.5785	-799.5006	R	coral	south
QUAD-1526	20.1341	317.2896	1.2096	-799.5006	R	coral	south
QUAD-1527	25.4888	296.7996	-0.9113	-799.5006	R	coral	south
QUAD-1528	24.6620	286.9756	-0.2056	-799.5006	R	coral	south
QUAD-1529	24.7800	287.1047	0.0890	-799.5006	R	coral	south
QUAD-153	6.5912	209.8751	-1.5966	-1053.9325	R	coral	head
QUAD-1530	24.1916	289.7594	-0.9244	-799.5006	R	coral	south
QUAD-1531	23.4549	283.4592	0.1010	-778.1688	R	coral	south
QUAD-1532	19.5857	256.2154	0.0000	-778.1688	R	coral	south
QUAD-1533	21.9507	256.0978	-0.9132	-778.1688	R	coral	south
QUAD-1534	24.3038	257.2717	-0.0724	-778.1688	R	coral	south
QUAD-1535	24.5930	255.2735	-2.2789	-727.1056	R	coral	south
QUAD-1536	28.9160	243.6597	-1.2589	-727.1056	R	coral	south
QUAD-1537	30.2000	254.9784	-2.2356	-730.2025	R	coral	south
QUAD-1538	38.1136	269.6753	1.3712	-730.2025	R	coral	south
QUAD-154	10.4950	214.8624	0.0000	-1053.9325	R	coral	head
QUAD-1540	32.3802	286.5163	1.4211	-709.1325	R	coral	south
QUAD-1541	32.1467	293.2014	0.3165	-709.1325	R	coral	south
QUAD-1543	33.5420	317.4725	0.0001	-709.1325	R	coral	south
QUAD-1544	37.2022	328.6099	1.0544	-709.1325	R	coral	south

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-1545	35.7629	349.5429	-0.0544	-699.3031	R	coral	south
QUAD-1547	25.8943	345.1429	-4.3800	-699.9163	R	coral	south
QUAD-1548	9.4596	344.7326	-2.9401	-699.9163	R	coral	south
QUAD-1549	26.9432	180.0876	4.3200	-697.0675	R	coral	south
QUAD-155	9.2549	235.8386	1.0178	-1053.9325	R	coral	head
QUAD-1550	18.3918	172.9747	0.0000	-697.0675	R	coral	south
QUAD-1551	8.7811	94.4758	3.3821	-697.0675	R	coral	south
QUAD-1552	29.5059	18.3922	-2.7022	-692.7769	R	coral	south
QUAD-1553	20.7848	337.6094	-0.2568	-692.7769	R	coral	south
QUAD-1554	20.1942	323.5871	0.0000	-682.7188	R	coral	south
QUAD-1555	16.6112	314.6529	-0.0001	-682.7188	R	coral	south
QUAD-1556	16.9176	321.4554	0.4889	-682.7188	R	coral	south
QUAD-1557	17.9055	286.6463	-0.0511	-670.8031	R	coral	south
QUAD-1558	17.9055	286.6463	-0.0511	-670.8031	R	coral	south
QUAD-1559	17.9055	286.6463	-0.0511	-670.8031	R	coral	south
QUAD-156	14.1889	232.1176	-0.1444	-1053.9325	R	coral	head
QUAD-1560	22.8965	297.1136	-0.8989	-670.8031	R	coral	south
QUAD-1561	24.4929	306.1808	0.5456	-670.8031	R	coral	south
QUAD-1562	22.2954	308.3955	0.9633	-670.8031	R	coral	south
QUAD-1563	17.6609	305.5982	-0.4177	-670.8031	R	coral	south
QUAD-1564	19.4263	297.2765	-2.2777	-670.8031	R	coral	south
QUAD-1565	22.7508	299.0214	0.8467	-652.2687	R	coral	south
QUAD-1566	22.5388	309.6583	-0.5322	-652.2687	R	coral	south
QUAD-1567	23.1113	302.2049	0.0000	-652.2687	R	coral	south
QUAD-1568	22.7410	290.6867	-1.4311	-652.2687	R	coral	south
QUAD-1569	25.1903	281.3539	-1.7322	-652.2687	R	coral	south
QUAD-157	12.4386	228.0216	2.1356	-1053.9325	R	coral	head
QUAD-1570	26.9303	279.5943	-0.0001	-612.6231	R	coral	south
QUAD-1571	27.6343	281.5819	-0.2400	-612.6231	R	coral	south
QUAD-1572	29.9193	278.9639	0.0000	-612.6231	R	coral	south
QUAD-1573	31.4611	277.6126	-0.1722	-612.6231	R	coral	south
QUAD-1574	33.7797	274.5194	-1.6044	-619.3037	R	coral	south
QUAD-1575	34.5862	270.0647	0.7756	-619.3037	R	coral	south
QUAD-1576	33.2479	267.0989	1.3433	-584.3669	R	coral	south
QUAD-1577	31.2490	265.9153	0.3022	-584.3669	R	coral	south
QUAD-1578	30.5884	267.4252	0.4510	-584.3669	R	coral	south
QUAD-1579	32.2212	278.3936	1.8870	-584.3669	R	coral	south
QUAD-158	5.5501	241.3410	2.0366	-1053.9325	R	coral	head
QUAD-1580	31.0170	267.5309	-0.7316	-584.3669	R	coral	south
QUAD-1581	27.7612	259.0244	-1.3028	-584.3669	R	coral	south
QUAD-1582	24.6922	253.8027	0.1471	-566.9631	R	coral	south
QUAD-1583	22.1173	256.5583	0.9079	-566.9631	R	coral	south
QUAD-1584	17.9270	265.8541	1.1923	-566.9631	R	coral	south
QUAD-1585	2.8153	317.6333	-1.3488	-693.4313	R	coral	south
QUAD-1586	3.1615	288.2888	0.0001	-693.4313	R	coral	south
QUAD-1587	3.8495	298.3428	-1.1400	-692.6225	R	coral	south
QUAD-1588	4.0014	299.5117	1.7255	-692.6225	R	coral	south
QUAD-1597	6.0542	277.7955	0.9697	-1051.6450	R	coral	south
QUAD-160	16.7813	227.1275	-0.5036	-1053.9325	R	coral	head
QUAD-1603	12.5066	286.3997	-4.9313	-1035.2262	R	coral	south
QUAD-1604	20.9274	288.1219	-0.0052	-1035.2262	R	coral	south
QUAD-1606	9.6856	229.1117	4.3524	-1035.2262	R	coral	south
QUAD-1607	24.8899	261.6071	4.6654	-1026.5881	R	coral	south
QUAD-1608	31.2283	231.7126	0.0000	-989.4037	R	coral	south
QUAD-1609	41.3668	240.5757	1.1178	-989.4037	R	coral	south
QUAD-161	14.6670	194.1242	1.3027	-1053.9325	R	coral	head
QUAD-1610	39.6184	233.3097	3.0701	-989.4037	R	coral	south
QUAD-1611	15.0092	260.1815	12.7455	-989.4037	R	coral	south
QUAD-1612	6.4709	124.8461	5.8634	-989.4037	R	coral	south
QUAD-1613	21.6103	181.0507	1.5466	-968.5331	R	coral	south

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-1614	17.8311	208.9742	-1.5011	-968.5331	R	coral	south
QUAD-1615	17.2748	229.1542	-0.1456	-968.5331	R	coral	south
QUAD-1616	18.9126	238.9085	-2.0490	-968.5331	R	coral	south
QUAD-1617	23.7309	241.2980	-2.0155	-968.5331	R	coral	south
QUAD-1618	26.8883	232.0264	0.3667	-946.3419	R	coral	south
QUAD-1619	27.6955	237.5763	-0.2000	-946.3419	R	coral	south
QUAD-162	11.4135	193.0493	-0.1444	-1053.9325	R	coral	head
QUAD-1620	27.4352	236.3048	0.0022	-946.3419	R	coral	south
QUAD-1621	26.7966	230.6198	0.2356	-946.3419	R	coral	south
QUAD-1622	24.4303	220.7646	0.1057	-936.1006	R	coral	south
QUAD-1623	25.1736	217.0730	-0.5557	-936.1006	R	coral	south
QUAD-1624	25.7894	214.5498	-0.1667	-936.1006	R	coral	south
QUAD-1626	20.8035	194.6490	3.0790	-936.1006	R	coral	south
QUAD-1627	26.3514	182.0631	-0.9000	-926.5894	R	coral	south
QUAD-1628	30.4587	175.1852	-1.3766	-926.5894	R	coral	south
QUAD-1629	27.7459	198.1785	-1.9044	-915.7175	R	coral	south
QUAD-163	11.7507	190.0285	0.0099	-1053.9325	R	coral	head
QUAD-1630	24.4880	203.7276	-2.4168	-901.3087	R	coral	south
QUAD-1631	18.7126	224.7116	0.9773	-901.3087	R	coral	south
QUAD-1632	22.3134	244.7600	0.0000	-879.2031	R	coral	south
QUAD-1633	22.7437	252.6277	-0.9513	-879.2031	R	coral	south
QUAD-1634	24.8959	250.2984	-0.5722	-879.2031	R	coral	south
QUAD-1635	28.1289	251.5052	-3.1536	-864.7662	R	coral	south
QUAD-1636	31.7768	270.1483	-3.9177	-864.7662	R	coral	south
QUAD-1637	32.0614	279.4579	-6.3828	-864.7662	R	coral	south
QUAD-1638	49.6557	271.1792	-10.1357	-807.1144	R	coral	south
QUAD-165	16.7593	189.9081	-2.6965	-1053.9325	R	coral	head
QUAD-1651	17.6844	60.4781	-0.0001	-852.3663	R	coral	south
QUAD-1652	17.1720	64.3700	0.0234	-852.3663	R	coral	south
QUAD-1653	6.0909	65.8768	-0.3455	-865.3937	R	coral	south
QUAD-1654	4.7646	134.0684	-0.4044	-870.7444	R	coral	south
QUAD-1655	4.7908	14.0410	0.2177	-870.7444	R	coral	south
QUAD-1658	6.2243	348.3544	0.5967	-874.5613	R	coral	south
QUAD-1659	6.9613	357.1311	-0.7122	-874.5613	R	coral	south
QUAD-166	13.7973	200.2164	1.2222	-1053.9325	R	coral	head
QUAD-1660	7.5891	343.5224	-2.0768	-870.0756	R	coral	south
QUAD-1661	7.3303	316.5399	0.2344	-870.0756	R	coral	south
QUAD-1662	5.7050	345.1293	0.6401	-870.0756	R	coral	south
QUAD-1663	8.8333	354.0179	-0.9178	-865.6356	R	coral	south
QUAD-1664	10.6709	339.2196	1.1181	-865.6356	R	coral	south
QUAD-1665	13.8323	314.3399	4.4547	-865.6356	R	coral	south
QUAD-1669	13.6096	284.0609	-0.1989	-841.9594	R	coral	south
QUAD-1670	18.0478	260.2230	-2.0334	-841.9594	R	coral	south
QUAD-1671	25.4720	249.1639	0.0000	-841.9594	R	coral	south
QUAD-1672	27.1627	246.2077	-0.4857	-841.9594	R	coral	south
QUAD-1673	24.0676	237.3872	-0.9567	-816.3694	R	coral	south
QUAD-1674	30.1521	244.7940	2.7756	-816.3694	R	coral	south
QUAD-1675	23.0434	258.2987	4.4880	-785.3318	R	coral	south
QUAD-1676	22.7767	240.2204	-4.9686	-785.3318	R	coral	south
QUAD-1677	45.4545	244.6967	7.0740	-785.3318	R	coral	south
QUAD-1678	20.1175	269.9270	4.7994	-785.3318	R	coral	south
QUAD-1679	19.3248	224.1242	4.6655	-755.6707	R	coral	south
QUAD-168	18.4235	197.4119	0.5010	-1053.9325	R	coral	head
QUAD-1686	16.0653	37.0058	0.4801	-786.6613	R	coral	south
QUAD-1687	7.8340	115.7973	-0.0001	-795.4188	R	coral	south
QUAD-1688	4.9982	132.4255	0.0000	-795.4188	R	coral	south
QUAD-1689	4.5035	117.4375	0.1155	-795.4188	R	coral	south
QUAD-169	18.2179	209.3082	0.0001	-1053.9325	R	coral	head
QUAD-1690	4.7082	118.4840	0.3278	-795.4188	R	coral	south
QUAD-1691	4.4790	122.5903	-0.4733	-798.6807	R	coral	south

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-1692	3.9129	173.0012	-0.6800	-798.6807	R	coral	south
QUAD-1693	3.7512	183.4491	-0.1288	-798.6807	R	coral	south
QUAD-1694	4.4510	218.9459	0.0989	-795.1356	R	coral	south
QUAD-1695	7.0279	227.1182	-0.7168	-795.1356	R	coral	south
QUAD-1696	8.2301	221.3714	1.1310	-795.1356	R	coral	south
QUAD-1697	7.0706	228.6493	-0.5455	-795.1356	R	coral	south
QUAD-1698	8.2552	61.7027	-0.0267	-792.0631	R	coral	south
QUAD-170	9.7446	207.5078	1.5436	-1053.9325	R	coral	head
QUAD-1700	1.7561	92.7271	-0.6578	-800.0475	R	coral	south
QUAD-1703	0.6660	47.9955	1.2488	-796.8638	R	coral	south
QUAD-1704	2.6893	26.0644	-0.0500	-796.8638	R	coral	south
QUAD-1705	2.1404	355.8654	-0.1232	-796.8638	R	coral	south
QUAD-1706	2.8068	301.8932	-1.7545	-796.8638	R	coral	south
QUAD-1707	4.0745	300.3047	-0.6855	-791.6732	R	coral	south
QUAD-1708	4.9718	298.6593	-0.2556	-791.6732	R	coral	south
QUAD-1709	6.0469	294.0310	-0.2466	-791.6732	R	coral	south
QUAD-171	14.0046	209.3150	0.7811	-1053.9325	R	coral	head
QUAD-1710	6.5778	297.8921	0.1956	-791.6732	R	coral	south
QUAD-1711	6.4231	307.8636	0.4955	-785.1887	R	coral	south
QUAD-1713	7.2173	324.4899	-0.7466	-785.1887	R	coral	south
QUAD-1714	7.4810	299.7809	-0.8911	-785.1887	R	coral	south
QUAD-1715	19.5422	280.5791	-0.7366	-762.7844	R	coral	south
QUAD-1716	25.2251	275.4101	-1.4034	-762.7844	R	coral	south
QUAD-1717	28.4825	268.3998	-0.9767	-762.7844	R	coral	south
QUAD-1719	23.5850	256.8953	-0.7654	-732.7850	R	coral	south
QUAD-172	7.9113	228.4761	3.0599	-1053.9325	R	coral	head
QUAD-1720	23.5981	259.8183	-0.4756	-732.7850	R	coral	south
QUAD-1721	26.7026	263.2719	-0.3455	-732.7850	R	coral	south
QUAD-1724	29.4739	266.8487	-1.0857	-705.8538	R	coral	south
QUAD-1725	33.8182	263.2658	2.0400	-705.8538	R	coral	south
QUAD-1726	31.2407	256.7787	3.8789	-705.8538	R	coral	south
QUAD-1729	36.4167	184.3135	2.9556	-695.1487	R	coral	south
QUAD-173	13.7964	221.1786	-0.0964	-1053.9325	R	coral	head
QUAD-1732	33.4198	197.5681	-1.5258	-695.1487	R	coral	south
QUAD-1734	35.7817	195.5305	-0.6556	-670.5950	R	coral	south
QUAD-1735	38.0298	192.7332	-0.6689	-670.5950	R	coral	south
QUAD-1736	38.5792	201.5647	-3.3900	-670.5950	R	coral	south
QUAD-1737	40.6559	211.6251	-0.6188	-670.5950	R	coral	south
QUAD-1738	39.5648	207.1845	5.8622	-652.7100	R	coral	south
QUAD-1739	36.5363	201.5231	1.0945	-652.7100	R	coral	south
QUAD-174	14.4593	234.1041	-0.6676	-1053.9325	R	coral	head
QUAD-1742	32.6660	206.8059	-1.2099	-652.7100	R	coral	south
QUAD-1743	27.9855	200.2622	2.5034	-649.8762	R	coral	south
QUAD-1745	7.2560	98.3553	-0.6521	-718.3362	R	coral	south
QUAD-1746	4.9877	157.3273	-0.6644	-718.3362	R	coral	south
QUAD-1747	7.2627	148.9852	0.2000	-718.3362	R	coral	south
QUAD-1748	7.1810	148.8539	-0.2101	-723.4925	R	coral	south
QUAD-1749	5.8485	158.1231	-0.1301	-723.4925	R	coral	south
QUAD-175	15.5055	227.3087	-2.6089	-1053.9325	R	coral	head
QUAD-1750	3.9184	160.7497	0.2355	-723.4925	R	coral	south
QUAD-1751	3.4430	160.0926	0.5768	-727.6625	R	coral	south
QUAD-1752	3.9355	158.4172	1.3221	-727.6625	R	coral	south
QUAD-1753	0.7481	179.1429	-0.4102	-727.6625	R	coral	south
QUAD-1754	4.5478	228.0022	-0.3845	-724.7087	R	coral	south
QUAD-1755	6.3818	210.7875	-0.9578	-724.7087	R	coral	south
QUAD-1756	7.4430	226.7663	-1.1544	-724.7087	R	coral	south
QUAD-1757	8.6085	241.2910	-0.2279	-710.7513	R	coral	south
QUAD-1758	9.1473	282.7868	-1.0855	-710.7513	R	coral	south
QUAD-1759	9.1473	282.7868	-1.0855	-710.7513	R	coral	south
QUAD-176	21.1732	212.0718	0.0001	-1053.9325	R	coral	head

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-1761	26.6073	286.5788	-1.1512	-710.7513	R	coral	south
QUAD-1762	32.9251	287.8145	-1.1834	-695.5306	R	coral	south
QUAD-1764	27.9211	267.9258	0.7444	-695.5306	R	coral	south
QUAD-1765	25.4681	268.9323	0.4768	-695.5306	R	coral	south
QUAD-1766	21.3734	270.1181	4.2068	-667.9637	R	coral	south
QUAD-177	22.7561	215.3415	-0.0601	-1053.9325	R	coral	head
QUAD-1771	14.9762	12.4979	-0.4332	-655.7581	R	coral	south
QUAD-1772	13.2175	322.8011	-0.7788	-655.7581	R	coral	south
QUAD-1773	12.6090	320.8055	1.0899	-655.7313	R	coral	south
QUAD-1775	1.6372	145.4463	-1.5566	-655.7313	R	coral	south
QUAD-1776	22.3460	136.6015	11.9523	-664.7056	R	coral	south
QUAD-1777	23.2810	131.0477	-0.8100	-664.7056	R	coral	south
QUAD-1778	21.8326	203.5645	6.3756	-672.1663	R	coral	south
QUAD-1779	23.3616	111.0528	-2.7924	-672.1663	R	coral	south
QUAD-178	24.3480	259.4877	-2.8818	-1053.9325	R	coral	head
QUAD-1780	22.3206	174.0248	-0.6501	-666.0538	R	coral	south
QUAD-1781	22.5480	201.2155	0.2166	-666.0538	R	coral	south
QUAD-1782	22.6935	207.6383	0.6711	-666.0538	R	coral	south
QUAD-1783	25.7200	215.0607	-0.8800	-657.3438	R	coral	south
QUAD-1784	21.1971	191.9466	1.6489	-657.3438	R	coral	south
QUAD-1785	24.5219	174.0684	-0.5767	-658.2137	R	coral	south
QUAD-1786	27.6205	191.4968	-4.0336	-658.2137	R	coral	south
QUAD-1787	29.6285	205.3310	1.2856	-643.6931	R	coral	south
QUAD-1788	27.6677	214.6339	0.6544	-643.6931	R	coral	south
QUAD-1789	28.3615	225.6463	-1.1166	-643.6931	R	coral	south
QUAD-179	22.5461	248.8483	-4.2696	-1053.9325	R	coral	head
QUAD-1790	28.2010	219.4337	-0.7322	-621.8838	R	coral	south
QUAD-1791	22.8714	206.2477	0.0000	-621.8838	R	coral	south
QUAD-1793	11.2614	90.9133	1.0112	-760.9519	R	coral	south
QUAD-180	25.1724	227.1750	4.3989	-1053.9325	R	coral	head
QUAD-181	19.9464	262.7268	0.3433	-1053.9325	R	coral	head
QUAD-182	30.0293	266.1790	-0.3270	-1053.9325	R	coral	head
QUAD-185	30.6256	257.6149	-0.6302	-1053.9325	R	coral	head
QUAD-186	19.7330	241.4139	6.2549	-1053.9325	R	coral	head
QUAD-187	25.5337	232.5502	-2.9008	-1053.9325	R	coral	head
QUAD-188	19.6635	243.8378	3.4451	-1053.9325	R	coral	head
QUAD-189	25.3095	266.0421	2.4861	-1053.9325	R	coral	head
QUAD-190	16.7869	272.8922	-0.4676	-1053.9325	R	coral	head
QUAD-191	25.7165	230.5381	5.2772	-1053.9325	R	coral	head
QUAD-192	31.8621	198.4253	-0.4289	-1053.9325	R	coral	head
QUAD-193	25.5007	202.8258	5.3123	-1053.9325	R	coral	head
QUAD-194	17.3070	160.8302	2.8068	-1053.9325	R	coral	head
QUAD-195	6.3396	144.7269	-0.6547	-1053.9325	R	coral	head
QUAD-196	5.5808	130.6297	0.3192	-1053.9325	R	coral	head
QUAD-197	3.2102	128.6472	0.0710	-1053.9325	R	coral	head
QUAD-198	3.1221	138.0763	-0.0601	-1053.9325	R	coral	head
QUAD-199	3.3448	167.4834	-0.0254	-1053.9325	R	coral	head
QUAD-200	2.4571	181.3580	0.0021	-1053.9325	R	coral	head
QUAD-201	2.4051	179.9979	0.0001	-1053.9325	R	coral	head
QUAD-202	2.9004	216.8487	-0.0266	-1053.9325	R	coral	head
QUAD-203	4.8188	236.2104	0.3829	-1053.9325	R	coral	head
QUAD-204	5.4402	250.5083	0.0001	-1053.9325	R	coral	head
QUAD-205	11.3854	253.4497	-0.5878	-1053.9325	R	coral	head
QUAD-206	13.1424	254.3703	0.0198	-1053.9325	R	coral	head
QUAD-207	14.1815	250.9073	-0.6836	-1053.9325	R	coral	head
QUAD-208	36.7964	268.7168	-2.1863	-1053.9325	R	coral	head
QUAD-209	39.9562	272.1519	-10.1447	-1053.9325	R	coral	head
QUAD-210	36.5438	263.6648	1.9485	-1053.9325	R	coral	head
QUAD-211	28.3324	267.2094	-1.5564	-1053.9325	R	coral	head
QUAD-212	22.1862	246.9769	-6.3122	-1053.9325	R	coral	head

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-213	29.8755	219.2835	2.7982	-1053.9325	R	coral	head
QUAD-214	19.8103	234.8171	2.2911	-1053.9325	R	coral	head
QUAD-215	13.2035	246.8167	2.0179	-1053.9325	R	coral	head
QUAD-216	20.4238	129.0811	0.2688	-1053.9325	R	coral	head
QUAD-217	16.6318	141.0663	-0.8788	-1053.9325	R	coral	head
QUAD-218	15.4790	166.6217	0.3311	-1053.9325	R	coral	head
QUAD-219	10.2418	161.6943	-0.1344	-1053.9325	R	coral	head
QUAD-220	6.1885	157.4627	-0.7299	-1053.9325	R	coral	head
QUAD-221	6.6820	177.2978	-0.5178	-1053.9325	R	coral	head
QUAD-222	6.9870	197.0472	-0.1877	-1053.9325	R	coral	head
QUAD-223	5.7760	215.8764	-0.2799	-1053.9325	R	coral	head
QUAD-224	5.3993	225.6790	-0.3800	-1053.9325	R	coral	head
QUAD-225	8.8538	243.1794	0.5656	-1053.9325	R	coral	head
QUAD-226	9.7205	234.0132	-0.4666	-1053.9325	R	coral	head
QUAD-227	14.7037	263.7685	1.4490	-1053.9325	R	coral	head
QUAD-228	17.9783	292.0081	-0.2555	-1053.9325	R	coral	head
QUAD-229	20.2238	290.6003	0.1122	-1053.9325	R	coral	head
QUAD-230	25.2652	296.9515	2.6444	-1053.9325	R	coral	head
QUAD-231	25.7993	309.5950	-1.2489	-1053.9325	R	coral	head
QUAD-232	29.4894	303.6188	0.0657	-1053.9325	R	coral	head
QUAD-233	19.1409	302.7518	0.2443	-1053.9325	R	coral	head
QUAD-234	21.2861	305.8506	0.6401	-1053.9325	R	coral	head
QUAD-235	21.1692	297.6735	0.0956	-1053.9325	R	coral	head
QUAD-236	24.8747	293.5536	2.2866	-1053.9325	R	coral	head
QUAD-237	25.2669	294.4975	0.7189	-1053.9325	R	coral	head
QUAD-238	26.1528	292.0801	0.4244	-1053.9325	R	coral	head
QUAD-239	25.2142	278.6429	-1.1810	-1053.9325	R	coral	head
QUAD-240	26.0975	266.3734	0.8012	-1053.9325	R	coral	head
QUAD-241	26.7358	306.7784	0.7189	-1053.9325	R	coral	head
QUAD-242	25.0648	300.6198	3.4000	-1053.9325	R	coral	head
QUAD-243	29.4322	310.0552	0.3778	-1053.9325	R	coral	head
QUAD-244	22.5252	289.2279	-0.2321	-1053.9325	R	coral	head
QUAD-245	26.8047	289.4253	0.3001	-1053.9325	R	coral	head
QUAD-246	27.5880	280.9243	-1.1000	-1053.9325	R	coral	head
QUAD-247	28.5823	277.8874	0.1012	-1053.9325	R	coral	head
QUAD-251	31.9553	278.5605	0.6133	-1053.9325	R	coral	head
QUAD-256	9.4592	101.3328	-0.0267	-1053.9325	R	coral	head
QUAD-257	7.5885	95.5249	-0.1044	-1053.9325	R	coral	head
QUAD-410	10.6741	251.7761	-1.3889	-655.0212	R	coral	head
QUAD-411	14.4055	223.1026	1.1500	-639.4207	R	coral	head
QUAD-412	11.0458	237.1453	0.0944	-637.9344	R	coral	head
QUAD-413	13.8849	247.7504	0.2077	-637.9344	R	coral	head
QUAD-414	16.4440	243.2347	-0.1512	-637.9344	R	coral	head
QUAD-415	14.9636	241.9059	0.1778	-621.8325	R	coral	head
QUAD-416	13.9482	246.1627	-0.0956	-621.8325	R	coral	head
QUAD-417	13.4744	245.8610	0.3279	-621.8325	R	coral	head
QUAD-418	10.6063	206.0499	1.7935	-621.8325	R	coral	head
QUAD-419	8.1950	171.1613	0.9594	-602.0587	R	coral	head
QUAD-425	18.7947	289.9288	-0.3011	-995.9069	R	coral	head
QUAD-426	22.0828	299.4996	-1.1512	-995.9069	R	coral	head
QUAD-613	28.3989	2.8209	-1.7517	-1007.5062	R	coral	flank
QUAD-614	28.3989	2.8209	-1.7517	-1007.5062	R	coral	flank
QUAD-615	30.6120	4.2307	-1.5720	-1007.5062	R	coral	flank
QUAD-616	30.0888	354.7464	-2.2537	-1007.1663	R	coral	flank
QUAD-617	28.2951	1.5938	2.0228	-1007.1663	R	coral	flank
QUAD-618	26.3163	10.5057	0.2162	-1007.1663	R	coral	flank
QUAD-619	26.5974	353.9207	-3.1005	-1007.1663	R	coral	flank
QUAD-620	30.5979	340.5385	-0.5145	-1007.1663	R	coral	flank
QUAD-621	34.3393	334.7831	0.0327	-1007.1663	R	coral	flank
QUAD-625	26.8777	336.3087	0.5910	-977.4469	R	coral	flank

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-626	28.4016	337.7443	0.3983	-957.7519	R	coral	flank
QUAD-627	28.4669	331.3599	0.3390	-901.8607	R	coral	flank
QUAD-628	25.7982	331.5266	-0.0099	-901.8607	R	coral	flank
QUAD-629	23.5932	323.9545	-0.8360	-890.5919	R	coral	flank
QUAD-630	22.9781	312.7050	-0.6593	-890.5919	R	coral	flank
QUAD-631	24.4191	301.6876	-2.6295	-890.5919	R	coral	flank
QUAD-632	24.8904	296.1593	-0.1721	-890.5919	R	coral	flank
QUAD-633	21.0173	303.4410	1.4951	-881.8156	R	coral	flank
QUAD-634	21.2866	316.9790	-0.2988	-881.8156	R	coral	flank
QUAD-635	21.7628	313.8766	-0.4038	-881.8156	R	coral	flank
QUAD-636	21.6653	312.4451	1.3499	-881.8156	R	coral	flank
QUAD-637	21.4849	316.9605	-0.0422	-865.9838	R	coral	flank
QUAD-638	18.1584	298.7521	-0.2368	-865.9838	R	coral	flank
QUAD-639	17.5610	282.5907	-1.1750	-865.9838	R	coral	flank
QUAD-640	12.8797	295.7871	0.9233	-850.1469	R	coral	flank
QUAD-641	14.5335	295.7429	0.4082	-850.1469	R	coral	flank
QUAD-642	13.7439	299.8251	0.2939	-850.1469	R	coral	flank
QUAD-643	14.1115	300.3430	0.0083	-832.0925	R	coral	flank
QUAD-644	16.3971	308.0567	0.2211	-832.0925	R	coral	flank
QUAD-645	16.9430	299.3994	-0.2351	-832.0925	R	coral	flank
QUAD-646	21.3916	298.3360	-1.1467	-801.7957	R	coral	flank
QUAD-647	23.8086	294.8428	-1.0361	-801.7957	R	coral	flank
QUAD-648	22.7725	298.0313	-0.3627	-801.7957	R	coral	flank
QUAD-649	23.9027	296.0618	0.0062	-801.7957	R	coral	flank
QUAD-650	25.2143	297.7220	-0.3588	-777.1993	R	coral	flank
QUAD-651	27.2961	297.7468	-0.9183	-777.1993	R	coral	flank
QUAD-652	30.1332	297.8999	-0.3928	-777.1993	R	coral	flank
QUAD-653	26.3706	293.2169	0.7384	-748.6031	R	coral	flank
QUAD-654	29.4221	286.7852	-2.3790	-698.2725	R	coral	flank
QUAD-655	33.3983	283.2127	-1.2127	-698.2725	R	coral	flank
QUAD-656	34.1972	282.3436	-1.0033	-698.2725	R	coral	flank
QUAD-657	38.6374	287.5779	-0.5300	-698.2725	R	coral	flank
QUAD-658	40.1919	290.9319	-0.8962	-698.2725	R	coral	flank
QUAD-659	40.1919	290.9319	-0.8962	-683.1956	R	coral	flank
QUAD-660	37.5927	290.0136	-0.5144	-683.1956	R	coral	flank
QUAD-661	37.5927	290.0136	-0.5144	-683.1956	R	coral	flank
QUAD-662	35.5021	293.8311	1.6361	-683.1956	R	coral	flank
QUAD-663	35.5021	293.8311	1.6361	-683.1956	R	coral	flank
QUAD-664	33.7742	321.5797	3.6517	-683.1956	R	coral	flank
QUAD-669	3.1401	126.1846	0.4822	-721.5819	R	coral	flank
QUAD-728	21.5540	302.3383	1.3299	-692.9500	R	coral	flank
QUAD-814	30.6483	8.8609	-2.1644	-795.3850	R	coral	flank
QUAD-846	37.3603	326.2095	-0.0266	-1020.7600	R	coral	flank
QUAD-847	36.7158	324.8369	-0.7566	-1020.7600	R	coral	flank
QUAD-848	36.7158	324.8369	-0.7566	-974.6287	R	coral	flank
QUAD-849	39.6388	312.7885	0.7539	-974.6287	R	coral	flank
QUAD-850	39.6388	312.7885	0.7539	-974.6287	R	coral	flank
QUAD-851	36.5703	310.3477	0.1949	-974.6287	R	coral	flank
QUAD-852	37.8026	305.3499	-0.6289	-974.6287	R	coral	flank
QUAD-853	37.8026	305.3499	-0.6289	-974.6287	R	coral	flank
QUAD-855	36.2152	304.5105	0.9977	-974.6287	R	coral	flank
QUAD-856	33.4107	305.8993	3.0505	-928.6212	R	coral	flank
QUAD-857	31.2461	303.1682	2.4872	-928.6212	R	coral	flank
QUAD-858	31.9015	310.0846	1.4556	-928.6212	R	coral	flank
QUAD-859	33.7950	303.1114	0.2346	-928.6212	R	coral	flank
QUAD-860	38.0761	293.5125	0.0372	-928.6212	R	coral	flank
QUAD-861	41.2909	296.5540	2.8755	-928.6212	R	coral	flank
QUAD-863	41.2657	290.0215	3.8823	-824.6763	R	coral	flank
QUAD-864	41.1132	300.0044	3.8183	-824.6763	R	coral	flank
QUAD-865	41.3963	294.0110	2.2789	-776.6256	R	coral	flank

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-866	43.8579	285.0184	2.1044	-776.6256	R	coral	flank
QUAD-867	42.0224	294.6279	2.5118	-776.6256	R	coral	flank
QUAD-868	42.2030	306.0093	2.8827	-776.6256	R	coral	flank
QUAD-870	43.4826	300.3975	2.7310	-776.6256	R	coral	flank
QUAD-872	37.1157	316.8265	2.5740	-776.6256	R	coral	flank
QUAD-873	37.7667	304.3796	4.0222	-730.2488	R	coral	flank
QUAD-874	36.1758	320.0004	3.3578	-730.2488	R	coral	flank
QUAD-875	36.1758	320.0004	3.3578	-730.2488	R	coral	flank
QUAD-876	36.4531	315.3626	0.7661	-730.2488	R	coral	flank
QUAD-877	39.3352	312.9019	-1.9295	-730.2488	R	coral	flank
QUAD-878	38.4308	309.4100	1.5671	-730.2488	R	coral	flank
QUAD-879	41.0819	304.4789	-0.1045	-730.2488	R	coral	flank
QUAD-880	41.0819	304.4789	-0.1045	-730.2488	R	coral	flank
QUAD-881	38.2260	294.5475	-0.2712	-730.2488	R	coral	flank
QUAD-882	37.9288	292.3802	-0.2511	-730.2488	R	coral	flank
QUAD-883	37.0130	291.5864	-2.1740	-694.2463	R	coral	flank
QUAD-884	37.7083	295.1366	0.0121	-694.2463	R	coral	flank
QUAD-885	41.3663	290.2839	-2.3979	-694.2463	R	coral	flank
QUAD-886	38.8181	281.1481	0.0066	-694.2463	R	coral	flank
QUAD-887	33.0933	271.6425	2.2051	-694.2463	R	coral	flank
QUAD-888	31.9854	291.4278	-3.5599	-694.2463	R	coral	flank
QUAD-889	31.0639	291.4153	-5.8561	-694.2463	R	coral	flank
QUAD-890	36.1480	297.3569	-0.1829	-694.2463	R	coral	flank
QUAD-894	7.9558	244.8241	2.3071	-694.8706	R	coral	flank
QUAD-897	24.4462	297.1584	0.0135	-969.0081	R	coral	flank
QUAD-898	25.5592	302.2296	-0.2705	-969.0081	R	coral	flank
QUAD-899	25.3741	306.4798	0.5889	-920.0406	R	coral	flank
QUAD-900	24.7819	305.8284	-0.1684	-920.0406	R	coral	flank
QUAD-901	24.8544	304.3238	-0.3384	-836.6244	R	coral	flank
QUAD-902	27.5884	305.1915	-1.4523	-836.6244	R	coral	flank
QUAD-903	30.5833	305.1120	-0.9843	-836.6244	R	coral	flank
QUAD-904	35.2332	308.3775	0.0795	-836.6244	R	coral	flank
QUAD-906	36.1251	309.8826	1.0860	-836.6244	R	coral	flank
QUAD-907	34.6649	308.6671	0.6578	-836.6244	R	coral	flank
QUAD-910	38.3143	307.7948	-1.2490	-800.5969	R	coral	flank
QUAD-913	41.1647	309.0984	-0.3949	-800.5969	R	coral	flank
QUAD-914	41.6875	309.5473	-1.1339	-800.5969	R	coral	flank
QUAD-915	41.6875	309.5473	-1.1339	-800.5969	R	coral	flank
QUAD-916	43.4382	311.1345	-0.9301	-800.5969	R	coral	flank
QUAD-917	44.0350	309.5561	-1.5405	-800.5969	R	coral	flank
QUAD-918	46.0518	310.4699	-0.9417	-800.5969	R	coral	flank
QUAD-919	46.0518	310.4699	-0.9417	-800.5969	R	coral	flank
QUAD-922	43.2105	309.5740	0.8839	-727.5988	R	coral	flank
QUAD-923	37.5807	312.4597	2.3493	-727.5988	R	coral	flank
QUAD-924	34.1663	318.3563	0.9266	-727.5988	R	coral	flank
QUAD-925	34.1663	318.3563	0.9266	-727.5988	R	coral	flank
QUAD-926	32.8430	320.0564	1.0589	-727.5988	R	coral	flank
QUAD-927	33.1515	322.9503	1.4395	-727.5988	R	coral	flank
QUAD-928	33.8568	322.5293	-0.0144	-727.5988	R	coral	flank
QUAD-929	37.4990	323.2123	0.6945	-720.4287	R	coral	flank
QUAD-930	38.2760	333.7121	2.5333	-720.4287	R	coral	flank
QUAD-931	38.2760	333.7121	2.5333	-720.4287	R	coral	flank
QUAD-932	34.6443	339.8848	4.9423	-720.4287	R	coral	flank
QUAD-933	27.4001	345.7648	3.5533	-720.4287	R	coral	flank
QUAD-934	27.4001	345.7648	3.5533	-720.4287	R	coral	flank
QUAD-935	25.8817	343.8862	-0.8333	-720.4287	R	coral	flank
QUAD-936	25.8817	343.8862	-0.8333	-720.4287	R	coral	flank
QUAD-937	38.2139	336.0902	-1.5176	-720.4287	R	coral	flank
QUAD-938	40.7681	339.4684	-1.0190	-715.2800	R	coral	flank
QUAD-939	43.4238	339.7788	1.5633	-715.2800	R	coral	flank

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-940	42.0280	346.0560	2.2534	-747.1269	R	coral	flank
QUAD-941	38.8507	350.5598	0.8112	-747.1269	R	coral	flank
QUAD-942	37.7984	350.6323	0.3761	-747.1269	R	coral	flank
QUAD-943	29.4844	354.0365	4.2395	-747.1269	R	coral	flank
QUAD-944	24.3735	1.4202	5.7161	-747.1269	R	coral	flank
QUAD-951	22.7303	311.8124	-0.5550	-972.1650	R	coral	flank
QUAD-952	22.7303	311.8124	-0.5550	-972.1650	R	coral	flank
QUAD-953	22.3208	310.8256	-0.0815	-972.1650	R	coral	flank
QUAD-954	22.7303	311.8124	-0.5550	-972.1650	R	coral	flank
QUAD-955	22.7303	311.8124	-0.5550	-972.1650	R	coral	flank
QUAD-956	22.7303	311.8124	-0.5550	-972.1650	R	coral	flank
QUAD-964	20.3676	331.9503	0.8056	-917.9419	R	coral	flank
QUAD-967	18.3788	330.0807	0.7589	-917.9419	R	coral	flank
QUAD-971	19.4078	325.8668	-0.1650	-869.8856	R	coral	flank
QUAD-972	19.2182	329.2030	-0.3055	-869.8856	R	coral	flank
QUAD-976	24.8582	329.6487	-0.1584	-869.8856	R	coral	flank
QUAD-981	29.7776	327.0751	-0.1750	-796.8969	R	coral	flank
QUAD-982	29.6178	326.6358	-0.9304	-796.8969	R	coral	flank
QUAD-983	28.2262	326.0000	-0.0822	-796.8969	R	coral	flank
QUAD-984	30.9276	323.4408	-0.6267	-796.8969	R	coral	flank
QUAD-986	37.7581	326.9321	0.8550	-772.7225	R	coral	flank
QUAD-987	35.5872	331.2751	1.3028	-772.7225	R	coral	flank
QUAD-988	33.1603	328.2342	0.6956	-772.7225	R	coral	flank
QUAD-989	33.3851	330.4280	1.5922	-717.6212	R	coral	flank
QUAD-990	30.6081	332.0569	1.7067	-717.6212	R	coral	flank
QUAD-991	27.5387	333.0059	1.3127	-717.6212	R	coral	flank
QUAD-992	27.5387	333.0059	1.3127	-717.6212	R	coral	flank
QUAD-993	27.1247	336.1450	-0.3616	-717.6212	R	coral	flank
QUAD-994	29.7186	336.9094	-0.6617	-701.4375	R	coral	flank
QUAD-995	30.9819	339.4213	-0.7672	-701.4375	R	coral	flank
QUAD-997	37.4360	318.6313	-2.9020	-1020.0956	R	coral	flank
QUAD-998	37.4360	318.6313	-2.9020	-1020.0956	R	coral	flank
QUAD-001	3.2529	293.5953	0.5400	-1019.4431	S	non-coral	head
QUAD-002	2.1978	330.2521	-0.6967	-1016.0344	S	non-coral	head
QUAD-003	2.1637	343.3376	-0.9378	-1012.0500	S	non-coral	head
QUAD-004	1.9193	320.9211	-1.3923	-1012.0500	S	non-coral	head
QUAD-005	1.5064	285.5627	-0.6010	-1012.0500	S	non-coral	head
QUAD-006	4.9291	208.7321	-0.7321	-1012.0500	S	non-coral	head
QUAD-007	5.3842	203.2902	0.5534	-1012.0500	S	non-coral	head
QUAD-008	5.3842	203.2902	0.5534	-1012.0500	S	non-coral	head
QUAD-009	4.4443	226.3324	-0.0366	-1008.7975	S	non-coral	head
QUAD-010	4.6372	214.8601	0.3090	-1008.7975	S	non-coral	head
QUAD-011	3.0041	228.4324	0.6568	-1008.7975	S	non-coral	head
QUAD-012	0.8970	328.2021	-0.0901	-1008.7975	S	non-coral	head
QUAD-013	2.3010	336.7486	-0.3323	-1007.1006	S	non-coral	head
QUAD-014	3.6298	287.7054	-0.4011	-1007.1006	S	non-coral	head
QUAD-015	4.5972	236.9556	-0.6733	-1007.1006	S	non-coral	head
QUAD-016	8.1701	228.3338	-0.7844	-1007.1006	S	non-coral	head
QUAD-017	8.4148	223.5389	-0.2344	-1007.1006	S	non-coral	head
QUAD-019	5.4791	304.4567	-0.2827	-1002.5018	S	non-coral	head
QUAD-020	7.3047	209.5552	-2.1923	-993.6450	S	non-coral	head
QUAD-021	16.3938	229.9600	1.5684	-991.5875	S	non-coral	head
QUAD-056	6.3906	215.0228	0.1833	-921.9675	S	non-coral	head
QUAD-057	5.2693	229.3235	-0.4744	-921.9675	S	non-coral	head
QUAD-058	6.4256	245.9383	-0.1832	-921.9675	S	non-coral	head
QUAD-059	7.7233	248.1638	-0.1157	-911.5069	S	non-coral	head
QUAD-060	9.0090	249.6384	-0.5233	-911.5069	S	non-coral	head
QUAD-061	13.5770	258.6839	-0.3922	-911.5069	S	non-coral	head
QUAD-062	17.0457	268.5099	-0.3345	-891.0294	S	non-coral	head
QUAD-064	17.9429	284.1864	0.3101	-899.1944	S	non-coral	head

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-075	2.8101	177.6153	-1.0790	-877.6544	S	non-coral	head
QUAD-076	4.4478	201.8020	-0.0001	-877.6544	S	non-coral	head
QUAD-077	0.5834	97.9929	-0.4277	-875.1881	S	non-coral	head
QUAD-078	2.6737	212.9348	-0.5189	-875.1881	S	non-coral	head
QUAD-079	5.9337	232.9187	-0.1511	-875.1881	S	non-coral	head
QUAD-080	2.5473	247.8649	0.2855	-875.1881	S	non-coral	head
QUAD-081	2.1953	251.4064	-0.0001	-869.4844	S	non-coral	head
QUAD-082	2.8924	260.5052	-0.3165	-867.1487	S	non-coral	head
QUAD-083	5.9569	274.6573	-2.2346	-867.1487	S	non-coral	head
QUAD-084	8.0611	278.3906	-0.5956	-867.1487	S	non-coral	head
QUAD-085	11.4792	282.6580	-0.4123	-854.3531	S	non-coral	head
QUAD-086	8.5408	256.8168	0.8955	-852.4738	S	non-coral	head
QUAD-087	6.5575	269.3075	1.0411	-847.6512	S	non-coral	head
QUAD-088	5.1330	286.2886	0.2133	-847.6512	S	non-coral	head
QUAD-089	3.7201	267.2573	0.3633	-847.6512	S	non-coral	head
QUAD-090	2.5544	258.1789	0.0621	-847.6512	S	non-coral	head
QUAD-091	3.0662	240.5703	-0.3234	-844.7819	S	non-coral	head
QUAD-092	5.5665	244.8514	-1.5600	-844.7819	S	non-coral	head
QUAD-093	7.3104	260.2009	0.8846	-844.7819	S	non-coral	head
QUAD-094	6.1327	274.8941	0.2122	-844.7819	S	non-coral	head
QUAD-095	5.5487	263.1025	0.0001	-844.7819	S	non-coral	head
QUAD-096	6.3693	244.3501	0.1467	-844.7819	S	non-coral	head
QUAD-097	8.6898	258.6959	-0.0234	-832.0413	S	non-coral	head
QUAD-098	8.7993	272.3445	-0.1289	-832.0413	S	non-coral	head
QUAD-099	11.7826	259.3484	0.0001	-823.0088	S	non-coral	head
QUAD-100	13.3579	254.2981	0.1932	-823.0088	S	non-coral	head
QUAD-101	12.0467	248.8661	0.4010	-823.0088	S	non-coral	head
QUAD-102	8.4373	258.0903	0.8923	-815.8694	S	non-coral	head
QUAD-103	8.6077	248.3217	-0.0845	-807.5425	S	non-coral	head
QUAD-104	9.0014	259.2672	0.7899	-807.5425	S	non-coral	head
QUAD-105	8.0112	260.9436	0.8779	-807.5425	S	non-coral	head
QUAD-106	7.8750	278.2441	0.3856	-807.5425	S	non-coral	head
QUAD-107	9.3014	277.3268	0.0287	-793.8406	S	non-coral	head
QUAD-108	9.2345	275.7062	-0.0156	-793.8406	S	non-coral	head
QUAD-1086	22.5301	321.3516	-1.2049	-939.5656	S	non-coral	flank
QUAD-1087	25.0188	319.8272	-0.4912	-939.5656	S	non-coral	flank
QUAD-109	9.8499	271.6415	-0.0446	-793.8406	S	non-coral	head
QUAD-110	8.5496	266.7646	0.3534	-779.9337	S	non-coral	head
QUAD-111	8.7680	244.0807	0.1677	-779.9337	S	non-coral	head
QUAD-1118	35.2870	351.7057	-0.1007	-799.3481	S	non-coral	flank
QUAD-1119	33.7664	354.0410	0.2000	-799.3481	S	non-coral	flank
QUAD-112	11.9418	251.4675	0.0711	-779.9337	S	non-coral	head
QUAD-1125	36.6582	353.7894	-1.7729	-792.8869	S	non-coral	flank
QUAD-1126	34.2238	355.1772	-0.7751	-792.8869	S	non-coral	flank
QUAD-1128	30.6701	341.6399	-2.5894	-754.1650	S	non-coral	flank
QUAD-113	12.1902	261.9805	0.5889	-779.9337	S	non-coral	head
QUAD-1130	31.3755	331.3051	-1.9690	-745.3775	S	non-coral	flank
QUAD-1131	32.6873	334.1876	-0.1255	-745.3775	S	non-coral	flank
QUAD-114	10.3525	275.1382	0.1257	-768.5513	S	non-coral	head
QUAD-1147	46.5265	286.6591	-0.8334	-923.0400	S	non-coral	flank
QUAD-1148	46.0722	287.6937	-1.4377	-771.0963	S	non-coral	flank
QUAD-115	13.0415	256.5186	-0.4334	-765.4037	S	non-coral	head
QUAD-116	11.4810	267.3503	0.2989	-765.4037	S	non-coral	head
QUAD-1168	7.4958	276.9759	1.1555	-1042.9006	S	non-coral	south
QUAD-1169	3.4883	263.7285	-1.0566	-1042.9006	S	non-coral	south
QUAD-1170	6.1564	298.5678	-0.1035	-1042.9006	S	non-coral	south
QUAD-1171	4.6473	223.8181	0.2499	-1034.6262	S	non-coral	south
QUAD-1172	7.7432	284.2134	-0.0081	-1042.9006	S	non-coral	south
QUAD-1173	6.5980	267.1357	-0.3290	-1042.9006	S	non-coral	south
QUAD-1174	5.0975	230.1073	-0.1776	-1042.9006	S	non-coral	south

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-1175	4.5379	288.7018	0.6152	-1034.6262	S	non-coral	south
QUAD-1176	9.5879	263.8150	-3.1218	-1042.9006	S	non-coral	south
QUAD-1177	7.3258	228.0482	-0.2168	-1034.6262	S	non-coral	south
QUAD-1178	5.0838	223.6281	-1.7108	-1034.6262	S	non-coral	south
QUAD-1179	3.5207	247.3093	-1.0920	-1031.0269	S	non-coral	south
QUAD-1180	8.6664	223.7004	-1.2156	-1025.7762	S	non-coral	south
QUAD-1181	6.3517	243.0837	-0.8967	-1031.0269	S	non-coral	south
QUAD-1182	6.5514	239.4108	-0.6130	-1025.7762	S	non-coral	south
QUAD-1183	8.9523	223.3787	-0.5080	-1025.7762	S	non-coral	south
QUAD-1184	6.9758	250.4917	0.3575	-1025.7762	S	non-coral	south
QUAD-1185	10.0168	229.2346	-0.1089	-1025.7762	S	non-coral	south
QUAD-1186	8.5618	239.6145	-1.6890	-1025.7762	S	non-coral	south
QUAD-1187	10.6437	232.2770	-0.6399	-1020.8013	S	non-coral	south
QUAD-1188	12.4681	234.9439	0.0000	-1020.8013	S	non-coral	south
QUAD-1189	13.9982	247.6860	-0.4501	-1020.8013	S	non-coral	south
QUAD-119	5.2958	267.3804	2.3689	-745.4631	S	non-coral	head
QUAD-1190	7.3268	242.4491	1.0754	-1020.8013	S	non-coral	south
QUAD-1191	7.4536	230.4185	-1.6279	-1020.8013	S	non-coral	south
QUAD-1192	10.5939	231.6033	1.9456	-1000.9587	S	non-coral	south
QUAD-1193	14.7009	241.1215	-3.3700	-1000.9587	S	non-coral	south
QUAD-1194	13.4954	251.2335	-4.5411	-1000.9587	S	non-coral	south
QUAD-1195	11.4238	207.8651	-0.2711	-987.3225	S	non-coral	south
QUAD-1196	5.5473	273.4605	0.3433	-987.1769	S	non-coral	south
QUAD-1197	15.5637	290.3994	0.5334	-987.3225	S	non-coral	south
QUAD-1198	17.1640	197.0923	-3.5546	-987.1769	S	non-coral	south
QUAD-1199	11.9422	243.5406	0.2377	-975.6394	S	non-coral	south
QUAD-120	2.4623	270.5927	0.0000	-745.4631	S	non-coral	head
QUAD-1200	13.0442	256.3236	-0.0001	-975.6394	S	non-coral	south
QUAD-1201	10.2544	264.1268	1.2512	-975.6394	S	non-coral	south
QUAD-1202	9.8933	253.2591	-2.4124	-963.9925	S	non-coral	south
QUAD-1203	8.2654	243.9562	-0.4619	-963.9925	S	non-coral	south
QUAD-1204	3.6080	257.9833	-2.6321	-963.9925	S	non-coral	south
QUAD-1205	6.9828	261.9205	-1.1097	-963.9925	S	non-coral	south
QUAD-1206	14.5219	195.4939	0.1512	-954.3918	S	non-coral	south
QUAD-1207	7.7760	185.7257	-0.8979	-954.3918	S	non-coral	south
QUAD-1208	14.0232	195.8488	-2.4844	-955.0800	S	non-coral	south
QUAD-1209	8.4263	209.6296	-4.9089	-944.3737	S	non-coral	south
QUAD-121	5.1743	222.8491	0.1723	-740.1456	S	non-coral	head
QUAD-1210	20.4529	210.0414	1.6023	-944.3737	S	non-coral	south
QUAD-1211	15.3924	168.7357	-0.5621	-955.0800	S	non-coral	south
QUAD-1212	8.4263	209.6296	-4.9089	-944.3737	S	non-coral	south
QUAD-1213	9.1105	179.2512	-2.2211	-955.0800	S	non-coral	south
QUAD-1214	8.4263	209.6296	-4.9089	-944.3737	S	non-coral	south
QUAD-1215	17.9338	165.3435	-0.0001	-955.0800	S	non-coral	south
QUAD-1216	17.0120	183.1878	0.7489	-955.0800	S	non-coral	south
QUAD-1217	20.8408	196.9092	-5.4523	-944.3737	S	non-coral	south
QUAD-1218	15.7899	198.7840	-2.3344	-944.3737	S	non-coral	south
QUAD-1219	20.8408	196.9092	-5.4523	-944.3737	S	non-coral	south
QUAD-122	7.6647	211.9251	0.2855	-735.9319	S	non-coral	head
QUAD-1220	18.5349	172.4781	-2.5557	-944.3737	S	non-coral	south
QUAD-1221	18.5349	172.4781	-2.5557	-944.3737	S	non-coral	south
QUAD-1222	18.5349	172.4781	-2.5557	-955.0800	S	non-coral	south
QUAD-1223	8.4263	209.6296	-4.9089	-944.3737	S	non-coral	south
QUAD-1224	8.4263	209.6296	-4.9089	-944.3737	S	non-coral	south
QUAD-1225	8.4263	209.6296	-4.9089	-944.3737	S	non-coral	south
QUAD-1226	12.6751	222.0512	-2.7488	-944.3737	S	non-coral	south
QUAD-1227	21.1668	212.7553	-0.0345	-944.3737	S	non-coral	south
QUAD-1228	14.3830	151.9306	-0.2900	-944.3737	S	non-coral	south
QUAD-1229	6.9315	183.7865	-2.1879	-944.3737	S	non-coral	south
QUAD-123	6.2388	224.0629	0.1890	-735.9319	S	non-coral	head

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-1230	13.5139	207.0448	-0.5145	-932.4231	S	non-coral	south
QUAD-1231	4.0179	334.0626	3.9955	-932.4231	S	non-coral	south
QUAD-1232	5.2801	286.1967	-1.8779	-932.4231	S	non-coral	south
QUAD-1233	8.2686	256.4470	-0.6545	-932.4231	S	non-coral	south
QUAD-1234	10.8153	256.0324	-0.2278	-915.7112	S	non-coral	south
QUAD-1235	9.9992	255.8797	0.4146	-909.6900	S	non-coral	south
QUAD-1236	9.2675	251.7870	-0.1733	-909.6900	S	non-coral	south
QUAD-1237	11.8106	258.2305	-0.6323	-909.6900	S	non-coral	south
QUAD-1238	10.8811	270.4632	-0.0001	-909.6900	S	non-coral	south
QUAD-1239	9.8883	286.0785	0.5279	-903.3881	S	non-coral	south
QUAD-1240	9.2625	274.4938	-0.2667	-903.3881	S	non-coral	south
QUAD-1241	7.2025	270.7430	-0.7090	-903.3881	S	non-coral	south
QUAD-1242	7.8259	263.2805	0.2877	-903.3881	S	non-coral	south
QUAD-1243	7.9717	251.9032	-0.0789	-895.9669	S	non-coral	south
QUAD-1244	7.3208	257.2271	0.2291	-895.9669	S	non-coral	south
QUAD-1245	7.5106	244.2238	-1.3644	-895.9669	S	non-coral	south
QUAD-1246	5.1529	255.1501	0.7645	-887.4912	S	non-coral	south
QUAD-1247	4.5860	254.9054	0.1732	-887.4912	S	non-coral	south
QUAD-1248	5.5997	263.0851	-0.6067	-884.1194	S	non-coral	south
QUAD-1249	8.4943	260.4504	-0.0067	-884.1194	S	non-coral	south
QUAD-125	6.9856	229.3760	0.0000	-732.0606	S	non-coral	head
QUAD-1250	12.5179	247.8701	0.4689	-875.6887	S	non-coral	south
QUAD-1252	12.1655	226.7857	2.7101	-875.6887	S	non-coral	south
QUAD-1253	5.2975	204.8919	-0.0557	-875.6887	S	non-coral	south
QUAD-1254	6.1690	223.4887	-0.3121	-875.6887	S	non-coral	south
QUAD-1255	4.6045	217.4737	0.2776	-873.1531	S	non-coral	south
QUAD-1256	6.0739	228.3861	-0.3690	-873.1531	S	non-coral	south
QUAD-1257	4.7700	250.9498	0.5412	-873.1531	S	non-coral	south
QUAD-1258	4.5892	249.6890	0.1545	-873.1531	S	non-coral	south
QUAD-1259	3.5691	241.8595	0.2512	-867.9106	S	non-coral	south
QUAD-126	0.4807	281.4652	0.4666	-728.1269	S	non-coral	head
QUAD-1260	6.3175	232.7490	-1.1223	-867.9106	S	non-coral	south
QUAD-1261	15.7013	210.7747	0.5945	-867.9106	S	non-coral	south
QUAD-1262	9.2358	173.4868	0.0001	-865.4163	S	non-coral	south
QUAD-1263	4.3181	245.9567	1.4767	-858.4094	S	non-coral	south
QUAD-1264	5.3899	277.3076	-1.1179	-858.4094	S	non-coral	south
QUAD-1265	7.9725	222.5892	0.0001	-858.4094	S	non-coral	south
QUAD-1266	2.5715	330.5264	3.5046	-850.2313	S	non-coral	south
QUAD-1267	7.1549	237.0573	1.9467	-850.2313	S	non-coral	south
QUAD-1268	3.6071	266.0575	0.0000	-850.2313	S	non-coral	south
QUAD-1269	4.8824	238.6461	0.7011	-850.2313	S	non-coral	south
QUAD-127	3.1572	347.1534	0.1009	-728.1269	S	non-coral	head
QUAD-1270	3.4955	222.8428	-1.6945	-838.2350	S	non-coral	south
QUAD-1271	13.6524	202.2045	0.2294	-838.2350	S	non-coral	south
QUAD-1272	13.1039	189.5892	3.5201	-834.7769	S	non-coral	south
QUAD-1273	3.7778	171.0209	2.4423	-829.4375	S	non-coral	south
QUAD-1274	4.2219	284.9138	0.0001	-829.4375	S	non-coral	south
QUAD-1275	4.6391	245.9186	-1.0156	-829.4375	S	non-coral	south
QUAD-1276	3.9151	248.4736	0.4779	-829.4375	S	non-coral	south
QUAD-1277	6.2342	214.3689	0.7422	-823.3937	S	non-coral	south
QUAD-1278	3.4589	246.4054	-0.6167	-823.3937	S	non-coral	south
QUAD-1279	10.8774	238.6215	-0.4857	-823.3937	S	non-coral	south
QUAD-128	8.3778	249.8080	0.4469	-1053.9325	S	non-coral	head
QUAD-1280	6.1009	254.1181	3.7134	-823.3937	S	non-coral	south
QUAD-1281	6.0578	251.9063	-1.7610	-818.3412	S	non-coral	south
QUAD-1282	6.3961	244.4665	1.6812	-818.3412	S	non-coral	south
QUAD-1283	4.8845	261.1080	-0.1799	-818.3412	S	non-coral	south
QUAD-1284	7.8602	252.7357	-0.2721	-818.3412	S	non-coral	south
QUAD-1285	9.5405	239.9264	-0.0001	-804.2900	S	non-coral	south
QUAD-1286	12.4694	227.6724	-0.0522	-804.2900	S	non-coral	south

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-1287	11.7055	224.5271	-0.7201	-804.2900	S	non-coral	south
QUAD-1288	7.8991	246.0129	2.8690	-804.2900	S	non-coral	south
QUAD-1289	7.3248	253.6328	1.6377	-804.2900	S	non-coral	south
QUAD-1290	7.5954	279.9690	-0.1177	-804.2900	S	non-coral	south
QUAD-1291	8.9444	263.0613	-0.4011	-793.0044	S	non-coral	south
QUAD-1292	10.7225	278.5033	-0.3677	-793.0044	S	non-coral	south
QUAD-1304	24.1187	324.2096	0.9034	-698.9894	S	non-coral	south
QUAD-1305	23.0200	320.1880	-3.4123	-698.9894	S	non-coral	south
QUAD-1309	18.8708	347.1360	3.4242	-692.5375	S	non-coral	south
QUAD-1310	18.8708	347.1360	3.4242	-692.5375	S	non-coral	south
QUAD-1311	14.3293	336.6086	0.8545	-719.6387	S	non-coral	south
QUAD-1312	14.3293	336.6086	0.8545	-719.6387	S	non-coral	south
QUAD-1313	11.2076	337.7495	-0.9567	-718.3319	S	non-coral	south
QUAD-1314	10.0040	336.7917	-1.1155	-718.3319	S	non-coral	south
QUAD-1316	8.2450	318.9174	0.0001	-718.3319	S	non-coral	south
QUAD-1322	6.1167	335.0558	-1.4545	-707.3962	S	non-coral	south
QUAD-1323	5.5030	316.0749	-1.0190	-721.3318	S	non-coral	south
QUAD-1340	6.9349	209.6892	-0.2466	-682.5631	S	non-coral	south
QUAD-1341	5.6623	224.7344	0.6533	-675.7519	S	non-coral	south
QUAD-1342	8.3829	206.5916	-0.1526	-675.7519	S	non-coral	south
QUAD-1343	9.4160	202.8664	-0.9083	-675.7519	S	non-coral	south
QUAD-1344	9.7085	205.3517	-1.4214	-675.7519	S	non-coral	south
QUAD-1345	15.8861	204.9142	0.0001	-657.4163	S	non-coral	south
QUAD-1346	22.7292	209.6350	-0.7844	-657.4163	S	non-coral	south
QUAD-1347	28.0693	208.3278	-1.4922	-657.4163	S	non-coral	south
QUAD-1348	25.8025	209.3162	2.0110	-654.1994	S	non-coral	south
QUAD-1349	1.0231	248.9418	6.0212	-654.1994	S	non-coral	south
QUAD-1351	23.4973	29.0674	0.0001	-662.3438	S	non-coral	south
QUAD-1352	28.7032	44.1656	-2.9312	-676.2506	S	non-coral	south
QUAD-1356	7.7401	21.3761	-0.4565	-674.7413	S	non-coral	south
QUAD-1361	3.8223	278.9457	-0.2955	-671.1057	S	non-coral	south
QUAD-1362	2.1152	295.0993	0.0000	-674.5244	S	non-coral	south
QUAD-1363	2.7875	320.8570	-0.0690	-674.5244	S	non-coral	south
QUAD-1364	2.8427	318.9472	-0.1132	-665.8187	S	non-coral	south
QUAD-1365	2.8564	285.2350	-0.3400	-665.8187	S	non-coral	south
QUAD-1366	2.6495	292.7788	0.0621	-665.8187	S	non-coral	south
QUAD-1367	2.0361	314.6818	-0.1556	-660.5938	S	non-coral	south
QUAD-1368	4.0134	282.9609	0.0233	-660.5938	S	non-coral	south
QUAD-1369	5.1849	275.4460	-0.2665	-660.5938	S	non-coral	south
QUAD-137	10.9330	239.8275	1.0433	-1053.9325	S	non-coral	head
QUAD-1370	6.4450	276.9203	0.1611	-657.3538	S	non-coral	south
QUAD-1371	7.3144	276.6795	-0.3554	-657.3538	S	non-coral	south
QUAD-1372	6.2694	265.3594	0.3611	-657.3538	S	non-coral	south
QUAD-1373	4.0054	267.2940	0.7134	-657.8756	S	non-coral	south
QUAD-1374	2.3883	288.4217	-0.4822	-654.7325	S	non-coral	south
QUAD-1375	3.2916	268.8370	0.0233	-654.7325	S	non-coral	south
QUAD-1376	3.0174	282.1690	0.1000	-654.7325	S	non-coral	south
QUAD-1377	3.2110	286.4964	-0.2689	-651.2750	S	non-coral	south
QUAD-1378	3.4527	272.4532	0.0344	-651.2750	S	non-coral	south
QUAD-1379	3.3086	285.9531	0.0289	-648.3100	S	non-coral	south
QUAD-1380	1.6941	275.3876	0.1445	-648.3100	S	non-coral	south
QUAD-1381	2.8926	277.6148	-0.0244	-649.5787	S	non-coral	south
QUAD-1382	2.8697	277.6583	-0.0954	-649.5787	S	non-coral	south
QUAD-1383	4.3389	287.0750	-0.0878	-647.4669	S	non-coral	south
QUAD-1384	2.2677	288.9942	-0.0001	-647.4669	S	non-coral	south
QUAD-1385	2.6407	271.8456	-0.1178	-645.3682	S	non-coral	south
QUAD-1386	2.4027	268.4820	-0.0222	-645.3682	S	non-coral	south
QUAD-1387	2.1822	267.0757	0.1167	-645.3682	S	non-coral	south
QUAD-1388	2.3450	277.4073	0.0723	-643.7913	S	non-coral	south

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-1389	2.1673	266.6333	-0.0001	-643.7913	S	non-coral	south
QUAD-1390	1.9632	265.3517	0.0611	-643.9357	S	non-coral	south
QUAD-1391	1.7128	249.0754	0.4955	-643.9357	S	non-coral	south
QUAD-1392	1.1781	231.0839	0.0378	-639.9606	S	non-coral	south
QUAD-1393	1.9911	262.1953	-0.1745	-639.9606	S	non-coral	south
QUAD-1394	1.9909	247.0732	0.1166	-639.9606	S	non-coral	south
QUAD-1395	1.8052	280.6680	0.2278	-638.1031	S	non-coral	south
QUAD-1396	1.7722	308.8021	-0.0134	-638.1031	S	non-coral	south
QUAD-1397	1.9945	308.3279	-0.0656	-638.1031	S	non-coral	south
QUAD-1398	2.0923	267.5128	-0.0268	-636.2950	S	non-coral	south
QUAD-1399	1.0426	328.7363	-0.0001	-636.2950	S	non-coral	south
QUAD-1400	3.1239	304.8431	0.0499	-636.2950	S	non-coral	south
QUAD-1401	3.2896	268.5450	0.5610	-633.2794	S	non-coral	south
QUAD-1402	3.4470	232.8347	-0.3333	-633.2794	S	non-coral	south
QUAD-1403	1.9081	286.8190	0.1779	-633.2794	S	non-coral	south
QUAD-1404	2.7840	280.0000	-0.0001	-633.2794	S	non-coral	south
QUAD-1405	1.4989	275.2967	-0.0721	-630.7794	S	non-coral	south
QUAD-1406	3.5633	236.8300	-0.1544	-630.7794	S	non-coral	south
QUAD-1407	2.7941	247.4779	0.2721	-628.8181	S	non-coral	south
QUAD-1408	3.0560	281.0999	-0.4034	-628.8181	S	non-coral	south
QUAD-1409	2.8123	276.4931	-0.1555	-628.8181	S	non-coral	south
QUAD-1410	1.6965	246.8018	-0.0001	-625.6806	S	non-coral	south
QUAD-1411	2.7991	258.8605	-0.1666	-625.6806	S	non-coral	south
QUAD-1412	2.1715	259.0188	0.0001	-624.0981	S	non-coral	south
QUAD-1413	1.4718	230.2816	0.0806	-624.0981	S	non-coral	south
QUAD-1414	2.5493	242.9888	0.0000	-624.0981	S	non-coral	south
QUAD-1415	2.3365	237.6276	0.2588	-622.2050	S	non-coral	south
QUAD-1416	1.0525	226.5313	-0.0887	-622.2050	S	non-coral	south
QUAD-1417	1.6290	249.2624	-0.1002	-622.2050	S	non-coral	south
QUAD-1418	0.5670	217.0095	-0.3010	-621.5112	S	non-coral	south
QUAD-1419	0.8799	252.7478	0.0000	-622.4981	S	non-coral	south
QUAD-1420	0.7563	278.4748	-0.1722	-622.0175	S	non-coral	south
QUAD-1421	1.8036	251.4860	0.0389	-622.0175	S	non-coral	south
QUAD-1422	0.8771	258.4840	0.2224	-622.0175	S	non-coral	south
QUAD-1423	1.4979	129.2240	0.7378	-620.8918	S	non-coral	south
QUAD-1424	1.0296	312.9012	0.0292	-620.8918	S	non-coral	south
QUAD-1425	1.3946	296.7449	-0.1421	-620.8918	S	non-coral	south
QUAD-1426	2.1386	231.2217	0.3789	-621.1044	S	non-coral	south
QUAD-1427	1.2295	112.8461	0.4288	-618.9006	S	non-coral	south
QUAD-1428	1.6450	120.2897	-0.0402	-618.9006	S	non-coral	south
QUAD-1429	1.5810	151.1140	0.0778	-619.2350	S	non-coral	south
QUAD-1430	2.0632	162.0831	-0.0967	-619.2350	S	non-coral	south
QUAD-1431	2.7348	186.6771	-0.0001	-619.2350	S	non-coral	south
QUAD-1432	1.5678	203.6633	-0.0943	-619.3369	S	non-coral	south
QUAD-1433	4.0992	289.7714	0.1178	-619.3369	S	non-coral	south
QUAD-1434	3.2592	296.9458	0.5214	-617.6013	S	non-coral	south
QUAD-1435	1.4134	218.0248	0.9173	-617.6013	S	non-coral	south
QUAD-1436	1.7397	138.7437	0.2766	-616.1606	S	non-coral	south
QUAD-1437	0.7083	270.7780	-0.1412	-616.4875	S	non-coral	south
QUAD-1438	1.4981	159.3551	-0.1266	-616.4875	S	non-coral	south
QUAD-1439	1.2077	212.3010	-0.0355	-616.4875	S	non-coral	south
QUAD-1440	1.7276	8.4744	0.8910	-614.5550	S	non-coral	south
QUAD-1441	3.0310	251.1453	0.0933	-614.5550	S	non-coral	south
QUAD-1442	1.3356	227.3579	0.4991	-614.5550	S	non-coral	south
QUAD-1443	4.1027	205.8153	-1.2642	-611.0056	S	non-coral	south
QUAD-1444	3.0364	305.3394	1.0875	-611.0056	S	non-coral	south
QUAD-1445	2.6008	215.6744	0.1788	-611.0056	S	non-coral	south
QUAD-1446	0.9441	96.2804	0.1442	-610.5693	S	non-coral	south
QUAD-1447	5.3971	174.7021	0.4169	-610.5693	S	non-coral	south
QUAD-1448	1.8287	124.3869	-0.3851	-609.6694	S	non-coral	south

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-1449	1.3942	121.3925	1.1651	-609.6694	S	non-coral	south
QUAD-1450	0.6202	118.3478	-0.5878	-609.6694	S	non-coral	south
QUAD-1451	2.3874	226.3495	0.4011	-608.5457	S	non-coral	south
QUAD-1452	4.4650	162.9446	1.2366	-608.5457	S	non-coral	south
QUAD-1453	5.8047	118.2510	0.3250	-608.5457	S	non-coral	south
QUAD-1454	3.5322	339.0314	-0.6467	-606.8019	S	non-coral	south
QUAD-1456	7.5612	289.4668	0.9800	-1034.2737	S	non-coral	south
QUAD-1457	10.3433	277.3800	-0.0002	-1034.2737	S	non-coral	south
QUAD-1458	11.2715	271.6132	-0.3644	-1034.2737	S	non-coral	south
QUAD-1459	12.4490	283.4310	0.2432	-1034.2737	S	non-coral	south
QUAD-1460	10.5503	291.2316	1.0337	-1022.9207	S	non-coral	south
QUAD-1461	10.9974	285.9239	-0.5824	-1022.9207	S	non-coral	south
QUAD-1462	10.6020	291.6679	-0.0997	-1022.9207	S	non-coral	south
QUAD-1463	10.5056	305.2842	0.3395	-1022.9207	S	non-coral	south
QUAD-1464	10.6780	312.9767	0.6318	-998.7200	S	non-coral	south
QUAD-1465	11.4199	315.2005	-0.0511	-998.7200	S	non-coral	south
QUAD-1466	11.8507	305.9142	-0.4667	-1008.6425	S	non-coral	south
QUAD-1467	11.3329	304.2057	-0.7355	-997.2244	S	non-coral	south
QUAD-1468	14.3049	291.0494	-0.4233	-997.2244	S	non-coral	south
QUAD-1469	10.0200	325.9389	-0.7645	-997.2244	S	non-coral	south
QUAD-1470	10.6270	310.8754	-1.8568	-986.5319	S	non-coral	south
QUAD-1471	10.5257	299.8761	-0.1334	-986.5319	S	non-coral	south
QUAD-1472	10.5679	285.4390	-0.0499	-986.5319	S	non-coral	south
QUAD-1473	11.2985	285.9956	-0.1723	-976.5394	S	non-coral	south
QUAD-1474	12.2523	282.9198	0.0000	-976.5394	S	non-coral	south
QUAD-1475	7.5072	293.6090	-0.0688	-976.5394	S	non-coral	south
QUAD-148	2.6137	233.9115	0.0001	-1053.9325	S	non-coral	head
QUAD-151	10.8225	217.2655	0.6177	-1053.9325	S	non-coral	head
QUAD-1589	5.4209	72.3832	4.8903	-1070.1787	S	non-coral	south
QUAD-159	9.1713	213.8056	2.3651	-1053.9325	S	non-coral	head
QUAD-1590	11.1688	47.1271	1.9509	-1070.1787	S	non-coral	south
QUAD-1591	13.1027	6.7023	-2.2255	-1070.1787	S	non-coral	south
QUAD-1592	15.1724	337.9205	-0.5991	-1070.1787	S	non-coral	south
QUAD-1593	8.8452	242.8535	-0.0713	-1062.1650	S	non-coral	south
QUAD-1594	6.0123	214.7188	-0.7554	-1062.1650	S	non-coral	south
QUAD-1595	9.1770	234.6302	2.3822	-1056.9844	S	non-coral	south
QUAD-1596	0.2710	282.8976	0.3033	-1051.6450	S	non-coral	south
QUAD-1598	3.0455	240.6789	-1.2889	-1051.6450	S	non-coral	south
QUAD-1599	2.7623	291.0534	-0.7574	-1051.6450	S	non-coral	south
QUAD-1600	3.2646	274.8891	-1.6179	-1047.3481	S	non-coral	south
QUAD-1601	4.3198	257.8457	-0.2021	-1047.3481	S	non-coral	south
QUAD-1602	5.5612	254.8851	-0.7078	-1047.3481	S	non-coral	south
QUAD-1605	14.1891	252.9587	7.1854	-1035.2262	S	non-coral	south
QUAD-164	12.4908	182.9899	0.0001	-1053.9325	S	non-coral	head
QUAD-1656	6.3521	352.8038	-0.0100	-872.9456	S	non-coral	south
QUAD-1657	7.4092	351.2527	0.3622	-875.2375	S	non-coral	south
QUAD-1666	9.0302	327.4736	-1.3144	-858.6669	S	non-coral	south
QUAD-1667	11.0468	292.6540	0.6578	-858.6669	S	non-coral	south
QUAD-1668	11.9232	290.5473	0.1112	-858.6669	S	non-coral	south
QUAD-167	12.5864	209.7658	-2.0767	-1053.9325	S	non-coral	head
QUAD-1760	18.0680	288.5614	-2.4766	-710.7513	S	non-coral	south
QUAD-1763	33.7677	285.3035	2.3457	-695.5306	S	non-coral	south
QUAD-1792	11.7572	82.8167	-1.6443	-760.9519	S	non-coral	south
QUAD-1794	9.3924	77.3311	-2.2632	-768.0925	S	non-coral	south
QUAD-1795	3.3398	72.0004	-0.0840	-768.0925	S	non-coral	south
QUAD-1796	5.3156	94.7082	1.8211	-768.0925	S	non-coral	south
QUAD-1798	2.2990	94.2602	0.1446	-768.7525	S	non-coral	south
QUAD-1799	6.3110	200.3904	-4.7652	-769.7150	S	non-coral	south
QUAD-1800	14.9481	263.9080	-0.5666	-769.7150	S	non-coral	south
QUAD-1801	4.1081	78.1069	0.7828	-769.7150	S	non-coral	south

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-1802	7.1405	84.4481	-6.2139	-770.8438	S	non-coral	south
QUAD-1803	0.8906	89.9466	-0.7062	-770.8438	S	non-coral	south
QUAD-1804	2.8027	114.7183	-0.0472	-770.8438	S	non-coral	south
QUAD-1805	2.7170	62.9105	-0.6365	-772.3638	S	non-coral	south
QUAD-1806	5.2748	134.1723	-1.3453	-772.3638	S	non-coral	south
QUAD-1807	6.5182	219.3166	2.2382	-772.3638	S	non-coral	south
QUAD-1808	3.6708	238.8722	1.4500	-770.9031	S	non-coral	south
QUAD-1809	0.6763	27.8056	-0.0478	-770.9031	S	non-coral	south
QUAD-1810	1.5852	72.3403	-2.1857	-770.9031	S	non-coral	south
QUAD-1811	4.4842	228.1034	-0.7902	-770.0187	S	non-coral	south
QUAD-1812	3.0602	206.7717	1.6769	-770.0187	S	non-coral	south
QUAD-1813	2.9608	34.4962	1.3035	-770.0187	S	non-coral	south
QUAD-1814	2.9595	32.0215	0.2867	-767.1288	S	non-coral	south
QUAD-1815	0.3008	109.3934	-0.9623	-767.1288	S	non-coral	south
QUAD-1816	3.0035	241.1313	-0.2136	-767.1288	S	non-coral	south
QUAD-1817	6.7395	221.4666	0.5468	-766.3375	S	non-coral	south
QUAD-1818	8.2212	286.6176	0.7514	-766.3375	S	non-coral	south
QUAD-1819	2.3493	341.1061	2.4671	-766.3375	S	non-coral	south
QUAD-1820	3.8396	21.0830	-2.6453	-762.4138	S	non-coral	south
QUAD-1821	1.1860	272.0550	-1.2850	-762.4138	S	non-coral	south
QUAD-1822	8.6523	189.7054	-0.8276	-762.4138	S	non-coral	south
QUAD-1823	54.7083	29.9652	23.8314	-759.9431	S	non-coral	south
QUAD-183	22.3208	275.6598	3.5513	-1053.9325	S	non-coral	head
QUAD-184	22.7439	256.2406	-0.5135	-1053.9325	S	non-coral	head
QUAD-253	28.2631	225.3461	3.6067	-1053.9325	S	non-coral	head
QUAD-254	10.1484	116.9250	0.2316	-1053.9325	S	non-coral	head
QUAD-255	10.4207	109.7644	-0.1360	-1053.9325	S	non-coral	head
QUAD-258	6.7424	100.4466	0.2972	-1053.9325	S	non-coral	head
QUAD-259	6.8943	109.8733	-0.1622	-1053.9325	S	non-coral	head
QUAD-260	7.8823	98.5453	0.5366	-1053.9325	S	non-coral	head
QUAD-261	7.7287	94.2734	0.4088	-1053.9325	S	non-coral	head
QUAD-262	7.5810	111.8135	-0.6794	-1053.9325	S	non-coral	head
QUAD-263	7.6602	114.6809	0.2133	-841.0156	S	non-coral	head
QUAD-264	7.6862	105.5871	0.2872	-840.2463	S	non-coral	head
QUAD-265	7.0949	104.6011	0.0538	-844.9612	S	non-coral	head
QUAD-266	5.9291	92.8364	-0.6334	-844.9612	S	non-coral	head
QUAD-267	5.2597	126.3829	-0.2478	-844.9612	S	non-coral	head
QUAD-268	6.0386	122.3590	0.0238	-844.9612	S	non-coral	head
QUAD-269	5.1113	118.2417	0.0527	-848.4988	S	non-coral	head
QUAD-270	4.9930	110.1723	0.0862	-848.4988	S	non-coral	head
QUAD-271	3.9722	105.8039	-0.3745	-843.8419	S	non-coral	head
QUAD-272	2.8674	141.8818	-0.0649	-843.8419	S	non-coral	head
QUAD-273	2.1030	147.0705	-0.0734	-845.4200	S	non-coral	head
QUAD-274	2.3716	165.0718	-0.1872	-845.4200	S	non-coral	head
QUAD-275	2.5218	149.6338	0.4233	-845.4200	S	non-coral	head
QUAD-276	2.3951	149.6338	0.4233	-845.4200	S	non-coral	head
QUAD-277	2.3951	135.0780	-0.3273	-845.4200	S	non-coral	head
QUAD-278	1.1803	183.1050	-0.0484	-845.4675	S	non-coral	head
QUAD-279	1.7176	159.6275	0.4022	-845.4675	S	non-coral	head
QUAD-280	1.2329	241.8325	-0.0756	-847.1225	S	non-coral	head
QUAD-281	0.1070	193.4614	-0.2665	-847.1225	S	non-coral	head
QUAD-282	3.4396	182.8860	-0.2628	-842.5125	S	non-coral	head
QUAD-283	3.7729	173.9886	-0.4072	-842.5125	S	non-coral	head
QUAD-284	3.2752	197.1399	-0.0032	-842.5125	S	non-coral	head
QUAD-285	2.7722	211.7736	-0.1504	-841.9106	S	non-coral	head
QUAD-286	2.2150	204.8926	-0.1149	-841.9106	S	non-coral	head
QUAD-287	2.6480	223.4209	-0.0017	-841.9106	S	non-coral	head
QUAD-288	1.2247	226.5829	0.0545	-840.6412	S	non-coral	head
QUAD-289	1.0204	174.6598	-0.0118	-840.6412	S	non-coral	head
QUAD-290	1.9442	190.5347	-0.2571	-837.5294	S	non-coral	head

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-291	2.3860	201.1216	-0.3516	-837.5294	S	non-coral	head
QUAD-292	1.4064	188.4952	0.1971	-836.9781	S	non-coral	head
QUAD-293	3.5133	153.4442	-0.5356	-836.9781	S	non-coral	head
QUAD-294	2.7846	164.4614	0.3771	-836.9781	S	non-coral	head
QUAD-295	2.5976	166.7800	-0.0656	-836.9781	S	non-coral	head
QUAD-296	1.2210	177.3272	-0.8061	-834.6956	S	non-coral	head
QUAD-297	2.6612	163.9614	-0.5017	-834.6956	S	non-coral	head
QUAD-298	3.0987	211.7298	-0.5488	-834.6956	S	non-coral	head
QUAD-299	3.4133	297.1916	-0.0666	-828.2206	S	non-coral	head
QUAD-300	0.6347	249.1613	-1.2545	-828.2206	S	non-coral	head
QUAD-301	2.0775	233.8142	0.0156	-828.2206	S	non-coral	head
QUAD-302	4.5289	235.1888	0.0879	-822.9807	S	non-coral	head
QUAD-303	4.6920	251.3633	0.6250	-822.9807	S	non-coral	head
QUAD-304	6.5204	241.1797	0.2216	-822.9807	S	non-coral	head
QUAD-305	9.7232	247.5714	-0.1923	-818.4375	S	non-coral	head
QUAD-337	5.0855	168.5953	-0.0479	-775.2781	S	non-coral	head
QUAD-338	3.4930	173.5591	0.4789	-775.2781	S	non-coral	head
QUAD-339	3.8620	161.6023	0.0744	-777.2325	S	non-coral	head
QUAD-340	3.0694	159.8670	0.0723	-777.2325	S	non-coral	head
QUAD-341	2.4989	141.8483	0.0078	-777.2325	S	non-coral	head
QUAD-342	4.5550	168.9634	-0.4121	-777.2325	S	non-coral	head
QUAD-343	2.1777	161.6719	0.7678	-776.5338	S	non-coral	head
QUAD-344	3.3271	166.0371	-0.4778	-772.9825	S	non-coral	head
QUAD-345	5.2111	182.9154	-0.3312	-772.9825	S	non-coral	head
QUAD-346	4.0814	172.8883	0.4312	-772.9825	S	non-coral	head
QUAD-347	1.8478	148.5194	0.1566	-772.9825	S	non-coral	head
QUAD-348	1.5300	137.0233	-0.1577	-774.2806	S	non-coral	head
QUAD-349	1.7094	200.9157	-0.2455	-774.2806	S	non-coral	head
QUAD-350	1.2719	183.2266	0.1978	-774.2806	S	non-coral	head
QUAD-351	1.7647	173.2408	-0.0978	-774.2806	S	non-coral	head
QUAD-352	0.7272	144.7089	0.1388	-774.2806	S	non-coral	head
QUAD-353	1.3453	354.4685	-0.1333	-774.3500	S	non-coral	head
QUAD-354	7.3635	193.1396	-0.9246	-774.3500	S	non-coral	head
QUAD-355	5.1476	186.2927	0.9890	-770.4269	S	non-coral	head
QUAD-356	0.5061	185.4964	0.4510	-769.4569	S	non-coral	head
QUAD-357	1.9036	190.7677	-0.0099	-769.4569	S	non-coral	head
QUAD-358	2.5924	224.4784	-0.1345	-769.4569	S	non-coral	head
QUAD-359	3.6966	182.8585	0.0667	-767.5419	S	non-coral	head
QUAD-360	2.0027	209.3251	0.1012	-767.5419	S	non-coral	head
QUAD-361	2.9149	204.5444	-0.8032	-767.5419	S	non-coral	head
QUAD-362	6.6154	200.2930	-0.1376	-767.5419	S	non-coral	head
QUAD-363	4.3314	208.3785	0.3168	-759.8744	S	non-coral	head
QUAD-364	0.5013	251.3944	0.3600	-759.8744	S	non-coral	head
QUAD-365	1.2492	199.4987	-0.8433	-759.8744	S	non-coral	head
QUAD-366	4.8823	209.1750	-0.5389	-759.8744	S	non-coral	head
QUAD-367	5.9537	208.9716	0.1312	-759.8744	S	non-coral	head
QUAD-368	3.8819	212.9864	0.7099	-759.8744	S	non-coral	head
QUAD-369	4.6011	219.7345	-0.2956	-755.9969	S	non-coral	head
QUAD-370	4.8857	222.6026	0.3701	-755.9969	S	non-coral	head
QUAD-371	4.5876	247.0253	0.6422	-755.9969	S	non-coral	head
QUAD-372	5.0354	253.1586	-0.0945	-755.9969	S	non-coral	head
QUAD-373	7.7451	246.1726	-0.6989	-750.2969	S	non-coral	head
QUAD-374	8.5056	246.0030	-0.3210	-743.3181	S	non-coral	head
QUAD-375	9.6642	241.8632	-0.0222	-743.3181	S	non-coral	head
QUAD-376	9.4408	246.8595	0.5056	-743.3181	S	non-coral	head
QUAD-377	4.5243	245.5178	0.5800	-739.1844	S	non-coral	head
QUAD-378	3.6695	217.4847	-0.2655	-739.1844	S	non-coral	head
QUAD-379	5.0417	224.0939	0.1022	-739.1844	S	non-coral	head
QUAD-380	3.9057	234.9227	0.1434	-735.7481	S	non-coral	head
QUAD-381	4.7358	229.6106	-0.3145	-735.7481	S	non-coral	head
QUAD-382	6.2553	222.6893	-0.2000	-735.7481	S	non-coral	head

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-383	6.0513	220.1751	0.2679	-729.5656	S	non-coral	head
QUAD-384	4.7362	227.1734	0.3466	-725.7181	S	non-coral	head
QUAD-385	5.9477	224.8813	-0.3054	-725.7181	S	non-coral	head
QUAD-386	5.5342	226.1268	0.2445	-725.7181	S	non-coral	head
QUAD-387	5.2880	234.3929	-0.3622	-725.7181	S	non-coral	head
QUAD-388	4.2705	273.7223	-0.0067	-722.0662	S	non-coral	head
QUAD-389	5.3535	253.4934	-1.0490	-722.0662	S	non-coral	head
QUAD-390	9.1344	225.2941	-0.2856	-722.0662	S	non-coral	head
QUAD-391	9.7956	232.4392	0.2234	-722.0662	S	non-coral	head
QUAD-392	8.3384	250.3430	0.3446	-722.0662	S	non-coral	head
QUAD-393	8.2497	252.7943	0.2855	-708.8350	S	non-coral	head
QUAD-394	9.1792	249.9859	-0.0767	-708.8350	S	non-coral	head
QUAD-395	8.2584	248.5121	0.3068	-708.8350	S	non-coral	head
QUAD-396	6.3070	265.7627	0.2877	-693.3275	S	non-coral	head
QUAD-398	7.7505	230.7897	-0.3134	-693.3275	S	non-coral	head
QUAD-399	7.0041	243.9184	0.5468	-693.3275	S	non-coral	head
QUAD-400	5.6324	256.1731	-0.0900	-685.2412	S	non-coral	head
QUAD-401	6.6005	244.7103	0.1533	-685.2412	S	non-coral	head
QUAD-402	5.7578	261.7559	0.3410	-685.2412	S	non-coral	head
QUAD-403	8.2772	273.2999	-0.3390	-685.2412	S	non-coral	head
QUAD-404	9.1076	266.6026	-0.7111	-669.6732	S	non-coral	head
QUAD-405	11.3746	249.7009	0.0590	-669.6732	S	non-coral	head
QUAD-406	10.6386	254.2988	-0.5111	-669.6732	S	non-coral	head
QUAD-407	12.2934	253.9725	0.1144	-669.6732	S	non-coral	head
QUAD-408	10.6302	261.8146	0.6468	-655.0212	S	non-coral	head
QUAD-420	14.9358	295.1156	-0.4247	-1039.0551	S	non-coral	head
QUAD-421	14.9358	295.1156	-0.4247	-1039.0551	S	non-coral	head
QUAD-422	14.9862	299.9970	0.0789	-1022.8819	S	non-coral	head
QUAD-423	18.3470	293.1413	-0.2001	-1022.8819	S	non-coral	head
QUAD-424	18.2410	292.5521	0.1711	-995.9069	S	non-coral	head
QUAD-427	21.7017	303.6288	-0.3112	-995.9069	S	non-coral	head
QUAD-428	19.4481	303.4680	1.5666	-983.4900	S	non-coral	head
QUAD-429	17.0490	301.9720	-0.4059	-983.4900	S	non-coral	head
QUAD-430	14.9961	304.3714	0.3022	-983.4900	S	non-coral	head
QUAD-431	15.0754	321.5860	-1.9438	-983.4900	S	non-coral	head
QUAD-432	15.0092	310.2278	-0.6899	-983.4900	S	non-coral	head
QUAD-433	16.9040	317.4821	-2.1402	-983.4900	S	non-coral	head
QUAD-434	14.6302	325.9785	0.4700	-970.3868	S	non-coral	head
QUAD-435	13.8567	310.0666	-0.0001	-970.3868	S	non-coral	head
QUAD-436	13.8483	302.4133	0.3400	-970.3868	S	non-coral	head
QUAD-437	13.7699	308.7234	-1.5745	-960.0925	S	non-coral	head
QUAD-438	11.9736	314.6552	0.9745	-960.0925	S	non-coral	head
QUAD-439	16.2550	313.1003	0.6066	-960.0925	S	non-coral	head
QUAD-440	12.9515	332.1473	0.0000	-949.5000	S	non-coral	head
QUAD-441	11.7657	330.3274	0.4443	-949.5000	S	non-coral	head
QUAD-442	8.3956	331.5394	-0.7010	-949.5000	S	non-coral	head
QUAD-443	12.3706	329.2625	1.1288	-931.0406	S	non-coral	head
QUAD-444	9.4236	330.2391	-0.1956	-931.0406	S	non-coral	head
QUAD-445	12.3720	311.6940	0.4755	-913.8419	S	non-coral	head
QUAD-446	9.4133	332.1299	0.6379	-913.8419	S	non-coral	head
QUAD-447	7.6000	338.5767	0.6733	-913.8419	S	non-coral	head
QUAD-448	10.2653	333.2209	-2.3655	-910.0625	S	non-coral	head
QUAD-449	12.4470	321.3762	-0.7724	-898.4619	S	non-coral	head
QUAD-450	8.0987	310.2805	0.0000	-898.4619	S	non-coral	head
QUAD-451	5.8874	316.5499	-1.6622	-890.9138	S	non-coral	head
QUAD-452	9.7226	322.9670	-0.4067	-890.9138	S	non-coral	head
QUAD-453	10.7403	315.0062	-0.0045	-890.9138	S	non-coral	head
QUAD-454	9.9247	309.3570	-0.2689	-890.9138	S	non-coral	head
QUAD-455	13.3284	305.4937	0.0000	-882.7706	S	non-coral	head
QUAD-456	9.8272	302.6585	0.4778	-882.7706	S	non-coral	head

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-457	10.0070	292.7053	-0.0001	-872.6537	S	non-coral	head
QUAD-458	9.7684	297.7993	0.1310	-872.6537	S	non-coral	head
QUAD-459	12.6676	295.8651	-0.6233	-872.6537	S	non-coral	head
QUAD-460	10.0100	297.9886	1.0611	-862.3025	S	non-coral	head
QUAD-461	11.2033	290.8598	-1.1944	-862.3025	S	non-coral	head
QUAD-462	11.5161	271.5855	-0.1733	-862.3025	S	non-coral	head
QUAD-463	12.0958	276.9350	-0.1311	-862.3025	S	non-coral	head
QUAD-464	11.8263	284.1599	-0.6689	-862.3025	S	non-coral	head
QUAD-465	11.7738	286.5699	-0.0178	-849.6119	S	non-coral	head
QUAD-466	11.0688	286.2990	0.9545	-840.6494	S	non-coral	head
QUAD-467	12.7115	289.0462	-0.8956	-840.6494	S	non-coral	head
QUAD-468	14.5828	287.0847	0.7301	-840.6494	S	non-coral	head
QUAD-469	11.8839	289.6859	-0.1556	-824.1844	S	non-coral	head
QUAD-470	18.6201	296.0517	0.0999	-824.1844	S	non-coral	head
QUAD-471	16.0711	298.1848	2.0523	-824.1844	S	non-coral	head
QUAD-472	13.1512	302.3997	0.4789	-824.1844	S	non-coral	head
QUAD-473	11.9279	299.9973	0.5944	-812.4506	S	non-coral	head
QUAD-474	7.0298	309.0299	1.4955	-812.4506	S	non-coral	head
QUAD-475	7.1505	290.8303	0.6011	-805.8169	S	non-coral	head
QUAD-476	8.4203	289.6897	0.6066	-805.8169	S	non-coral	head
QUAD-477	9.7608	290.5715	-0.1733	-805.8169	S	non-coral	head
QUAD-478	13.6481	296.7473	-0.4456	-791.7137	S	non-coral	head
QUAD-479	16.9970	289.7720	-1.1534	-791.7137	S	non-coral	head
QUAD-480	22.0201	285.1740	-0.8256	-791.7137	S	non-coral	head
QUAD-481	23.3610	283.1141	-0.0001	-791.7137	S	non-coral	head
QUAD-482	15.6060	290.6249	0.6312	-757.4100	S	non-coral	head
QUAD-483	13.6321	300.1569	-0.1968	-757.4100	S	non-coral	head
QUAD-484	18.3482	293.3151	-0.1266	-743.3331	S	non-coral	head
QUAD-486	22.8729	288.8609	-0.4823	-743.3331	S	non-coral	head
QUAD-487	25.1927	287.2504	0.0388	-728.9519	S	non-coral	head
QUAD-488	25.0598	287.1086	0.0000	-728.9519	S	non-coral	head
QUAD-489	20.2950	287.2414	1.8156	-728.9519	S	non-coral	head
QUAD-490	11.1103	296.2971	0.8365	-728.9519	S	non-coral	head
QUAD-491	9.9828	302.4706	-1.0355	-728.9519	S	non-coral	head
QUAD-492	11.0988	307.3241	0.1055	-718.2525	S	non-coral	head
QUAD-493	8.8094	309.9102	0.3168	-709.2250	S	non-coral	head
QUAD-494	9.4009	312.1779	0.0835	-709.2250	S	non-coral	head
QUAD-495	23.0138	304.6441	0.0541	-1232.8269	S	non-coral	head
QUAD-496	23.0138	304.6441	0.0541	-1216.8362	S	non-coral	head
QUAD-497	24.8787	307.0057	-1.0505	-1216.8362	S	non-coral	head
QUAD-498	25.4436	309.1019	-0.6267	-1216.8362	S	non-coral	head
QUAD-499	22.5314	307.7060	-0.0106	-1216.8362	S	non-coral	head
QUAD-500	19.5496	297.9667	-0.7189	-1216.8362	S	non-coral	head
QUAD-501	19.5496	297.9667	-0.7189	-1216.8362	S	non-coral	head
QUAD-502	20.1616	304.0168	-5.1501	-1216.8362	S	non-coral	head
QUAD-503	21.9850	296.2353	-1.8544	-1216.8362	S	non-coral	head
QUAD-504	23.7579	303.2374	-2.0841	-1196.1656	S	non-coral	head
QUAD-505	25.8374	306.0626	0.2065	-1196.1656	S	non-coral	head
QUAD-506	20.7271	299.5714	0.6815	-1174.6188	S	non-coral	head
QUAD-507	19.4073	296.9047	-0.0446	-1174.6188	S	non-coral	head
QUAD-508	18.8647	296.7564	-0.1956	-1174.6188	S	non-coral	head
QUAD-509	18.8671	294.2429	-0.3979	-1154.3862	S	non-coral	head
QUAD-510	22.5787	300.1953	-2.6772	-1154.3862	S	non-coral	head
QUAD-511	28.0052	310.3882	-2.9556	-1154.3862	S	non-coral	head
QUAD-512	27.1902	311.2487	-0.2161	-1154.3862	S	non-coral	head
QUAD-513	23.3736	302.1490	0.2285	-1154.3862	S	non-coral	head
QUAD-514	20.5683	297.4738	1.6412	-1154.3862	S	non-coral	head
QUAD-515	18.2281	301.3420	0.3533	-1133.3281	S	non-coral	head
QUAD-516	17.9277	302.9149	0.2985	-1133.3281	S	non-coral	head
QUAD-517	16.0413	304.9734	0.6619	-1133.3281	S	non-coral	head

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-518	17.0202	307.1960	-0.0933	-1133.3281	S	non-coral	head
QUAD-519	19.3742	314.6618	-0.3043	-1086.9525	S	non-coral	head
QUAD-520	18.5067	310.5234	0.7222	-1075.2694	S	non-coral	head
QUAD-521	16.5486	301.3928	-0.0309	-1075.2694	S	non-coral	head
QUAD-522	15.3628	281.4653	3.2938	-1075.2694	S	non-coral	head
QUAD-523	12.7609	252.5182	3.0831	-1075.2694	S	non-coral	head
QUAD-524	14.4144	236.9593	-2.0541	-1075.2694	S	non-coral	head
QUAD-525	13.3297	261.1218	-2.3049	-1075.2694	S	non-coral	head
QUAD-526	15.0438	308.5715	-4.2219	-1062.6182	S	non-coral	head
QUAD-527	18.3002	323.3049	-3.6422	-1062.6182	S	non-coral	head
QUAD-528	22.9933	339.3592	-2.1876	-1062.6182	S	non-coral	head
QUAD-529	24.1797	347.6423	1.5593	-1062.6182	S	non-coral	head
QUAD-530	21.8748	344.4958	2.8944	-1023.8337	S	non-coral	head
QUAD-531	17.0321	333.8283	1.2845	-1023.8337	S	non-coral	head
QUAD-532	17.3459	325.5127	0.5740	-1023.8337	S	non-coral	head
QUAD-533	16.3649	318.7365	-0.2267	-1023.8337	S	non-coral	head
QUAD-534	21.6635	305.6756	0.4810	-1023.8337	S	non-coral	head
QUAD-535	22.5751	308.3354	0.2151	-1023.8337	S	non-coral	head
QUAD-536	22.3312	310.7765	0.3389	-1008.0363	S	non-coral	head
QUAD-537	19.0695	314.2383	0.3979	-1008.0363	S	non-coral	head
QUAD-538	17.8005	315.4417	0.2067	-1008.0363	S	non-coral	head
QUAD-539	20.4233	301.9519	0.1044	-1008.0363	S	non-coral	head
QUAD-540	19.8253	298.9584	-0.0001	-975.5644	S	non-coral	head
QUAD-541	20.1457	315.6350	-1.7255	-954.4156	S	non-coral	head
QUAD-542	20.2260	314.9329	-1.0368	-954.4156	S	non-coral	head
QUAD-543	21.9815	313.7899	0.3878	-954.4156	S	non-coral	head
QUAD-544	17.3108	313.6005	-0.0057	-939.3557	S	non-coral	head
QUAD-545	18.0523	304.1696	0.8188	-939.3557	S	non-coral	head
QUAD-546	18.9838	292.5193	0.4094	-939.3557	S	non-coral	head
QUAD-547	19.5182	303.8876	0.2236	-939.3557	S	non-coral	head
QUAD-548	16.9837	300.2642	1.2911	-923.8725	S	non-coral	head
QUAD-549	18.9391	300.1101	-1.1268	-923.8725	S	non-coral	head
QUAD-550	20.2043	307.5969	0.3953	-910.0625	S	non-coral	head
QUAD-551	17.7767	298.1837	0.4077	-910.0625	S	non-coral	head
QUAD-552	16.7486	293.0458	1.7739	-910.0625	S	non-coral	head
QUAD-553	16.1391	292.9621	0.4154	-891.3675	S	non-coral	head
QUAD-554	14.9368	299.7234	0.9091	-891.3675	S	non-coral	head
QUAD-555	19.0758	294.1388	1.1049	-891.3675	S	non-coral	head
QUAD-556	17.5320	292.7070	0.8153	-891.3675	S	non-coral	head
QUAD-557	21.3377	329.5678	3.6747	-891.3675	S	non-coral	head
QUAD-558	19.5605	319.7334	1.7120	-874.5938	S	non-coral	head
QUAD-559	15.4375	315.4515	1.8575	-874.5938	S	non-coral	head
QUAD-560	27.6591	308.8321	-8.3343	-874.5938	S	non-coral	head
QUAD-561	16.4305	251.6911	-0.7951	-857.0556	S	non-coral	head
QUAD-562	15.9252	279.0565	0.2339	-846.1831	S	non-coral	head
QUAD-563	22.4512	308.6297	-4.8503	-846.1831	S	non-coral	head
QUAD-564	25.1204	304.6037	1.7531	-846.1831	S	non-coral	head
QUAD-565	12.4297	286.6084	-0.3829	-846.1831	S	non-coral	head
QUAD-566	11.9945	260.6862	-0.2230	-846.1831	S	non-coral	head
QUAD-567	6.7591	260.9004	-0.0001	-837.7706	S	non-coral	head
QUAD-568	7.7137	293.1839	-1.5050	-837.7706	S	non-coral	head
QUAD-569	6.0124	277.6432	-0.2874	-837.7706	S	non-coral	head
QUAD-570	12.2404	279.6810	-1.3604	-837.7706	S	non-coral	head
QUAD-571	12.8569	287.8054	0.4531	-822.6244	S	non-coral	head
QUAD-572	10.1347	276.7322	0.4126	-822.6244	S	non-coral	head
QUAD-574	10.9374	311.4282	0.1122	-822.6244	S	non-coral	head
QUAD-575	9.9204	301.6884	-0.2643	-812.3768	S	non-coral	head
QUAD-576	8.5150	313.1511	2.0835	-812.3768	S	non-coral	head
QUAD-577	10.5439	307.3315	0.0001	-812.3768	S	non-coral	head
QUAD-578	8.9750	288.7828	-1.6806	-812.3768	S	non-coral	head

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-579	15.5260	321.7460	0.1416	-790.4406	S	non-coral	head
QUAD-580	11.3652	316.4167	0.6257	-785.5156	S	non-coral	head
QUAD-581	8.9036	336.6343	2.5626	-785.5156	S	non-coral	head
QUAD-582	9.9108	306.0073	-0.4955	-785.5156	S	non-coral	head
QUAD-583	11.1736	288.4315	-1.0579	-775.1294	S	non-coral	head
QUAD-584	7.1894	277.2056	0.7023	-775.1294	S	non-coral	head
QUAD-585	6.6290	310.5363	-1.2493	-775.1294	S	non-coral	head
QUAD-586	9.8297	321.8910	-5.3323	-775.1294	S	non-coral	head
QUAD-587	12.1121	300.2234	0.2680	-775.1294	S	non-coral	head
QUAD-588	11.4930	322.6196	-2.7980	-759.1625	S	non-coral	head
QUAD-589	18.6833	307.8399	-0.6158	-734.6575	S	non-coral	head
QUAD-590	22.3174	310.6787	-10.1620	-734.6575	S	non-coral	head
QUAD-591	20.2861	314.9686	-2.4763	-708.5831	S	non-coral	head
QUAD-592	18.8989	313.2798	-0.7139	-708.5831	S	non-coral	head
QUAD-593	31.2628	313.6869	-9.3694	-708.5831	S	non-coral	head
QUAD-594	27.5026	326.4301	0.3075	-708.5831	S	non-coral	head
QUAD-595	34.5739	320.9798	-0.9003	-708.5831	S	non-coral	head
QUAD-599	15.4426	328.8049	1.0454	-687.4257	S	non-coral	head
QUAD-600	11.6327	322.7589	1.0565	-671.9900	S	non-coral	head
QUAD-601	4.5232	316.0105	0.4166	-667.9637	S	non-coral	head
QUAD-602	4.7555	323.8424	-0.0745	-667.9637	S	non-coral	head
QUAD-603	4.9732	341.1142	0.0966	-667.9637	S	non-coral	head
QUAD-604	4.1099	341.9864	0.0621	-667.9637	S	non-coral	head
QUAD-605	4.1033	340.0758	-0.1000	-665.4350	S	non-coral	head
QUAD-606	4.5090	326.1582	0.1478	-665.4350	S	non-coral	head
QUAD-607	4.6004	320.8977	-0.3112	-665.4350	S	non-coral	head
QUAD-608	6.0403	308.3589	0.3134	-665.4350	S	non-coral	head
QUAD-609	3.4141	298.1568	1.0256	-649.9750	S	non-coral	head
QUAD-610	4.8250	302.3927	-0.0455	-649.9750	S	non-coral	head
QUAD-611	4.6641	306.3180	0.9943	-649.9750	S	non-coral	head
QUAD-612	3.7498	335.3792	0.1633	-649.9750	S	non-coral	head
QUAD-622	30.7593	341.5234	-0.5916	-977.4469	S	non-coral	flank
QUAD-623	27.6716	343.4385	-0.1983	-977.4469	S	non-coral	flank
QUAD-665	1.8050	170.5119	-0.4044	-717.0612	S	non-coral	flank
QUAD-666	2.5429	176.8980	0.0484	-717.0612	S	non-coral	flank
QUAD-667	5.7831	118.9397	-0.0156	-719.7568	S	non-coral	flank
QUAD-668	2.9976	120.4438	0.2972	-719.7568	S	non-coral	flank
QUAD-670	4.9525	132.4980	-0.0356	-721.5819	S	non-coral	flank
QUAD-671	5.1408	145.4775	-0.1583	-721.5819	S	non-coral	flank
QUAD-672	3.5913	156.0061	-0.8213	-721.5819	S	non-coral	flank
QUAD-673	2.8440	204.7597	-0.1404	-727.0594	S	non-coral	flank
QUAD-674	2.9362	209.1432	0.1484	-727.0594	S	non-coral	flank
QUAD-675	0.6778	97.5155	0.0210	-727.0594	S	non-coral	flank
QUAD-676	0.2027	12.7928	0.5250	-728.2537	S	non-coral	flank
QUAD-677	1.6364	104.0255	0.0712	-728.2537	S	non-coral	flank
QUAD-678	2.4693	121.1908	0.1294	-728.2537	S	non-coral	flank
QUAD-679	2.8373	123.7784	-0.0684	-728.2537	S	non-coral	flank
QUAD-680	3.1324	114.5488	-0.1089	-728.2537	S	non-coral	flank
QUAD-681	2.1463	186.7784	0.1562	-728.1318	S	non-coral	flank
QUAD-682	1.8457	135.5084	0.5033	-728.1318	S	non-coral	flank
QUAD-683	2.3986	124.5312	0.1573	-728.1318	S	non-coral	flank
QUAD-684	1.9023	170.7136	0.1133	-726.1975	S	non-coral	flank
QUAD-685	2.3386	152.8548	0.2007	-725.1000	S	non-coral	flank
QUAD-686	3.3581	149.1732	0.1173	-725.1000	S	non-coral	flank
QUAD-687	4.3033	182.1784	-0.1349	-725.1000	S	non-coral	flank
QUAD-688	2.6079	197.1590	0.2395	-725.1000	S	non-coral	flank
QUAD-689	1.5459	152.6910	0.1166	-724.4525	S	non-coral	flank
QUAD-690	2.2057	160.9966	-0.3622	-724.4525	S	non-coral	flank
QUAD-691	2.1534	172.9008	0.2733	-724.4525	S	non-coral	flank
QUAD-692	1.0541	154.7770	0.2134	-728.4263	S	non-coral	flank

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-693	2.0334	113.7712	0.2549	-728.4263	S	non-coral	flank
QUAD-694	1.5265	110.3422	-0.6811	-729.1188	S	non-coral	flank
QUAD-695	0.5429	244.0601	-0.2233	-729.1188	S	non-coral	flank
QUAD-696	0.9226	221.1507	0.4306	-729.1188	S	non-coral	flank
QUAD-697	2.6294	94.9950	-0.1279	-729.1188	S	non-coral	flank
QUAD-698	2.5459	116.6424	-0.1417	-728.7412	S	non-coral	flank
QUAD-699	0.7165	58.7197	-0.1523	-728.7412	S	non-coral	flank
QUAD-700	1.2455	127.7329	-0.1738	-729.4313	S	non-coral	flank
QUAD-701	1.8838	135.3928	0.1545	-729.4313	S	non-coral	flank
QUAD-702	2.1515	116.4641	-0.0956	-729.4313	S	non-coral	flank
QUAD-703	0.8600	127.7074	-0.1351	-731.8438	S	non-coral	flank
QUAD-704	0.4417	106.2219	0.0967	-731.8438	S	non-coral	flank
QUAD-705	1.4972	75.3821	0.5200	-731.8438	S	non-coral	flank
QUAD-706	2.6616	64.9360	0.1801	-731.8438	S	non-coral	flank
QUAD-707	2.1981	68.6878	-0.1399	-732.5756	S	non-coral	flank
QUAD-708	1.3775	60.1031	0.1456	-732.5756	S	non-coral	flank
QUAD-709	0.7966	50.1469	0.0004	-732.5756	S	non-coral	flank
QUAD-710	2.0834	83.7004	0.3383	-732.5756	S	non-coral	flank
QUAD-711	1.4329	81.5570	-0.3510	-732.8187	S	non-coral	flank
QUAD-712	1.0528	317.0794	0.0332	-732.8187	S	non-coral	flank
QUAD-713	1.2307	88.8747	-0.1071	-732.8187	S	non-coral	flank
QUAD-714	0.1898	71.7988	0.0178	-733.5457	S	non-coral	flank
QUAD-715	0.7099	71.9087	0.1595	-733.5457	S	non-coral	flank
QUAD-716	0.4884	14.3969	-0.0662	-734.1219	S	non-coral	flank
QUAD-717	1.0700	274.3036	0.0466	-737.2050	S	non-coral	flank
QUAD-718	1.3583	281.7423	-0.1190	-737.2050	S	non-coral	flank
QUAD-719	2.0089	272.5395	-0.2157	-736.5450	S	non-coral	flank
QUAD-720	2.6269	277.6534	0.0183	-736.5450	S	non-coral	flank
QUAD-721	5.4825	301.1776	-0.1823	-729.4981	S	non-coral	flank
QUAD-722	12.6718	294.4695	-0.6818	-729.4981	S	non-coral	flank
QUAD-723	12.6718	294.4695	-0.6818	-715.4981	S	non-coral	flank
QUAD-724	15.2978	303.3544	0.5478	-715.4981	S	non-coral	flank
QUAD-725	22.0025	311.6490	-0.4712	-694.7238	S	non-coral	flank
QUAD-726	22.0025	311.6490	-0.4712	-694.7238	S	non-coral	flank
QUAD-732	15.7209	311.7491	-0.8634	-1231.4551	S	non-coral	flank
QUAD-733	15.8204	318.2402	-0.2466	-1231.4551	S	non-coral	flank
QUAD-734	15.0182	304.9590	-0.9452	-1231.4551	S	non-coral	flank
QUAD-735	17.7635	311.3458	0.0143	-1231.4551	S	non-coral	flank
QUAD-736	14.2834	309.5984	0.1012	-1182.0519	S	non-coral	flank
QUAD-737	18.5384	310.5819	0.7007	-1182.0519	S	non-coral	flank
QUAD-738	21.3902	326.5372	-0.5077	-1168.0475	S	non-coral	flank
QUAD-739	28.2701	329.0967	-2.8409	-1168.0475	S	non-coral	flank
QUAD-740	29.6015	328.5334	-0.5927	-1168.0475	S	non-coral	flank
QUAD-741	28.6598	329.2973	0.2930	-1168.0475	S	non-coral	flank
QUAD-743	29.3905	330.4898	-1.5966	-1168.0475	S	non-coral	flank
QUAD-744	30.9326	331.7592	0.5594	-1168.0475	S	non-coral	flank
QUAD-745	33.2104	328.9928	-0.2501	-1147.9399	S	non-coral	flank
QUAD-746	32.1987	330.0415	1.3236	-1147.9399	S	non-coral	flank
QUAD-747	32.3391	329.9416	-1.6779	-1093.6606	S	non-coral	flank
QUAD-748	35.6218	328.2621	1.2178	-1093.6606	S	non-coral	flank
QUAD-749	32.2873	330.5216	0.8271	-1093.6606	S	non-coral	flank
QUAD-751	30.7739	333.0154	-0.2279	-1093.6606	S	non-coral	flank
QUAD-752	31.5397	335.7627	-0.6257	-1073.1312	S	non-coral	flank
QUAD-753	31.6565	335.3224	0.0437	-1073.1312	S	non-coral	flank
QUAD-755	34.4629	328.4375	-0.4608	-1073.1312	S	non-coral	flank
QUAD-756	32.1990	326.2684	0.9445	-1073.1312	S	non-coral	flank
QUAD-757	30.0688	327.1395	0.9305	-1073.1312	S	non-coral	flank
QUAD-758	28.0556	332.7056	-0.2240	-1054.6469	S	non-coral	flank
QUAD-759	29.5863	336.1417	-0.5652	-1054.6469	S	non-coral	flank
QUAD-760	32.2330	333.9494	-0.4382	-1054.6469	S	non-coral	flank

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-761	32.8585	332.8614	0.3362	-1054.6469	S	non-coral	flank
QUAD-762	30.0668	335.0209	1.3676	-1006.6256	S	non-coral	flank
QUAD-765	23.0825	331.6701	-0.8983	-992.2650	S	non-coral	flank
QUAD-766	26.0716	324.6495	-1.0491	-992.2650	S	non-coral	flank
QUAD-767	27.5854	329.7151	0.0443	-992.2650	S	non-coral	flank
QUAD-768	26.6487	329.3105	0.2340	-992.2650	S	non-coral	flank
QUAD-769	27.8327	327.1785	-1.3539	-992.2650	S	non-coral	flank
QUAD-770	30.6541	326.3871	-0.7827	-992.2650	S	non-coral	flank
QUAD-785	30.7953	344.1525	0.0178	-856.4131	S	non-coral	flank
QUAD-803	30.3823	11.8573	-0.2644	-797.2087	S	non-coral	flank
QUAD-806	33.6511	8.5594	0.3005	-797.2087	S	non-coral	flank
QUAD-807	30.5161	11.1037	1.6167	-797.2087	S	non-coral	flank
QUAD-812	27.5068	10.3170	-2.4044	-795.3850	S	non-coral	flank
QUAD-813	27.5068	10.3170	-2.4044	-795.3850	S	non-coral	flank
QUAD-824	22.5592	337.0426	0.2178	-754.0200	S	non-coral	flank
QUAD-834	7.0172	330.2329	-0.3578	-735.3868	S	non-coral	flank
QUAD-835	6.3274	331.8302	0.1894	-734.2162	S	non-coral	flank
QUAD-836	6.1396	336.5990	-0.3644	-734.2162	S	non-coral	flank
QUAD-837	5.9875	329.2726	-0.4417	-734.2162	S	non-coral	flank
QUAD-838	7.1951	329.4285	-0.7471	-734.2162	S	non-coral	flank
QUAD-839	6.9157	331.9962	0.2549	-734.2162	S	non-coral	flank
QUAD-841	4.3138	333.9408	0.2962	-717.3862	S	non-coral	flank
QUAD-842	4.2220	320.2757	0.3027	-717.3862	S	non-coral	flank
QUAD-843	2.9517	320.3780	0.3789	-717.3862	S	non-coral	flank
QUAD-844	2.4793	326.5135	-0.4111	-717.3862	S	non-coral	flank
QUAD-845	2.4793	326.5135	-0.4111	-717.3862	S	non-coral	flank
QUAD-891	36.1480	297.3569	-0.1829	-686.1437	S	non-coral	flank
QUAD-892	35.5934	291.2357	0.9496	-686.1437	S	non-coral	flank
QUAD-893	20.3688	278.6773	3.7607	-694.8706	S	non-coral	flank
QUAD-895	19.4018	296.8972	0.0440	-969.0081	S	non-coral	flank
QUAD-896	23.0000	295.3322	-0.9294	-969.0081	S	non-coral	flank
QUAD-905	36.1251	309.8826	1.0860	-836.6244	S	non-coral	flank
QUAD-909	36.7783	307.4695	-0.2945	-800.5969	S	non-coral	flank
QUAD-911	39.4337	307.9739	-0.3260	-800.5969	S	non-coral	flank
QUAD-912	40.1698	308.6794	0.3101	-800.5969	S	non-coral	flank
QUAD-945	8.3320	68.4985	5.2618	-747.1269	S	non-coral	flank
QUAD-946	19.8840	179.4005	-0.9861	-751.0669	S	non-coral	flank
QUAD-947	16.4694	175.4027	0.1772	-753.8187	S	non-coral	flank
QUAD-948	15.2867	174.5311	-0.1407	-753.8187	S	non-coral	flank
QUAD-949	12.4770	178.7773	-0.1394	-762.6063	S	non-coral	flank
QUAD-950	12.8632	162.1711	0.1060	-762.6063	S	non-coral	flank
QUAD-958	21.7815	316.3532	1.3966	-957.2687	S	non-coral	flank
QUAD-959	19.2120	319.4418	0.6666	-957.2687	S	non-coral	flank
QUAD-960	17.4296	318.5459	0.3282	-957.2687	S	non-coral	flank
QUAD-961	17.6923	319.9863	0.4449	-957.2687	S	non-coral	flank
QUAD-962	20.0943	321.7545	0.1745	-930.3531	S	non-coral	flank
QUAD-963	21.6895	326.7033	0.0250	-930.3531	S	non-coral	flank
QUAD-965	20.0539	331.0909	0.2823	-917.9419	S	non-coral	flank
QUAD-966	20.4002	329.0901	0.5051	-917.9419	S	non-coral	flank
QUAD-968	15.6843	330.1458	-0.0694	-917.9419	S	non-coral	flank
QUAD-969	16.8938	329.5905	-0.9265	-917.9419	S	non-coral	flank
QUAD-973	21.9999	324.2334	-0.0617	-869.8856	S	non-coral	flank
QUAD-974	24.5159	325.2949	-0.1877	-869.8856	S	non-coral	flank
QUAD-975	25.4344	327.4868	0.8650	-869.8856	S	non-coral	flank
QUAD-977	25.6463	326.5495	-0.3505	-869.8856	S	non-coral	flank
QUAD-978	28.9791	321.6647	-0.3604	-848.1937	S	non-coral	flank
QUAD-979	28.3554	322.6273	-0.3577	-848.1937	S	non-coral	flank
QUAD-980	28.6280	324.5580	-0.4222	-796.8969	S	non-coral	flank
QUAD-999	41.6551	320.7094	-2.3217	-1020.0956	S	non-coral	flank
QUAD-018	3.2124	283.5228	1.4510	-1002.5018	SD	non-coral	head

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-054	4.9106	167.0618	0.6443	-926.4288	SD	non-coral	head
QUAD-055	4.8429	187.4302	-1.0611	-921.9675	SD	non-coral	head
QUAD-117	9.2346	284.7585	0.3779	-754.2250	SD	non-coral	head
QUAD-118	8.0878	275.7547	-0.4702	-750.6531	SD	non-coral	head
QUAD-124	9.0365	234.7484	-0.7022	-732.0606	SD	non-coral	head
QUAD-1315	6.7856	308.1737	-0.3811	-718.3319	SD	non-coral	south
QUAD-1317	6.0653	301.0412	-1.7289	-714.1044	SD	non-coral	south
QUAD-1318	6.0351	307.5388	-0.1944	-714.1044	SD	non-coral	south
QUAD-1319	6.2078	320.1898	-0.8466	-714.1044	SD	non-coral	south
QUAD-1320	5.7775	317.8050	0.4813	-707.3962	SD	non-coral	south
QUAD-1321	9.7662	348.3616	-0.1833	-707.3962	SD	non-coral	south
QUAD-1324	4.8419	342.2661	0.2626	-715.8431	SD	non-coral	south
QUAD-1325	5.1908	344.8752	-0.8204	-715.8431	SD	non-coral	south
QUAD-1326	3.5929	255.2627	-0.2367	-715.8431	SD	non-coral	south
QUAD-1327	5.1063	257.6143	-0.0389	-715.8431	SD	non-coral	south
QUAD-1328	5.5504	257.9647	-0.1057	-709.4437	SD	non-coral	south
QUAD-1329	5.9243	258.3634	0.1649	-709.4437	SD	non-coral	south
QUAD-1330	8.6337	234.1030	0.0799	-709.4437	SD	non-coral	south
QUAD-1331	7.9273	242.5860	-0.5333	-702.4287	SD	non-coral	south
QUAD-1332	8.7149	247.8055	-1.1946	-702.4287	SD	non-coral	south
QUAD-1333	10.8097	243.5652	-0.3290	-702.4287	SD	non-coral	south
QUAD-1334	8.3538	239.4373	-0.0354	-700.1650	SD	non-coral	south
QUAD-1335	8.0916	243.3771	-0.4367	-700.1650	SD	non-coral	south
QUAD-1336	9.6981	236.7643	-0.6356	-700.1650	SD	non-coral	south
QUAD-1337	10.3266	229.5810	0.2566	-700.1650	SD	non-coral	south
QUAD-1338	7.0717	231.5769	0.2560	-682.5631	SD	non-coral	south
QUAD-1339	8.9992	207.1479	0.6451	-682.5631	SD	non-coral	south
QUAD-1350	18.2197	29.7606	1.1744	-662.3438	SD	non-coral	south
QUAD-1353	16.4264	38.1314	-1.1577	-676.9269	SD	non-coral	south
QUAD-1354	19.6540	25.8726	-0.9612	-676.9269	SD	non-coral	south
QUAD-1355	12.7493	21.3991	-0.0001	-676.9269	SD	non-coral	south
QUAD-1357	5.6671	21.9277	-0.1832	-674.7413	SD	non-coral	south
QUAD-1358	2.3832	352.5036	-0.2744	-674.7413	SD	non-coral	south
QUAD-1359	1.6627	316.9022	-0.0610	-674.7413	SD	non-coral	south
QUAD-1360	1.4031	330.4413	-0.1765	-671.1057	SD	non-coral	south
QUAD-1797	3.8151	109.0581	-0.2476	-768.0925	SD	non-coral	south
QUAD-306	8.2911	240.5949	0.4089	-818.4375	SD	non-coral	head
QUAD-307	5.8470	243.8500	0.3546	-818.4375	SD	non-coral	head
QUAD-308	4.7737	268.9473	-0.5110	-806.5512	SD	non-coral	head
QUAD-309	4.5677	248.8336	-0.1179	-806.5512	SD	non-coral	head
QUAD-310	4.3537	284.9332	-1.0922	-806.5512	SD	non-coral	head
QUAD-311	3.9123	263.6566	-0.0573	-806.5512	SD	non-coral	head
QUAD-312	0.6648	301.3385	0.3818	-803.4925	SD	non-coral	head
QUAD-313	1.0676	279.3517	0.2050	-803.4925	SD	non-coral	head
QUAD-314	2.5530	224.5730	-0.0501	-803.4925	SD	non-coral	head
QUAD-315	2.4717	223.4890	0.1323	-803.4925	SD	non-coral	head

Table A.3. Quadrat number, seabed terrain features, substrate type, habitats and site locations

Quadrat	Slope (°)	Aspect (°)	Rugosity	Depth (m)	Substrate	Habitat	Site location
QUAD-316	2.1261	225.3031	-0.5377	-803.1150	SD	non-coral	head
QUAD-317	3.6822	247.8628	-0.2090	-803.1150	SD	non-coral	head
QUAD-318	4.2950	242.6288	0.1600	-803.1150	SD	non-coral	head
QUAD-319	4.3207	204.8038	-0.3312	-803.1150	SD	non-coral	head
QUAD-320	6.9903	199.2607	0.0801	-803.1150	SD	non-coral	head
QUAD-321	6.7916	198.5573	0.6022	-802.1731	SD	non-coral	head
QUAD-322	3.7106	222.2565	0.4101	-802.1731	SD	non-coral	head
QUAD-323	3.8581	216.8786	0.6321	-802.1731	SD	non-coral	head
QUAD-324	3.5395	230.4301	-0.0045	-802.1731	SD	non-coral	head
QUAD-325	2.1940	247.2644	1.0034	-796.7250	SD	non-coral	head
QUAD-326	2.1193	336.1592	0.3299	-796.7250	SD	non-coral	head
QUAD-327	2.0654	335.8327	0.2922	-796.7250	SD	non-coral	head
QUAD-328	1.5301	258.1207	-0.4434	-791.7263	SD	non-coral	head
QUAD-329	3.4218	234.6641	-0.1754	-790.1025	SD	non-coral	head
QUAD-330	4.6320	235.0098	-0.0145	-790.1025	SD	non-coral	head
QUAD-331	4.9539	226.7262	0.2321	-790.1025	SD	non-coral	head
QUAD-332	2.1693	235.6976	0.1223	-786.9031	SD	non-coral	head
QUAD-333	1.1485	235.9519	-0.1111	-786.9031	SD	non-coral	head
QUAD-334	4.7025	204.6694	-0.2589	-786.9031	SD	non-coral	head
QUAD-335	4.8161	181.8982	0.0566	-786.8438	SD	non-coral	head
QUAD-397	6.5543	249.9873	0.0744	-693.3275	SD	non-coral	head
QUAD-409	8.7064	289.3982	0.2911	-655.0212	SD	non-coral	head
QUAD-485	20.1725	289.9010	0.0612	-743.3331	SD	non-coral	head
QUAD-573	8.9850	296.0883	1.4824	-822.6244	SD	non-coral	head
QUAD-624	26.6774	334.0277	0.1418	-977.4469	SD	non-coral	flank
QUAD-772	30.8576	326.3643	-0.5100	-944.8269	SD	non-coral	flank
QUAD-781	26.0382	340.1541	0.1285	-932.3019	SD	non-coral	flank
QUAD-782	27.2049	340.3734	-0.1096	-932.3019	SD	non-coral	flank
QUAD-783	28.8318	342.4900	0.2228	-916.4275	SD	non-coral	flank
QUAD-784	28.8318	342.4900	0.2228	-916.4275	SD	non-coral	flank
QUAD-786	29.4682	349.2203	0.6082	-856.4131	SD	non-coral	flank
QUAD-788	32.3316	351.8520	-1.0938	-856.4131	SD	non-coral	flank
QUAD-798	31.8805	3.6154	-0.1185	-858.4431	SD	non-coral	flank
QUAD-804	31.9380	11.1303	-0.5422	-797.2087	SD	non-coral	flank
QUAD-809	27.7937	14.9601	-0.1650	-797.2087	SD	non-coral	flank
QUAD-829	18.3045	344.0541	0.6771	-754.0200	SD	non-coral	flank
QUAD-840	5.0748	341.8290	0.0932	-734.2162	SD	non-coral	flank

Appendix 7

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