

Using biological traits analysis to investigate ecological functioning of cold-water coral reefs



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Thesis presented for the degree of Doctor of Philosophy

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There is the sea, vast and spacious, teeming with creatures beyond number –
living things both large and small

Psalm 104:25

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Abstract

Cold-water coral reefs are fragile, slow growing systems that are found in all oceans. Past research has focused on the species assemblages found on cold-water coral reefs. The species found on cold-water coral reefs are representative of the species assemblages found in the surrounding waters, with almost no true obligate reef species. No past studies have attempted to determine if biological traits differ on and off the reef, or between reef zones. Norwegian cold-water coral reefs are well-studied; however, the sites that have been identified as likely cold-water coral reefs in South Africa remain under-studied. This thesis leverages the well-documented Norwegian reefs as a means to predict functioning on South African reefs. To this end, the following questions are addressed: 1) does the location of cold-water reefs off the coast of Norway account for variations in species assemblages, 2) are the functional traits on and near cold-water coral reefs related to environmental factors, and 3) does the location of the reef account for variations in trait assemblages? Video transects conducted on coral reefs by the Norwegian habitat mapping program MAREANO (www.Mareano.no) were used to investigate taxonomic and trait differences between nine reef sites off the coast of Norway. The relationships between taxa found at the sites and the environmental conditions were investigated using ordination, specifically, distance-based redundancy analysis (db-RDA). Traits were assigned to each taxon observed using fuzzy coding (0-3). Information for these trait codes was obtained from The Arctic Traits Database, Polytraits, MARLIN, and FishBase. Traits were assigned for 59 taxa that were not included in established trait databases via literature review. The relationships between biological traits and environmental factors were investigated using a combined RLQ fourth-corner method. Additionally, the community-weighted means of traits were investigated using redundancy analysis (RDA). The species assemblages were significantly influenced by the longitude and latitude of the site, in addition to other environmental variables. The result of the RDA performed on community-weighted means indicated that longitude and latitude explained a significant proportion of the variance in biological traits. The burrow dwelling trait was found to be significantly associated with sandy mud and pebble bottom types, and negatively associated with coral substrata. This was the only significant trait association, indicating that cold-water coral reefs might not have a defined trait assemblage associated with the reef structure. However, it could also be indicative of substantial “area of influence” around each reef, since all subsamples were taken within 400m of a cold-water coral reef, and the majority of sites had coral within 100m. More comparative studies between the results of biological trait analyses and sampling methods (video vs grab vs trawl, etc.) are required in order to quantify observation biases in traits as a result of sampling methodology or experimental design. The findings of this thesis support the idea that reefs aggregate local species, offering refuges and benefits, rather than acting as a host to true obligate reef species.

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In the words of Captain Haddock: “Billions of blue blistering barnacles”. What a journey this doctorate has been.

Chapter 1

Introduction

Abstract

In this chapter, the general framework for the thesis as a whole is set out. Cold-water coral reefs are found in all the world's oceans and are known hotspots for biodiversity. Reefs in the northern Atlantic have been well studied. The reefs are made up of three different zones (living coral, dead coral, and coral rubble), each of which provide different habitat features attracting different taxa. In general, Bivalvia, Polychaeta and Echinodermata are associated with the living and dead parts of the reef. Past studies have identified suspension feeding as associating with the living and dead reef zones, while deposit feeding dominated the dead reef zones. Little is known about cold-water corals in South African waters, but it is hypothesised that the taxa present would have similar functionality to those on other cold-water coral reef systems. The species found on cold-water coral reefs can be affected by the location of the reef and the local framing of the reef. Thus, a more functional approach is necessary to compare reefs over large distances. Biological traits can be used to compare ecosystems and, if these traits are functional, they can be used to infer functioning of these systems. Understanding biological traits and their functional implications feeds into building ecosystem models that can be used to better investigate the flow of energy on cold-water coral reefs. In order to address the hypothesised general functioning of cold-water coral reef systems, two hypotheses were addressed. The first of these is that the geographical location of reef sites will explain at least in part the species found on them, since the local species pool changes with location. Local species pools can be the result of restriction of species movements between largely separated areas; however, on the scale of this thesis they are likely the result of local environmental factors that were not measured in the dataset. The second was that environmental factors other than location will explain the traits found on cold-water coral reefs, and that the reefs themselves will have similar trait profiles. Reefs are expected to have similar trait profiles, since traits group taxa that are functionally similar together. Similarly functioning systems will have similar trait profiles, thus the trait profile generated from well-studied cold-water coral reef systems can be used to infer the trait profile on other reefs. The expected traits can be related back to the local species pool, thus predicting what taxa might be found on South African reefs.

1.1 Introduction

1.1.1 Research concept

Species can be seen as a collection of specific functional traits. The prevalence of these functional traits in a system can provide information on how similar systems with different species might function, and allow for functional comparison without considering the impact of species diversity between

sites (de Juan et al., 2022).

Cold-water coral reefs are found around the world, yet the flow of energy on these reefs is relatively understudied. Of particular interest is the “aggregation effect” that cold-water coral reefs seem to have, where the abundance of marine organisms on the reef is greater than off the reef (Price2021; Fosså et al., 2002; Costello et al., 2005; Roberts et al., 2006; Henry and Roberts, 2016). Both benthic and pelagic organisms are found on cold-water coral reefs (e.g Mortensen and Fosså, 2006; Kutti et al., 2014). Thus, cold-water coral reefs may play an important role in benthic-pelagic coupling, through both vertical and horizontal transfers.

The hypothesis that trophic interactions, mediated by the presence of *Lophelia pertusa* (Linnaeus, 1758) (now synonymous with *Desmophyllum pertusum* (Linnaeus, 1758) (Addamo et al., 2016)), accounted for the increased abundance of many taxa observed on cold-water coral reefs was investigated by de Haast (2019) using a trophic model. The research made use of data for the general southern Benguela as no data existed for local cold-water coral reefs, although reefs were suspected to be present in the southern Benguela. de Haast (2019) found that trophic interactions alone did not account for the increased abundance observed on cold-water coral reefs. This finding suggested that cold-water coral reefs should be modelled using platforms that allow for the modelling of physical nutrient movement. Furthermore, de Haast (2019) did not make use of data from actual reef observations but rather assumed that the biomass of species found on cold-water coral reefs was related directly to the biomass of species in the broader ecosystem.

This project will build off the findings of de Haast (2019) overcoming the data deficiency in South African waters by quantifying similarities and differences between Norway reefs in terms of biological traits. Using biological traits rather than species allows for transferable generalisations about cold-water coral reef systems in other parts of the world. Such conceptual generalisations allow for targeted research questions to be proposed, potentially unlocking funding for direct sampling.

1.2 Framework

1.2.1 Cold-water coral reefs

Cold-water corals are a globally distributed subset of the paraphyletic group of corals (Roberts et al., 2009). Despite the attention given to their tropical counterparts, the majority of coral species are found at depths greater than 50m (i.e. 65% of 5160 known species in 2007, Cairns, 2007; Roberts et al., 2009). All cold-water corals are azooxanthellate and thus obtain all their energy from consumption (Carlier et al., 2009; Roberts et al., 2009). Cold-water corals are not contained by a single clade within the coral group. Instead, cold-water coral species are spread across nearly all families of corals. As such, there are both reef-building and non-reef building species of cold-water corals. Both forms are found in all the world's oceans (Freiwald et al., 2021). The first record of cold-water corals is from Norway in 1752 (English translation: (Pontoppidan, 1755)); however, these corals were likely known to fishers before this. Older research uses the term “deep-water coral” to refer to cold-water corals. This term, however, is a misnomer as it implies that all of these organisms are found at “depth”. While some cold-water corals have been recorded at depths in excess of 3000m (Squires, 1959) in Trondheimsfjorden, Norway, the coral *Paragorgia arborea* has been observed at depths as shallow as 30m

(Svensen et al., 1998). Cold-water corals are not sensitive to pressure; thus, they are able to survive over a vast range of depths. They are instead temperature sensitive, hence the preferred nomenclature (Buhl-Mortensen et al., 2014).

Lophelia pertusa is both the most studied and a cosmopolitan reef-building cold-water coral species; these factors make it ideal for discussing the environmental range of cold-water corals in general (de Haast, 2019). Temperature, salinity and sea water density restrict the range of cold-water corals. For *L. pertusa* the temperature range is between 4°C and 14°C (Roberts et al., 2006; Freiwald et al., 2009; Roberts et al., 2009; Davies and Guinotte, 2011) and salinities between 33 and 37 are tolerated (Freiwald, 2002). Cold-water coral reefs are restricted to waters with sigma-theta densities between 27.35 to 27.65 kg m⁻³ (Dullo et al., 2008). Cold-water corals are not pressure sensitive. However, the density of sea water is non-linearly related to pressure, salinity and temperature. Pressure is directly related to depth, thus, the density requirement of cold-water corals can restrict them to specific depth zones in different water masses. In addition to these environmental requirements, cold-water coral reefs are typically found in relatively swift currents (Thiem et al., 2006; Oakham, 2009). *Lophelia pertusa* is a passive suspension feeder that utilizes a wide range of food sources ranging in size from dissolved organic matter (DOM) to mesozooplankton (Duineveld et al., 2007; van Oevelen et al., 2009; Mueller et al., 2014). *Lophelia* is found across almost the full extent of the depth range over which cold-water corals are found; it has been observed in Trondheimsfjorden at depths of 50m (Mortensen and Fosså, 2001) while Squires (1959) reports depths in excess of 3000m.

It was previously thought that cold-water coral reefs obtained their organic carbon from methane seeps (Hovland et al., 1994; Henriot et al., 1998; Hovland and Risk, 2003). This hypothesis has since been refuted; little overlap was found between the species observed on gas seeps and cold-water coral reefs (Cordes et al., 2008). The hypothesis was further refuted by the $\delta^{13}\text{C}$ signatures of cold-water corals which are inconsistent with the consumption of gas seep supported food sources (Duineveld et al., 2004). This suggests that photosynthetic primary production supports the carbon requirement of cold-water corals (Duineveld et al., 2004; Davies et al., 2009). However, surface production from the water above the reefs cannot represent the only source of nutrients for cold-water corals (Khripounoff et al., 2014). Hydrodynamics, including internal waves and tidal effects, play a critical role in providing allochthonous food to cold-water coral reefs (Mienis et al., 2007; de Froe et al., 2022). Inherent in this is the concept that the benthic habitat of cold-water corals must then interact with the pelagic habitat in which primary production takes place.

Lophelia pertusa reefs are hotspots for biodiversity (Dons, 1944; Rogers, 1999; Weaver et al., 2004; Henry and Roberts, 2016) across multiple spatial scales (Mortensen and Fosså, 2006). These reefs can take on a number of different shapes (Buhl-Mortensen et al., 2010). However, regardless of shape, the reef is made up of three distinct regions: live *Lophelia*, dead *Lophelia*, and *Lophelia* rubble (Buhl-Mortensen et al., 2010). This zonation pattern has been observed on a *Lophelia* outside the Northern Atlantic (Ghana: Buhl-Mortensen et al. (2017a); however, descriptions of other reefs outside the North Atlantic do not focus on zonation). This pattern of zonation was originally described for a “mound” shaped *Lophelia* reef, where the live *Lophelia* zone was found on the top of the reef, above the dead *Lophelia* zone (Buhl-Mortensen et al., 1995). All cold-water coral reefs have these zones; however, they are not always linearly distributed as in examples of cigar shaped reefs. The zones can be spread

out vertically or in a more patch work patter. However, given that the zones are related to reef growth there order is consistent; living coral representing the growing edge, followed by older dead coral, with coral rubble on the edges.

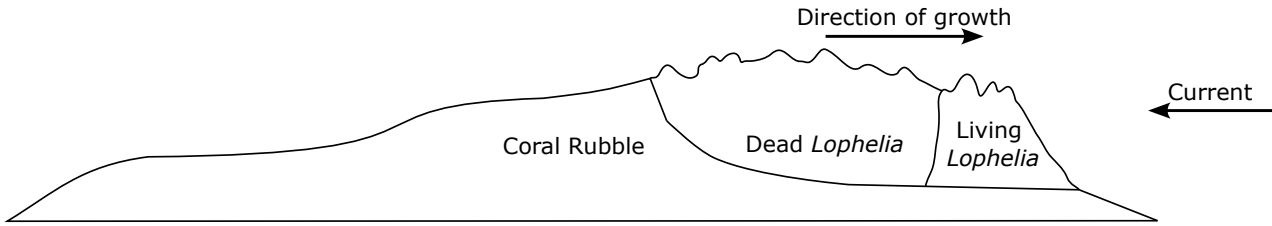


Figure 1.1: Simplified schematic of the reef zones for a cigar shaped reef, adapted from Buhl-Mortensen et al. (2017b). The transition between regions is smoother than the diagram suggests, particularly between the living and the dead zone. Diagram not to scale.

The live *Lophelia* zone is made up of the living and actively feeding part of the corals; the branches are covered with polyps (Buhl-Mortensen et al., 2017b). As this is the actively feeding part of the coral reef it is most often found oriented such that a fresh supply of nutrients is available (Buhl-Mortensen et al., 2017b), either at the top of the reef (Buhl-Mortensen et al., 1995) or facing the current (Buhl-Mortensen et al., 2010; Kutti et al., 2014; Cathalot et al., 2015; Buhl-Mortensen et al., 2017b). This is also the youngest part of the reef and its location represents the growing edge of the reef (Buhl-Mortensen et al., 2010). There is relatively low species richness associated with this part of the reef (Mortensen and Fosså, 2006; Buhl-Mortensen, 2017). The presence of a thin layer of living tissue over the corals (coenosarc) prevents attached organisms from easily colonising this zone (Freiwald et al., 2004; Buhl-Mortensen et al., 2017b). One of the notable examples of an attached organism in this zone is the polychaete *Eunice norvegica*, which associates with the actively feeding coral polyps (Buhl-Mortensen, 2001). The polychaete feeds on larger particles that are trapped by the coral polyps. This is possible as the coral polyps take longer to handle these particles compared to smaller ones, allowing time for *E. norvegica* to grab the particles from the coral polyps (Buhl-Mortensen, 2001; Mueller et al., 2013). Feeding studies have shown that there is no negative effect on the corals' carbon uptake in the presence of *Eunice norvegica* (Jensen and Frederiksen, 1992). Laboratory experiments suggest that the presence of *E. norvegica* plays a role in reef aggregation (Roberts, 2005), potentially by increasing calcification (Mueller et al., 2013). While there are no known predators of cold-water corals, *E. norvegica* attacks organisms that would otherwise invade the coral surface (Buhl-Mortensen, 2001). This, along with the presence of the coenosarc, explains the lack of biofouling in the live *Lophelia* zone.

The dead *Lophelia* zone represents the coral skeleton that was overgrown by new generations of *Lophelia*. As they are overgrown the older generations die out, most likely as a result of reduced water flow which limits the food supply (Buhl-Mortensen et al., 2017b). The lack of active *Lophelia* polyps leave the branches open to colonisation by other species (López Correa et al., 2005). This zone is found directly adjacent to the live *Lophelia* zone (Buhl-Mortensen et al., 1995; Mortensen and Fosså, 2006), representing the older portion of the reef. The lack of a coenosarc allows for colonisation by attached species. The sponge *Protanthea simplex* was found to dominate Additionally, mobile organisms, including fish, use the skeleton as a refuge (Buhl-Mortensen, 2017). As a result, the dead *Lophelia* zone has the highest species richness on the reef (Jensen and Frederiksen, 1992; Buhl-Mortensen et al., 1995; Buhl-Mortensen, 2017).

The coral rubble is the trailing edge of the reef. This is made up of degraded and broken coral fragments. In vertically orientated reefs the coral rubble zone is found at the base (Buhl-Mortensen et al., 1995). In current swept reefs this zone is found trailing the reef (Buhl-Mortensen, 2017). While this zone lacks the coenosarc present in the living zone, it also lacks the complex 3D structure of the coral skeleton in the dead *Lophelia* zone. This zone has the lowest species diversity of the three; however, species abundance is higher than in the living *Lophelia* zone (Mortensen and Fosså, 2006). Relative to the other two zones, this zone has a higher abundance of deposit feeders (Mortensen and Fosså, 2006). Beazley et al. noted a significant increase in cerianthid tube anemones in this zone during *Lophelia* reef recovery.

These regions each provide a different set of features to the reef community, therefore different species are associated with each region (Buhl-Mortensen, 2017). There are multiple spatial scales present within each reef, the reef as a whole differs from the surrounding seafloor; however, within the reef there are the reef zones. Even within the reef zones there are patches of other substrata. These multiple spatial scales present within the reef mean that these areas must all be considered when the functioning of the reef is discussed. Given that *Lophelia* reefs are hotspots for biodiversity, it is worth mentioning the taxa that are associated with them. In the next section taxa will be discussed as being associated with cold-water coral reefs; however, there are very few obligate cold-water coral reef species (i.e. only found on cold-water coral reefs) (Buhl-Mortensen et al., 2017b).

The prevalence of the three major feeding types (suspension-feeding, deposit-feeding, and predation) differs between the reef zones. Suspension-feeding is most prevalent in the live and dead *Lophelia* zones, while deposit feeders are most prevalent among the coral rubble (Mortensen and Fosså, 2006). Predation is less common than other feeding methods across all the reef zones and, in Mortensen and Fosså (2006), it was observed as being least common in the dead *Lophelia* zone. When comparing abundances on and off the reef, Henry and Roberts (2007) found that suspension feeders were significantly more abundant on the reef, while the inverse was true for deposit feeders. This is indicative of different sets of biological traits being associated with on and off the reef, as well as with the different reef zones. The distribution of biological traits on cold-water coral reefs, and the implications of these distributions on the understanding of reef function.

1.2.2 Taxa associated with *Lophelia* reefs

The taxa associated with *Lophelia* reefs have been studied on several reefs across the Atlantic. These studies make use of a range of different sampling techniques: grabs (Jensen and Frederiksen, 1992; Mortensen and Fosså, 2006), video footage from remotely operated vehicles (Mortensen and Fosså, 2006), triangular dredges (Mortensen and Fosså, 2006), and box cores (Henry and Roberts, 2007). When discussing these studies, caution must be taken to differentiate between the most abundant taxa, greatest richness, and most diverse, the latter taking into account both abundance and richness. For instance, Jensen and Frederiksen (1992) observed 13 different species of *Bivalvia* associated with dead *Lophelia*. There were 910 individuals, which made them the most abundant taxa present in the dead *Lophelia* zone but not the most species-rich group. Caution is advised as, given the range of papers discussed here, not all include descriptions of abundance, richness, and diversity. Additionally, counts are not directly comparable unless standardised to the same unit.

On the Faroe shelf when both the live and dead *Lophelia* samples were considered, the three most abundant groups were Polychaeta, Bivalvia, and Echinodermata (Jensen and Frederiksen, 1992). This agrees in part with the most abundant phyla collected from Sula Reef, Rødberg, Nordleksa, Midfjord, and Selliggrunnen, which found the phyla Foraminifera, Annelida (which contains Polychaeta) and Mollusca (which contains Bivalvia) to be the most abundant (Mortensen and Fosså, 2006). Porifera, while neither the most abundant nor species rich of the groups observed on *Lophelia* reefs, are strongly associated with the reef habitat. This is evident by the repeated presences of this group on sampled *Lophelia* reefs (e.g. Jensen and Frederiksen, 1992; Buhl-Mortensen et al., 1995; Henry and Roberts, 2007; Roberts et al., 2008; Buhl-Mortensen et al., 2017a). Their association with the reef is supported by their near absence from the surrounding seafloor is noted on the Porcupine Seabight (Southwest of Ireland) (Henry and Roberts, 2007), and their link to nutrient recycling on reefs (Rix et al., 2016, see section 1.2.3).

In Norwegian waters *Sebastes* species (redfish) are commonly observed on *Lophelia* reefs (Buhl-Mortensen et al., 1995; Järnegren and Kutti, 2008). Costello et al. (2005) observed pregnant *Sebastes* on a Norwegian reef. On *Lophelia* and *Madrepora oculata* reefs in the Central Mediterranean *Conger conger*, *Helicolenus dactylopterus*, and *Polyprion americanus* were found to be more abundant on reef environments compared to non-reef environments (D’Onghia et al., 2012). The fish associated with *Lophelia* reef in the Central Mediterranean differ from those in Norwegian waters; where *Brosme brosme*, *Galeus melastomus*, *Chimaera monstrosa* are found to aggregate on the reef (Freiwald, 2002; Costello et al., 2005; Kutti et al., 2014).

In addition to the specific fish taxa associating with cold-water coral reefs mentioned above, fishers have reported increased catch in the waters surrounding cold-water coral reefs for years (Fosså et al., 2000). Such is the recognised importance of cold-water coral reefs to fishers in Norway, that in the early 1990s they contacted the Institute for Marine Research out of concern about decreased catches, which they attributed to damaged reefs (Fosså et al., 2002). Fosså et al. (2002) made a number of important findings. First, through the use of ROV and multibeam echo sounders, they were able to confirm that fishers were very adept at identifying the locations of reefs. Second, they showed that bottom trawling had damaged between 30% and 50% of the *Lophelia* reefs in Norwegian waters. Finally, they showed that fish aggregate on cold-water coral reefs. Further studies support the claim that there is increased abundance of fishes on cold-water coral reefs compared with the surrounding waters (Costello et al., 2005; Mortensen et al., 2005; D’Onghia et al., 2012; Kutti et al., 2014). Fish caught on cold-water coral reefs tend to be larger than those caught in non-coral habitats (Husebø et al., 2002).

1.2.3 Functioning of cold-water coral reef systems

Benthic-pelagic coupling is defined as the linking of the benthic and pelagic zones, as a result of flows of nutrients and energy (Griffiths et al., 2017). This traditionally is viewed as the sinking of pelagic material to the benthos (e.g. Suess, 1980; Smetacek, 1985); however, the inverse is also possible. While the term sinking implies a passive event, zooplankton exhibit diel vertical migration and thus actively take part in benthic-pelagic coupling (Hutchinson, 1967).

Changes in the biomass of benthic organisms can impact the rest of the water column. In Chesapeake Bay, oyster beds used to provide a hard substrate, in an otherwise sandy sediment (Coen et al., 1999). A period of overfishing followed by disease reduced these oyster beds. The loss of oyster beds resulted in a massive decrease in water filtration (Kemp et al., 2005). The reduction in water filtration resulted in changes to the plankton concentrations in the water, altering the trophic dynamics of the benthos. This study, based on an estuarine system, highlights the importance of benthic-pelagic coupling, even in well-mixed systems. The massive 3-D structure of cold-water coral reefs (Roberts et al., 2006) is more structurally complex than these oyster beds. However, in both cases the loss of hard substrate might have abiotic impacts on other organisms. Likewise, cold-water corals and part of their associated fauna are suspension feeders (Duineveld et al., 2007; van Oevelen et al., 2009; Mueller et al., 2014). As with the loss of oyster beds, the loss of a cold-water coral reef would result in altered trophic dynamics in the region.

Cold-water coral reefs require external energy sources; since the $\delta^{13}\text{C}$ values on a studied reef were inconsistent with gas seeps (Duineveld et al., 2004), the external energy source that they utilise must be derived elsewhere. Lipid analysis of two species of cold-water coral, *L. pertusa* and *Madrepora oculata*, suggests that zooplankton formed a major part of their diet (Kiriakoulakis et al., 2005). The consumption of zooplankton by *Lophelia* (Freiwald, 2002) has been observed. The utilisation of both phytoplankton and zooplankton as nutrient sources has also been suggested by isotopic analysis on the reef (Duineveld et al., 2004; Carlier et al., 2009; Dodds et al., 2009; Mueller et al., 2014). The $\delta^{13}\text{C}$ signatures observed by Carlier et al. (2009) indicate that the carbon used as an energy source was of photosynthetic origin. In addition to the cold-water corals themselves, the community found on cold-water coral reefs must obtain their energy from somewhere. Both isotopic (Duineveld et al., 2007) and fatty acid (Kiriakoulakis et al., 2004) analysis indicates that the cold-water coral community is supported by phytodetritus. Apart from phytodetritus, the cold-water coral community relies on zooplankton as an energy source, indicated by food-web modelling (van Oevelen et al., 2009) and combined fatty acid analysis and isotope analysis (Kiriakoulakis et al., 2005; van Oevelen et al., 2018a). Seasonal changes in the colour of *Lophelia pertusa* have been detected, this change was hypothesised to be the result of increased consumption of calanoid copepods which contain the red pigment astaxanthin (Osterloff et al., 2019). These colour changes, coupled with increased polyp activity, in the period following a spring bloom suggest a heavy reliance of the diurnally migrating zooplankton *Calanus finmarchicus*. Fish on cold-water coral reefs have been observed using zooplankton as an energy source (Husebø et al., 2002). All of these studies show that the nutrients that enter cold-water coral reef systems as a result of currents or the sinking of organic material originate from surface waters. The availability of food has been linked to the rate at which physiological processes take place in cold-water corals (Naumann et al., 2011), highlighting the importance of nutrient supply. Food supply on cold-water coral reefs is linked to both surface production and local hydrodynamics, thus in some areas it is not consistent throughout the year (Khripounoff et al., 2014). This scaling of physiological processes might explain how some reefs are able to sustain themselves in these areas.

Despite their lack of zooxanthellae, cold-water corals produce a comparable amount of dissolved organic matter (DOM) to their tropical counterparts (Wild et al., 2008). Wild et al. (2008) raised the question of how azooxanthellate cold-water corals are able to spare the energy required to produce large amounts of DOM. This question has not been answered to date. However, the carbon to nitrogen

ratio (C:N) of cold-water coral derived DOM is lower than that of tropical corals (Wild et al., 2008; Rix et al., 2016). Tropical corals are found in oligotrophic waters (Muscatine and Porter, 1977), where nitrogen is often the limiting nutrient, which is not the case on cold-water coral reefs (de Froe et al., 2019). Incorporating nitrogen rich compounds into the coral mucus, while retaining more carbon, might explain the similar release rates between cold-water and tropical corals (Ward, 2008; Rix et al., 2016).

Cold-water corals are not the only sessile organisms present on the reef that are known to feed on planktonic groups. Sponges (Porifera) are found on both tropical (Wulff, 2001) and cold-water coral reefs (Fosså et al., 2000; Husebø et al., 2002; Roberts et al., 2006; Cordes et al., 2008). A large proportion (50-80%) of the coral mucus secreted by both cold-water and tropical corals is quickly dissolved in the water as DOM (Wild et al., 2004; Wild et al., 2008). Sponges have the ability to utilise DOM (de Goeij et al., 2013; Rix et al., 2016). While it was found that sponges on tropical reefs in the Caribbean did not associate with coral but rather with a ready source of particulate organic carbon (POC) (Lesser, 2006), it is likely that at depth where POC is limited the ability of sponges to recycle coral-derived DOM links them to the cold-water coral food-web. Furthermore, cold-water corals feed on a different size class of zooplankton to their associated sponges (Witte et al., 1997; Pile and Young, 2006), which means that the sponges' ability to utilise DOM gives them indirect access to more nutrients. Sponges have predators, cold-water corals do not; grazing on sponges may provide a route for carbon to re-enter the pelagic food web. Ecosystem modelling using a modified Ecopath with Ecosim model found it impossible to make the energy transferred up the food-web by the sponge loop significantly large without unbalancing the pelagic components by demanding too much energy from pelagic derived zooplankton in order to support the coral mucus production required (de Haast, 2019). Cold-water corals obtain at least some of their energy from lateral import into the reef system (Davies et al., 2009). This model did not include a term for lateral flow, which could explain why the impact of the sponge loop could not be made significant. When lateral flow is considered the sponge loop would act to capture and retain carbon in the system rather than allowing it to simply flow through. This feature may explain why cold-water coral reefs act as areas of aggregation.

The enhanced carbon recycling observed in cold-water coral regions in Norway supports the hypothesis that cold-water corals play a role in carbon cycling (White et al., 2012). de Froe et al. (2019) conclude that cold-water coral reefs play a role in carbon and nitrogen cycling at the habitat scale. These findings suggest that cold-water coral reefs are hotspots for benthic-pelagic coupling. Sponges, as mentioned before, are important in benthic-pelagic coupling (Lesser, 2006; Pile and Young, 2006). Cold-water corals and sponges are suspension feeders (Pile and Young, 2006); however, sponges actively divert water over their feeding apparatus (active filter feeder) while cold-water corals grab particles that float pass their feeding apparatus (passive suspension feeder). In Additionally their feeding preferences differ, with cold-water corals selectively handling their food particles, utilising a wide range of different size classes ranging from dissolved organic matter (DOM) to zooplankton such as *Meganycetophanes norvegica* and *Artemia* (~10mm) (Roberts and Anderson, 2002; Mueller et al., 2014). Sponges non-selectively filter large quantities of water (Gage and Tyler, 1991), consuming particulate carbon (POC) and ultrazooplankton, both of which are on the order of $10\mu m$ (Witte et al., 1997; Pile and Young, 2006). The differences in feeding method and size preference means that there is no competition between deep-water sponges and cold-water corals for food. The versatile diets of deep-water

sponges suggests that they play a role in both nitrogen and carbon cycling on cold-water coral reefs (Kazanidis et al., 2018).

In the open ocean only between 1% and 3% of primary production reaches depths of 1500m (Lutz et al., 2002). The diel vertical migration (DVM) of zooplankton is capped at depths on the order of hundreds of metres (Hutchinson, 1967). Cold-water corals are commonly associated with areas where hydrodynamic conditions would support the supply of both nutrients and food (Duineveld et al., 2004; Kiriakoulakis et al., 2007; Duineveld et al., 2012), or elevated features such as seamounts, banks and ridges (Freiwald et al., 2004; Roberts et al., 2006; Roberts et al., 2009) that might place them in the depth range of migrating zooplankton. This supports the idea that lateral flow into the system supplements the flow of food from the pelagic zone. While many cold-water coral reefs are found in areas where the conditions are “favourable”, healthy reefs have been observed in “unfavourable” conditions such as low pH (Georgian et al., 2016) or low oxygen concentrations (Hanz et al., 2019). What is notable about the reefs in these “unfavourable” conditions is that primary production in these areas is high (Georgian et al., 2016; Hanz et al., 2019). A high-resolution study of Eastern Atlantic cold-water coral reefs found that hydrographic and biogeochemical conditions are secondary for cold-water coral health (Juva et al., 2020). Rather, healthy reefs are associated with sites where local hydrodynamics ensure a good supply of food (Juva et al., 2020). These findings impact predictions about how cold-water coral reefs respond to climate change scenarios. They also suggest that there is a strong link between the corals themselves and the pelagic zone. While connected, it is conceptually important to consider the separation of surface production, the water column through which it must pass and the benthos. This is because, as nutrients move between these “compartments” there are biological and physical forces that can influence both the quantity and quality of nutrients that reach the reef. The importance of local hydrodynamics cannot be underestimated in its ability to support and retain nutrients in the reef system and thus must be included in any ecosystem model of a cold-water coral reef.

Understanding the hydrodynamics of reefs is important when considering the impact that benthic suspension feeders have on the water column. The assumption that the water column is well-mixed can lead to overestimates for the amount of energy that reaches benthic suspension feeders (Ackerman et al., 2001). This is especially true for deep-water environments where mixing of water layers is reduced. Ecosystem models are a tool, not just for predicting how pressures will affect the whole ecosystem, but also, to investigate pathways and interactions that are difficult to measure in situ, such as benthic-pelagic coupling (Griffiths et al., 2017).

1.2.4 The state of knowledge of cold-water corals in South Africa

There are cold-water corals in South African waters (Department of Environmental Affairs, 2014; Samaai et al., 2020; Filander et al., 2021); however, these systems are understudied (Sink, 2016). In general offshore and deep water habitats in South Africa are undersampled (Sink2019). A literature search on Primo using the parameters of either the title or subject containing “South Africa” (or variants of Africa) and any field containing “cold-water coral” (or variants of coral), returned only seven results. These results consisted of a masters thesis (de Haast, 2019), two newspaper articles, two technical reports (Sink et al., 2012; Department of Environmental Affairs, 2014) and two journal articles (Atkinson, 2009; Stevenson et al., 2015). A similar search on the SCOPUS database yielded no results.

The first paper returned by this search was de Haast (2019), the master’s dissertation that this doctorate aims to build upon. The findings of this study are described in the introduction to this chapter; however, it is worth reiterating that they in part indicate that more specific data for cold-water coral reef systems is needed in order to model the system. The lack of data representing species observations on cold-water coral reefs highlights the understudied nature of these habitats in South African waters.

Two of the results returned are the same newspaper article related to an operation by the South African government to determine the optimal location for future marine protected areas called “Operation Phakisa”. It is worth noting that the Primo search did not return any of the technical reports on Operation Phakisa. Further literature related to Operation Phakisa that was returned by this search contains the statement that cold-water coral habitats are poorly understood in South African waters (Sink, 2016). In the four years since this statement was made no literature focused on observing cold-water coral reefs in South African waters have been published. Furthermore, not a single result returned by this search related to observational studies, highlighting the lack of accessible information regarding the locations and observations of cold-water coral habitats in South Africa.

The technical reports related to Operation Phakisa are important for understanding the state of knowledge about cold-water coral reefs in South Africa. Two of these documents, Department of Environmental Affairs (2014) and Sink et al. (2012), outline some of the suspected locations of cold-water corals in South African waters. Some of these suspected sites are thought to include the reef-building *Lophelia*. Papers that do mention the locations of cold-water corals such as Atkinson (2009) and Stevenson (2003) do not focus on the corals. As of the end of the first quarter of 2023, no published peer-reviewed articles detailing the sampling, location, or function of cold-water coral reefs in the South African Exclusive Economic Zone (EEZ) existed. However, (Samaai et al., 2020) published a still taken from footage, related to a gas extraction project, dating back to 2001 indicating the presence of reef density cold-water corals in the South African EEZ. This reef location has not been further sampled in the two decades since. Unpublished reports by the Department of Agriculture, Fisheries and Forestry (DAFF) indicate the presence of live corals resembling *Lophelia*, no detailed or dedicated publication has been made regarding this findings.

While cold-water coral reefs in South African waters have not been sampled, reefs off the west coast of Africa have been identified. *Lophelia* reefs have been observed off the coast of Namibia (Hebbeln et al., 2017), Ghana (Buhl-Mortensen et al., 2017a) and Angola (Le Guilloux et al., 2009). The major eastern boundary current that the Angolan and Namibian reefs are found in extends into South African waters (Shannon and Nelson, 1996). Furthermore, predictive modelling indicates habitats suitable for five different reef forming cold-water corals; *Enallopsammia rostrata*, *Goniocorella dumosa*, *Lophelia pertusa*, *Madrepora oculata*, *Oculina varicosa* and *Solenosmilia variabilis* (Davies et al., 2008; Davies and Guinotte, 2011). This supports the existence of *Lophelia* reefs in South African waters, which is in accordance with observations of *Lophelia* during other sampling activities (e.g. Stevenson, 2003; Atkinson, 2009). Additionally, *Solenosmilia variabilis* a strong reef forming cold-water coral is known to be present in the Agulhas region from historic reports (von Marenzeller, 1904), and from more recent reports along the coasts of the Eastern Cape and KwaZulu-Natal (Cairns and Keller, 1993;

Filander et al., 2021).

1.2.5 Cold-water corals outside of South Africa

Cold-water corals are found in all of the world's oceans (Roberts et al., 2006) (Figure 1.2). The majority of known reefs are in the northern Atlantic (Freiwald et al., 2004). However, the prevalence of known cold-water coral reefs in the northern Atlantic is likely the result of sampling bias (Freiwald et al., 2017). The process of sampling cold-water coral reefs is both time consuming and expensive (Freiwald et al., 2004). In recent years more reefs in the southern hemisphere have been identified (Freiwald et al., 2017). One of the countries that has enjoyed a long history of research and protection of cold-water coral reefs is Norway. There are more than 1200 verified reefs off the coast of Norway and more than 6000 indicated from bathymetry data (Buhl-Mortensen et al., 2017b). All known cold-water coral reefs have been protected to some degree in Norwegian waters since 1999.

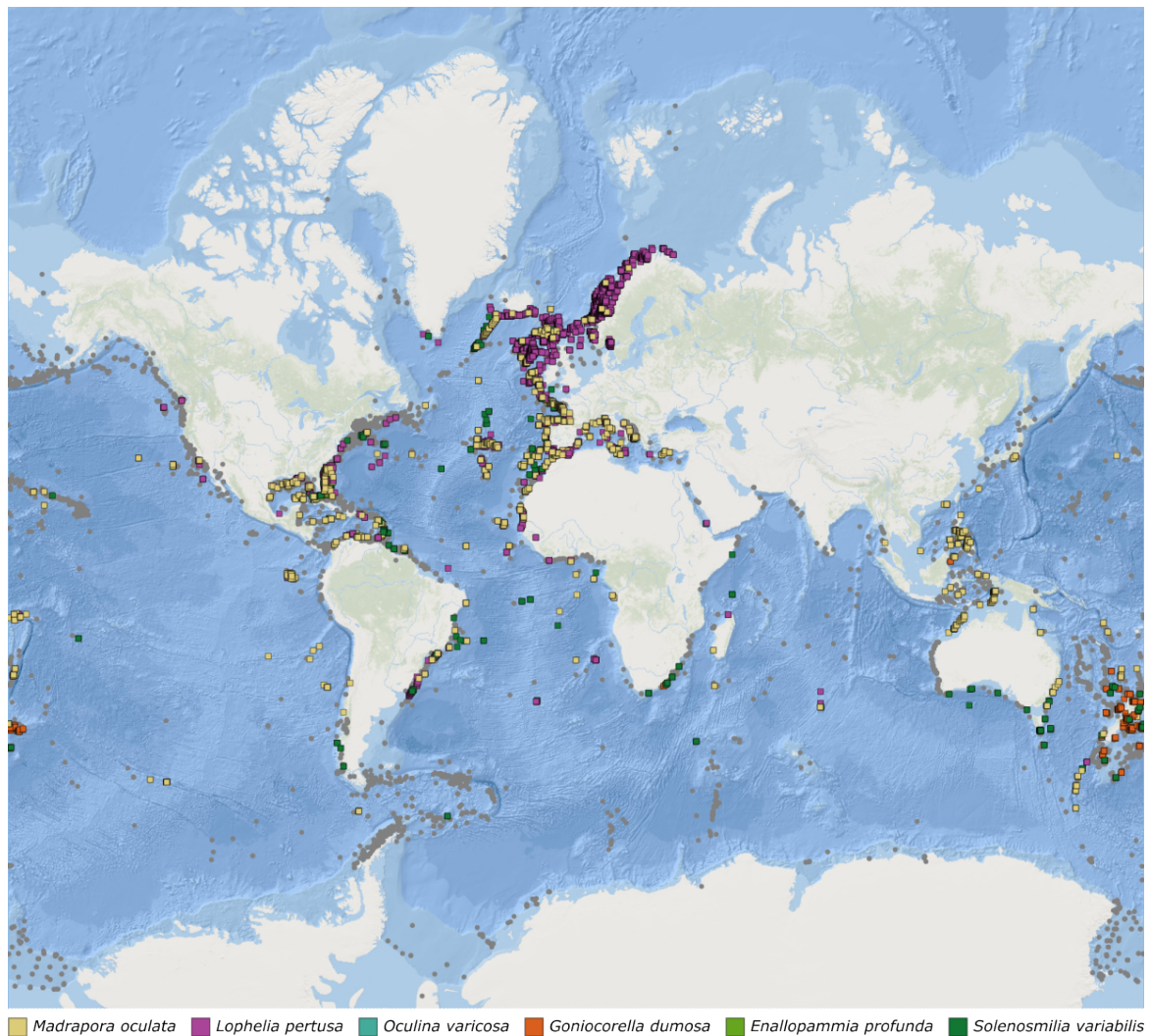


Figure 1.2: The global locations of cold-water coral observations, rendered from Freiwald et al. (2021) using QGIS and the ESRI world ocean base map. Coloured squares represent reef-forming cold-water coral observations, grey points represent observations of non reef-forming cold-water corals. Map data are exhaustive; however, sites markers overlap in areas of high observation densities.

The global distribution of cold-water corals raise questions about how these reefs function; a generalised

model represents an opportunity to investigate this based on what is currently known about these systems. The species assemblages on cold-water coral reefs are related to the local species pool, environmental conditions, and physical structures (biotic and abiotic), collectively this can be referred to as the local framing of the reef (Buhl-Mortensen et al., 2010). Geographical position of the reef is part of the local framing and can be significant at relatively small scales (e.g. longitude was significant at 88.8km (Buhl-Mortensen, 2017)). While common taxa found on reefs can be compared and related to the local species assemblages, when considering the “functioning” of the reef a more generalised approach might be beneficial.

1.2.6 Comparing ecosystems

A comparison of the cold-water coral systems along the coast of Norway in terms of function necessitates the use of terms such as “ecosystem functioning”. No firm definition for this term exists (Bellwood et al., 2019). In the context of this thesis, the term refers to the net effect of the function of organisms in the ecosystem, particularly in relation to the storage and transfer of energy. This ecological definition of ecosystem function was put forward by Bellwood et al. (2019). It is in line with Southwood’s (1977) conclusion that the characteristics of an ecosystem are the result of the different population strategies of organisms in the ecosystem and the interactions between them.

“Do these sets of observations differ significantly?” This is one of the fundamental questions that can be asked in science. Likewise, in ecology, one of the fundamental questions become, “Do these areas/groups differ?” There are a multitude of methods for comparing habitats in terms of ecology. These methods can be seen as starting with the relatively simple comparisons between abundance and diversity indices across sites. Even at this end of the scale, there are options to run tests that focus on sites (one-way ANOVA and equivalents) (McDonald, 2014), or on the relationships between the indices and environmental conditions at the sites (two-way and crossed ANOVAs) (Dufour et al., 1995). At the other end of the scale are multivariate statistical methods where the whole species assemblage is used as the response variables (Field et al., 1982; Dufour et al., 1995; McGarigal et al., 2000). Again in these methods, environmental variables can be included.

There are a number of approaches to describing the functioning of communities of marine organisms. These include trophic grouping, functional group analysis, and comparison of indices (Bremner et al., 2006). However, the function of a whole ecosystem is too complex to be described by any single variable (Giller et al., 2004). For example, two systems with similar species richness and abundances do not necessarily function similarly. This supports the use of multivariate methods for comparing ecosystems in terms of their functioning. The response variable for multivariate analysis need not simply be the species found in the two systems. Bremner et al. (2006) highlights the use of traits rather than species in such analyses. This assertion is of particular importance when comparing systems where the species present are expected to differ.

1.2.7 Biological trait analysis

A biological trait is, at a fundamental level, a proxy for the performance of the organism (Violle et al., 2007). Violle et al. (2007) suggest that a trait be defined as a feature that is measurable at an individual level, with no reference to the environment. Biological trait analysis is a method born

of templet theory (Bremner et al., 2003). The central idea of the templet theory is that ecological strategies manifest as characteristics and evolve as a response to habitat (Southwood, 1977). Using templet theory as the foundation for a biological trait analysis has been shown to be ecologically valid (Townsend and Hildrew, 1994). Biological trait analysis focuses on the functioning of the assemblage rather than the species found in it. As such, biological trait analysis is resistant to biogeographical variation, making it a useful tool for assessing the ecosystem functioning of large-scale benthic environments (Bremner et al., 2003). It also makes this method useful for comparisons between regions (Bremner, 2008; Törnroos et al., 2015; Beauchard et al., 2017). Here, the discussion focuses on the marine branch of this theory. However, it should be noted that from its original conception the theory developed into both marine and terrestrial applications (Törnroos, 2014). Many of the terrestrial applications are based on plants (Törnroos, 2014). Systems do not need to be converted into large matrices representing all the traits present, as many of these will be shared across large numbers of taxa. Furthermore, it is impractical to obtain trait information for every trait present in many systems (de Juan et al., 2022). Rather, a few defining traits are required to define a system (Fauchald and Jumars, 1979). Thus, the biological traits chosen to represent the system should be the traits that best define the functioning of a system or contrast it from other systems. Rare traits should not be summarily discounted when considering highly conserved traits as they might represent rare function (Koutsidi et al., 2020). Bremner et al. (2003) made use of nine traits representing life history, morphology, and behaviour in order to maximise the differences between taxa. When comparing systems using biological trait analysis, the goal is to maximise, within reason, the differences between the taxa. Retaining strongly conserved traits across the taxa, reduces the ability of the analysis to detect differences.

Feeding method and body size are inherently important traits. The method by which organisms feed directly affects their ability to interact with each other in the form of both predator-prey relationships and competition for food sources. The metabolic rate, growth rate, reproductive rate, and mortality of organisms is directly linked to their body size (Brown et al., 2004). In addition, trophic interactions are also linked to body size as they determine what predators an organism is likely to have, and what prey it can consume.

Biological trait analysis are not influenced by differences in taxonomic composition thus they allow for comparisons between areas from different regions (Bremner, 2008; Törnroos et al., 2015; Beauchard et al., 2017). In addition to comparing the functioning of systems, the distribution of biological traits within community assemblages can be used to make a range of inferences about the systems' functioning and response to changes. An example of one such inference is whether or not functional gaps will be filled if a species becomes extinct. The more evenly a trait or series of traits is represented in a community, the more likely that such a gap will be filled by other species (Törnroos, 2014). Specific climate change examples are mentioned in chapter 4 (Eklöf et al., 2015; Frainer et al., 2017). More generally traits can be used to understand function changes as a result of environmental or anthropogenic changes (e.g. Tillin et al., 2006; de Juan et al., 2007; Fleddum et al., 2013; Bolam et al., 2014; Degen and Faulwetter, 2019; Dong et al., 2021).

1.2.8 Use of biological trait analysis and ecosystem modelling

Groups of biological traits, in conjunction with a species matrix, can be converted into functional groups (Bremner et al., 2006). This allows for a statistical approach to functional grouping. The use of species groups in ecosystem modelling results in unnecessarily complex models. Each additional group in a model adds additional links. If this group is functionally the same as another group in the model, then no new information has been added to the model. Thus, maintaining two species as modelling units just because they are different species adds unnecessary complexity to the model. In addition to the trait-based approach to functional grouping, care must be taken to ensure that species grouped together have similar rate variables (growth rate, production rate, etc.) and that they share similar predators and prey (Fulton et al., 2003). Using the raw traits in the model would not provide enough information, because animals sharing certain traits would not meet Fulton et al.’s (2003) requirement of similar predators and prey. For example, an increase in the filter feeder trait would imply more predation pressure on the small body size trait. However, without information on actual predator-prey interactions, it is not clear what other traits would decrease as certain small organisms are consumed. While understanding which traits affect each other is useful, the lack of nested information prevents dynamic runs based on trophic interactions.

Ecosystem modelling allows for experiments, in the form of scenarios, to be run on a simulated system. Running experiments (which would otherwise be impractical or unethical) in simulated space allows for the investigation of links between groups. There exists a vast range of ecosystem models (Fulton, 2010). Some examples of these include: mass balanced models such as Ecopath with Ecosim (Christensen and Walters, 2004), a bottom-up version of EwE with physical coupling ECO-TRAN (Steele, 2009), the biogeochemical and trophic based European Regional Seas Ecosystem Model (ERSEM) (Butenschön et al., 2016), and the coupled physical transport and biogeochemical Integrated Generic Bay Ecosystem Model (IGBEM) (Fulton et al., 2004). Given the wide range of models available, understanding the objectives of the modelling experiment is important when picking which model to use. Cold-water coral reefs are complex ecosystems. The aggregation effect of these reefs adds complexity to the food web, as a wide range of species may interact on the reefs. Furthermore, the physical structure of the reef differs from the open ocean, altering predation risk. Nutrient flow on the reef is governed by hydrodynamic processes, and nutrient recycling take place on the reef. Understanding the traits found on cold-water coral reefs will help improve future models by assisting in identifying and highlighting important energy pathways.

1.3 Hypotheses

A number of hypotheses and aims have been set out based on the framework presented.

Energy enters cold-water coral reef systems by the sinking of food sources from the pelagic zone and the retention of lateral import. The species on the reef make use of these food sources, interacting with other reef species and moving through the reef system. Understanding these ecological interactions can be achieved by addressing two questions: “Does the species composition differ between different cold-water coral reefs, based on their geographical positions and local environmental conditions?” and “Are the functional traits on cold-water coral reefs similar between different reef locations?”.

The first question arises because the species found on the reef are related to the local species pool (Buhl-Mortensen et al., 2010) and longitude was a significant factor in species assemblage on a reef at relatively small scales (88.8km) (Buhl-Mortensen, 2017). It is therefore hypothesised that the geographical position will be a significant factor for explaining the species composition found on cold-water coral reefs.

The next question is based on conclusions regarding the hypothesis related to question one: “if species assemblage differs between the reefs, could the same be said about the biological traits present on the reef?” This question generates four hypotheses: 1) the biological trait profile of the taxa found on the reefs are similar across reefs regardless of geographic position, 2) depth is a significant driver of differences in the biological trait profile, 3) the presence of individual trait modalities (EI burrowing, swimming, ect.) are influenced by the substrata present, and 4) cold-water coral reefs in the region function similarly, as indicated by the presence of similar biological traits on the reef.

The final aim of this thesis is to present, if present, a generalised trait profile for cold-water coral reef sites based on these well-studied reefs. These generalised traits can then be used to discuss traits, and potential species that might be present on under-studied cold-water coral reef sites.

1.4 Structure

This thesis consists of five chapters. The next three chapters will directly investigate the hypotheses and questions posed. The final chapter will synthesise the findings and place them in context.

Chapter two will focus on comparing the species observed on nine different cold-water coral reef sites along the coast of Norway. This chapter will seek to answer the question, “does the species assemblage differ between cold-water coral reefs based on their geographical positions and local environmental conditions?”. The data used in this chapter come from the MARine aREAL database for NORwegian sea areas (MAREANO). A sample of reefs from this dataset will be analysed using multivariate statistical methods. The purpose of this analysis is to investigate which environmental factors related to the bottom type and location of cold-water corals, drive the community structure found on these reefs.

In order to perform a biological trait analysis on the taxa observed in the data, the biological traits of these taxa must be identified. Chapter three will use literature sources to systematically detail the traits of taxa observed on the reef sites, that were not otherwise described in biological trait databases. This chapter will thus complete the trait matrix for the taxa observed on the different cold-water coral reefs. Each entry in this chapter will be written such that it is understandable in isolation. While this will result in some repetition, it will ensure that the chapter acts as a useable stand-alone resource.

Building on the findings of chapters two and three, chapter four will focus on the biological traits present on the cold-water coral reef sites that were investigated in chapter two. In this chapter, the fauna observed on the reefs will be represented by biological traits. The prevalence of the different biological traits between the different reef sites will then be compared and related to the environmental factors using similar multivariate methods to those in chapter two. The aim of this chapter is dependent on the results of chapter two. If the fauna observed on the reef sites are similar, then

their traits will be similar, and chapter four will focus on the differences between the microhabitats within the reefs. If chapter two indicates that the fauna differs between the reefs, this chapter will seek to answer the second question, “are the functional traits on cold-water coral reefs similar between different reefs?”.

The final chapter will focus on synthesising the findings of the previous research chapters. This chapter will describe a conceptual model, based on the biological traits, which will focus on better understanding energy flows on cold-water coral reefs. Finally, this chapter will place the findings of the thesis into the context of the South African system, and lay out what future steps can be taken to improve the local application of the model.

Chapter 2

Comparing cold-water coral reefs:

How do species assemblages differ based on coral coverage and reef location?

Abstract

Lophelia pertusa reefs are known to form complex 3-dimensional structures with distinctive zonation. These reefs are known to be biodiversity hotspots, with increased abundances of local taxa present on the reef compared to the surrounding seafloor. Within the reef system, biodiversity and species association differ between the different reef zones. This study aimed to identify drivers of taxonomic variation both between different reef sites, and within reefs based on substratum type. Data were obtained for nine *Lophelia* reef sites off the coast of Norway. These data were obtained from processed video transects taken using the video platform, CAMPOD as part of the MAREANO program. Processed data described the species composition on the reefs, covering all organisms visible in the footage. In addition to counts for both sessile and mobile fauna, depth, geographical position and substratum coverage were recorded. Each video line was separated into 100m video sequences; these sequences were used to investigate whether species assemblages on the reefs were related to the depth, substratum present, and/or geographical position. The depths, substratum coverage, co-ordinate position, and steepness of the reefs were described and covariant variables identified. Multi-level pattern analysis was used to identify relationships between taxa and the most common substratum type present. The multivariate statistical method, distance based redundancy analysis (db-RDA), was used to identify relationships between the environmental variables of depth, longitude, latitude, and substratum type, and the species assemblages. The presence of burrows were found to be associated with sites where the most common substrata was not related to coral. Both analyses indicated that the sponge, *Mycale lingua*, was associated with the live coral. The percentage of live coral coverage was found to be the most significant explanatory factor for species assemblage, followed by depth, latitude, longitude, percentage cover of coral rubble, and percentage cover of pebbles. The absence of the known cold-water coral symbiote, *Eunice norvegica*, suggests that the detection levels of fauna capable of hiding in the coral matrix using this sampling method might have been low. The species found on these cold-water coral reefs were found to be influenced by both the depth and the geographical location of the reef, in addition to the presence of cold-water coral related substrata.

2.1 Introduction

Cold-water coral reefs are relatively common in the Northeast Atlantic and, by extension, in Norwegian waters (Dons, 1944). The presence of cold-water coral reefs in Norwegian waters has been known since the mid 1700s (Pontoppidan, 1752). Typically, these reefs are constructed by the cosmopolitan *Lophelia pertusa* (Linæus, 1758), now synonymous with *Desmophyllum pertusum* (Linæus, 1758) (Addamo et al., 2016). As *Lophelia pertusa* remains the more common name in the literature, this thesis will continue to use it for clarity. The prevalence of known cold-water coral reefs in the Northern Atlantic is likely the result of sampling bias (Freiwald et al., 2017). In Norway, the cross field program, MARine aREAL database for NORwegian sea areas (MAREANO), has been running since its initiation by the Central Government of Norway in 2005. The project aims to describe the Norwegian seabed in terms of geography, biology, and chemistry. As of 2016, MAREANO has mapped around 131 000 km² of the Norwegian seafloor (Buhl-Mortensen et al., 2015a). The MAREANO project is currently, as of Jan 2023, still active and focusing on the second phase.

Lophelia reefs form complex 3-dimensional structures and are biodiversity hotspots (Dons, 1944; Jensen and Frederiksen, 1992; Rogers, 1999; Weaver et al., 2004; Mortensen and Fosså, 2006; Henry and Roberts, 2016). In addition to the biodiversity and increased abundance associated with the cold-water coral reef as a whole, the different sections of the reef have different biodiversities and species associated with them (Buhl-Mortensen et al., 1995). The live *Lophelia* zone has relatively low biodiversity (Mortensen and Fosså, 2006; Buhl-Mortensen, 2017). Notably, there are few attached organisms in this zone (Freiwald et al., 2004). The highest biodiversity on the reef is found in the dead *Lophelia* zone (Jensen and Frederiksen, 1992; Buhl-Mortensen, 2017). While, the biodiversity observed on the coral rubble zone is between that of the living and dead zones. Several species of fish are also common on *Lophelia* reefs (Husebø et al., 2002; Costello et al., 2005; Kutti et al., 2014).

Few of the species that are associated with the increased biodiversity on cold-water coral reefs are obligate reef species (Buhl-Mortensen et al., 2017b). The species assemblage found on the reef is related to the local species assemblage (Buhl-Mortensen, 2017). Thus, in accordance with Tobler's first law of geography, close reefs are more closely related than far reefs (Tobler, 1970).

There are several multivariate methods for relating species to environmental factors (Borcard et al., 2018). Data obtained from the MAREANO program have been analysed using detrended correspondence analysis (DCA) (Dolan et al., 2009; Buhl-Mortensen, 2017). While video datasets of cold-water coral reefs, collected using a similar methodology to the MAREANO projects, have also been analysed using constrained correspondence analysis (CCA) (Mortensen and Buhl-Mortensen, 2005a). In investigating benthic community structure on tropical reef sites, Bierwagen et al. (2018) used constrained distance-based redundancy analysis (db-RDA) based on Bray-Curtis dissimilarities. Ordination methods can broadly be grouped into two categories. These are, unconstrained ordination methods, where only the species table is analysed, and constrained analyses, where both species and environmental tables are analysed (Borcard et al., 2018). In order to include environmental information in an unconstrained ordination, an indirect analysis between the ordination axis and the data are required (Legendre and Legendre, 2012). This is referred to as indirect gradient analysis (ter Braak, 1995). Constrained methods are thus direct gradient analysis, as both the species and environmental vari-

ables are considered in the same analysis. Constrained methods, such as CCA, db-RDA, and RDA, allow for a direct test between the response and explanatory variables, and should therefore produce more readily interpretable results (ter Braak, 1995; Legendre and Legendre, 2012). ter Braak et al. (2012) recommends the use of db-RDA for datasets where the explanatory variables are mixed between quantitative and qualitative. The db-RDA method allows for the use of non-euclidean dissimilarities such as the Bray-Curtis (Legendre and Anderson, 1999).

This chapter focused on video data obtained from the MAREANO program. However, over all the MAREANO program collected data using multiple methods. This data has been used to address multiple research questions. Most of cold-water coral research based off MAREANO data has focused on habitat mapping (Buhl-Mortensen et al., 2014; Diesing and Thorsnes, 2018; Jarna et al., 2019; Sundahl et al., 2020). The aim of this chapter was to determine whether species assemblages differed between nine different cold-water coral reefs off the coast of Norway and, if so, to identify the drivers of these differences. It was hypothesised that longitude and/or latitude would be a significant explanatory variable for differences in species composition between these reefs. No past study utilising MAREANO data has compared the taxa found on cold-water coral reefs across the geographical scale used in this chapter.

2.2 Methods

2.2.1 Data structure

The numerical data used in this study were generated from MAREANO cruises, where they make use of the video platform CAMPOD. This video platform utilises a high-definition colour video camera (Sony HDC-X300) which is tilted forward at a 45° angle, two 400W lights, a pair or quadrat of lasers, and a depth sensor (Buhl-Mortensen et al., 2015a). The platform can be fitted with other accessories. The dataset analysed in this chapter contained information obtained from a positioning transponder attached to the CAMPOD (Appendix B) Each video transect is bookended by a period where the CAMPOD is stationary on the seafloor, focusing on details within appropriately 6m² of the CAMPOD. Thereafter, the CAMPOD is towed at a speed of 0.7 knots at about 1.5m above the seafloor.

Real-time video observations were made onboard the vessel during MAREANO video lines. These coarse onboard observations recorded the reef zone and any species that could be identified in real-time. Video footage underwent detailed analysis at a later point, where all taxa visible were identified (Appendix A) and counted and substratum types were recorded as percentage coverage. The standards for defining the different sediment types used in the MAREANO survey were based on a modified version of Folk and Ward's (1957) scale, the definitions for which were listed in a standard report (Bøe et al., 2010). This standard makes use of the Wentworth scale for grain size classifications (Table 2.1). These defined substrata (Table 2.2) are reported in colour to distinguish them from generic descriptions of substrata. The coarse onboard data for 167 reefs sampled between 2006 and 2016 were used to select reefs; detailed datasets from these selected reefs were used for the actual reef comparisons.

Table 2.1: Grain sizes used by the MAREANO project, based on the Wentworth (1922) scale, note that the size category gravel is referred to as pebble in this dataset.

Grain Classification	Size (mm)
Clay	<0.002
Silt	0.002-0.063
Sand	0.063 - 2
Gravel/Pebble	2 - 64
Cobble	64 - 256
Boulder	>256

Table 2.2: The substratum types present in this dataset, this is a subset of the substratum types used by the MAREANO project. Based on a modified Folk and Ward (1957) scale used for the sediment types. The coral substrata are based on the presence of coral and are classified on neither the Folks nor Wentworth scales. See section 2.2.3 for detailed explanation on the use of Live Coral, which differs from the MAREANO definition.

Substratum Name	Definition
Sandy mud	Clay:silt ratio between 1:2 and 2:1
	Clay + silt > 50%
	Sand < 50%
	Gravel < 2%
Sand	Sand > 90%
	Clay + silt < 10%
	Gravel < 2%
Pebble	Gravel/pebble > 80%
Cobble	Dominant grain size is cobble
Clay and Sponge spicules	Bioclastic material
	Sponge spicules embedded in clay
Boulder	Dominant grain size is boulder
Live Coral	Living <i>Lophelia</i> or <i>Madrepoda</i> present
Dead <i>Lophelia</i>	Dead <i>Lophelia</i> present
Coral Rubble	Coral rubble present

2.2.2 Reef selection

A set of inclusion criteria were applied to these observations and reefs not matching these were discarded at each step. The first criterion was that the reef had to be “well sampled”; this was defined as containing at least 100 onboard observational events. The purpose of this selection criterion was to ensure that the selected sites would have sufficient observations of substrata for the presence of a reef to be established.

Cold-water coral reefs are made up of three distinctive sections, namely, coral rubble, dead *Lophelia*, and live *Lophelia* (Buhl-Mortensen et al., 1995). A fourth zone, dead coral blocks, was described by Buhl-Mortensen et al. (2010). However, while coarse onboard datasets recorded all four of these bottom types, this additional zone was not used in the detailed datasets. Reefs were selected if each of these substratum types represented between 10% and 75% of the substrata observed. In practice, this meant that the upper limit for any individual reef substrata was 60%. This criterion was used to ensure that cold-water coral reef sites were selected and that these reefs represented all components of a cold-water coral reef.

The criteria for percentage coverage of each coral type were removed to identify sites that represented extreme latitudes and longitudes of the study region. On inspection, only the extreme western site at the middle latitudes was retained for the analysis. The northern reef contained coral substrata; however, it was considered to represent only part of a reef as it contained no dead coral, and therefore was not included in the analysis. The geographical location of the included reefs (figure 2.1) indicates, that even without including, those sites the geographical spread of data covered approximately 450km along the west coast of Norway.

The selection criteria selected three reefs for which data were inaccessible. These reefs were: The southernmost reef R1066, which was near reef R0994. The easternmost reef near the middle of the latitude range reef R0947. And, reef R1121 which was located between reefs R1108 and R1130.

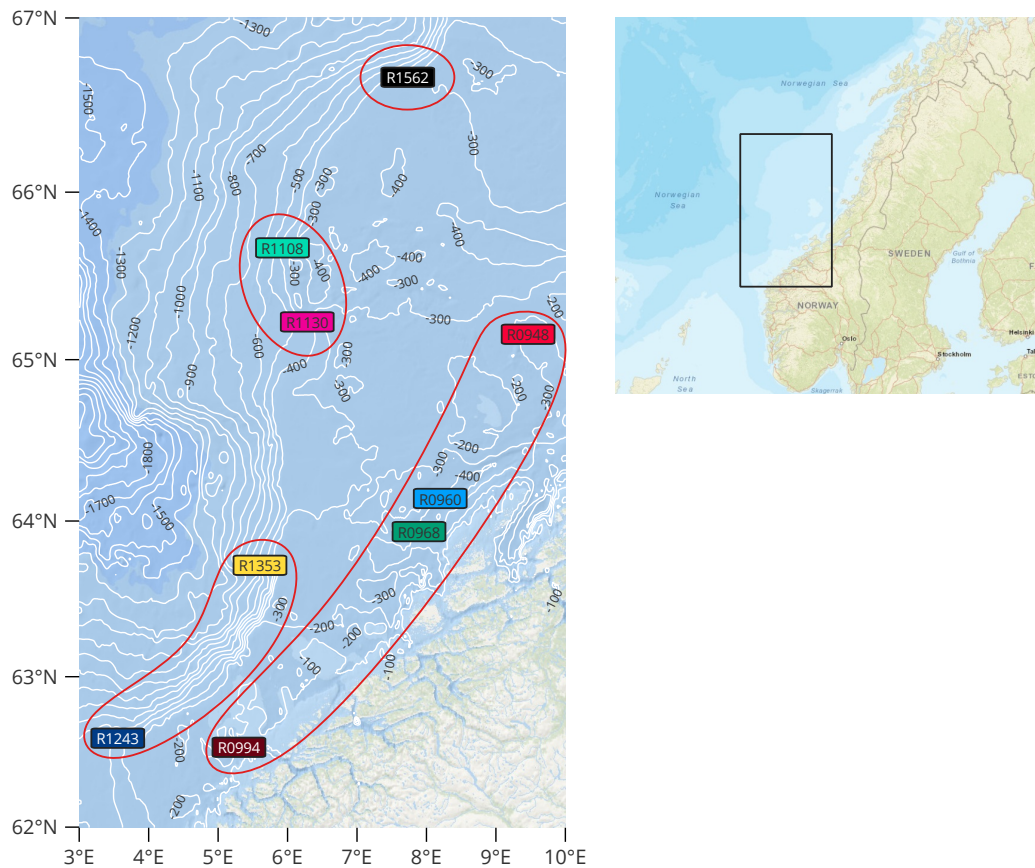


Figure 2.1: The locations of the nine reef sites used in this study. The depth contours are displayed in white at 100m intervals starting from 100m below sea level. Reefs are coloured for consistency with figures 2.8 to 2.11. Differences in text colour are solely for readability. The location of the contour map relative to the Norwegian Sea is indicated by the bounding box on the smaller map.

2.2.3 Subsampling

The detailed data for each reef site were subsampled based on 100m video sequences. As part of the sampling method, the CAMPOD was stationary at the beginning and end of the video lines, only data from when the CAMPOD was moving were used in this chapter. The coordinates and depth of the CAMPOD were logged every time a taxon or change in substrata composition was recorded. The geosphere package (Hijmans, 2019) was used to convert the differences between coordinates into

distances. The sum of these distances was used to calculate a cumulative distance from the starting point, which could then be used to divide the video line into sequences.

In order to obtain average percentage cover for each substratum type in each video sequence, a dummy observation of the last substratum composition was added at each 100m mark. This was done so that the averages could be calculated as mean percentage cover by each substratum per metre. The taxa observed were summed over the 100m subsections, and these total observation counts were corrected for the variable field of view. While the CAMPOD is maintained at a height of 1.5m from the seabed, it is impossible for it to be at this exact height at all times. Two laser pointers set at a distance of 10cm apart were used to calculate the field of view based on the screen size. Counts were divided by the field of view, therefore, the community matrix produced represents the observed density of taxa (counts per 100m²), with each row of the matrix representing a 100m video sequence.

Attention should be drawn to how substratum type was recorded in the data. The percentage of the seafloor covered by each of the 16 different substratum types was recorded from the video frames. However, this was not done for each frame of the video, rather it was recorded every time the percentage cover of these substrata visibly changed. The substratum types used in the data sets from the earlier part of the sampling period differed slightly; these differences were addressed after data extraction and combination. Substratum types that were not seen at any of the selected sites were dropped from the dataset, leaving nine different types (figure 2.4). Two of the nine remaining substratum types were not included in the earlier datasets, namely, **clay and sponge spicules** and **sandy mud**. At reef R1243 (figure 2.1) the branching coral genus *Madrepora* was observed frequently enough that it was recorded as a substrata. Since no substrata class existed for *Madrepora*, it was recorded as the rarely used **clay and sponge spicules**, with a comment attached to each observation attesting that it represented a *Madrepora* reef. Since *Madrepora* corals are branching and reef-forming, and these observations coincided with the presence of a *Lophelia* reef, a decision was taken to combine these into a substrata named **live coral**, as the observations represented living reef-forming corals. Given the low presence of **clay and sponge spicules** this substratum was not used in the multivariate analyses.

The mean depth of each video sequence was calculated as mean depth observed over the 100m video sequences. Minimum and maximum depth represented the shallowest and deepest points of each video sequence. The steepness of each video sequence, referred to as gradient, was calculated as the average change in depth per metre travelled. The gradient was calculated by determining the change in depth per metre between each point. The absolute values of these differences were averaged across the video sequence. Appendix B contains a summary of the position, depth, gradient and substrata for each of the 59 video sequences.

2.2.4 Data sanitisation

The raw observations in the data were sanitised using the following set of firm rules. The list of unique taxonomic observations were ran against the WoRMS database (WoRMS Editorial Board, 2021) using R. All names in the list that returned valid WoRMS listings were considered to be correct. The list was then sorted alphabetically to manually locate clear typographical errors, such as double key strokes in an otherwise valid name.

Some taxonomic observations were relatively coarse; in these cases morphotype was often recorded. Morphotypical descriptions in this dataset made use of any combination of colour, size or shape. For example, “Porifera big white”, “Porifera white big”, and “Big white Porifera”. These observations were considered to represent diversity and were thus not merged into a single group; however, this necessitated consistency in labelling. Along with the manual changes, a set of regular expression (regex) based rules were applied to detect patterns within the observational names. These rules ensured that descriptive observations were listed by taxonomic level, then size, and then colour across all sites, and ensured that abbreviations and separators were consistent. Using the same example as above, all these observations were relabelled as “Porifera white big”. A python script read in each raw datafile, and each observation was checked and automatically cleaned up according to the rules included in the script. These corrected observations were written to a new column, which was verified by random inspection to ensure that the changes were logically applied. This method was used to ensure that these naming conventions were applied consistently across all the reef sites, and to any sites that were added to the study.

2.2.5 Statistical analysis

Unless otherwise stated, all data extraction, analysis, and plotting was performed using R (Version 4.2.1 R Core Team, 2022). The total abundances, taxonomic richness, and diversity of the 59 video sequences were calculated. The Shannon index (Shannon, 1948) was used as a measure of diversity. The mean depths of the video sequences were binned into 100m starting at 250m. Additionally, categorical variables representing the type of coral substrata present in each video sequence and the most common substratum type were calculated. The presence of coral was calculated based on the presence of each of the three coral substratum types (Living, Dead and Rubble). No minimum threshold was used for coral type present, and video sequences could have multiple coral types present. When two coral types were present, the combination was noted. The shorthand “all” was used when all three were present and, likewise, “none” when no coral was present in the sequence. Two different methods of representing the most common substratum present were used. The first method assigned a substratum type to each video sequence if that substratum represented more than 50% of the video sequence; this was referred to as the dominant substratum. In cases where no dominant substratum was present, the variable was assigned the value of “none”. Alternatively, the most common substratum type was also calculated for each video sequence. In this case, the most common substratum that represented more than 33% of the observed substratum types in the video sequence was assigned. If no substratum represented at least 33% of the video sequence, the most common substratum variable was set to “heterogeneous”.

An analysis of variance (ANOVA) was used to determine whether the Shannon index differed significantly between the different categorical variables. Dominant substratum, most common substratum, the presence of coral, binned depth, the interaction term between dominant substratum and coral presence, and the interaction term between most common substratum and coral presence were considered for the ANOVA. Forward selection based on the Akaike Information Criterion (AIC) was used to determine which variables should be retained in the final ANOVA; this was performed using `stepAIC` (Venables and Ripley, 2002). In addition to diversity indices, the relationship between the taxonomic observations and the most common substratum types were investigated using multi-level pattern analysis (Dufrêne and Legendre, 1997), using `multipratt` (De Caceres and Legendre, 2009). Pearson’s

phi coefficient of association was used to determine the association between taxonomic abundances and the most common substratum present (Chytrý et al., 2002).

The mean depth and gradient for each reef site were calculated from the video sequences. For both variables significant differences between the reefs sites were tested for using separate ANOVAs, a tukey test was used to identify which reefs differed. Percentage coverage of each substrata were averaged across video sequences on each reef. The substrata composition of the reefs were compared using a chi-squared goodness of fit test.

The Pearson product moment correlation coefficient and associated p-value were calculated for each pair of environmental variables (Harrell Jr, 2022). The results of these tests were visualised as a correlation plot (Wei and Simko, 2021). Variables with a significant ($p < 0.05$) correlation coefficient greater than 0.7 were considered to be highly correlated. Additional plotting and linear regression were used to investigate significant ($p < 0.05$) correlation coefficients that were between 0.55 and 0.7.

For the multivariate analyses (other than the multi-level pattern analysis), only taxa that were observed in 5 or more of the 59 video sequences (8%) were included. The value of 5 was chosen as none of the reefs contained fewer than 5 video sequences. Thus if, a taxon was only observed on a single reef it would not automatically be dropped from the dataset. This reduced the number of observed taxa from 167 to 59. This subsetting was performed to reduce the impact that rare taxa, that are not representative of the community structure, would have on the multivariate analyses (Legendre and Legendre, 2012; Brasil et al., 2020). The variance in the abundance of observed taxa was large, therefore the data were fourth-root transformed.

Non-metric multidimensional scaling (MDS) was performed using the **vegan** package (Oksanen et al., 2019) in order to visualise the species assemblage data. Bray-Curtis dissimilarity was used for the MDS analysis. Three dimensions were used ($k=3$) in order to reduce the overall stress of the ordination. Environmental vector fitting (**envfit**, **vegan** (Oksanen et al., 2019)) was used to identify significant species ($p < 0.01$) for plotting.

The community structure and its relationship to the environmental variables were examined using distance-based redundancy analysis (db-RDA). This analysis was conducted using Bray-Curtis dissimilarity. The **capscale** function was used to conduct this analysis (**vegan**: Oksanen et al., 2019). Model selection was performed using **ordistep**, which bases model selection on the Akaike Information Criterion (AIC). The stepping was done in both directions. Starting with $y \sim 1$, new explanatory variables are added at each step and those already included in the model are removed. The single addition or deletion that results in the best AIC is kept and the process is repeated. Permutational multivariate analysis of variance using Bray-Curtis distances was performed using **adonis2** (**vegan**: Oksanen et al., 2019). This distance based linear model used the environmental factors that were contained in the final db-RDA model. The results of this analysis indicated the main drivers of community structure.

2.3 Results

Diversity indices

This study included nine reef sites, and each site contained six or seven 100m video sequences. Thus, 59 100m video sequences were included, covering a total distance of 5.9km. The majority (93%) of video sequences represented areas that were considered to have a most common substratum type (single substratum accounting for >33% of substrata coverage present). The four video sequences that did not have a most common substratum were all dominated (>50% coverage) by the coral-related substrata. Taxonomic richness ranged between 10 and 38 taxa per sample, with a mean of 24 taxa per sample. Total abundance was more variable, ranging from 25 organisms per 100m² to 2219 organisms per 100m². The mean value was 302.3 organisms per 100m². Eight of the video sequences had abundances of over 500 organisms per 100m². Seven of these eight top video sequences represent reef R1562, where the different Porifera groups accounted for the majority of observations. In particular, the morphotype Porifera Coral ranged between 161.3 to 1098.7 observations per 100m². While the total abundance of taxa within the video sequences varied by three orders of magnitude, the Shannon index of the video sequences was relatively narrow, with a minimum value of 1.3, a maximum of 3.0, and the mean was 1.8.

The Shannon index was significantly different between samples based on the most common substratum type and the presence of different coral zones in the sample (table 2.3). The Shannon index was larger on samples where the most common substratum was sandy mud compared to those where it was coral rubble, and live or dead coral (figure 2.2A). Visual inspection of the mean Shannon index and coral presence suggests that the significant results found by the ANOVA were likely influenced by a video sequence that contained both live coral and coral rubble (figure 2.2A).

Table 2.3: ANOVA results comparing Shannon's index based on the most common substratum present and the different coral reef zone combinations (Living, dead, rubble, all combinations present in the dataset, and the absences of coral). Columns represent degrees of freedom (df), the sum of squares, mean squares, F statistic (F) and the associated p-value. ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$

	df	Sum of Sq	Mean Sq	F	Pr(>f)	
Most common	6	6.62	1.10	14.86	1.94×10^{-9}	***
Coral present	5	1.17	0.23	3.20	0.016	*
Residuals	47	3.49	0.07			

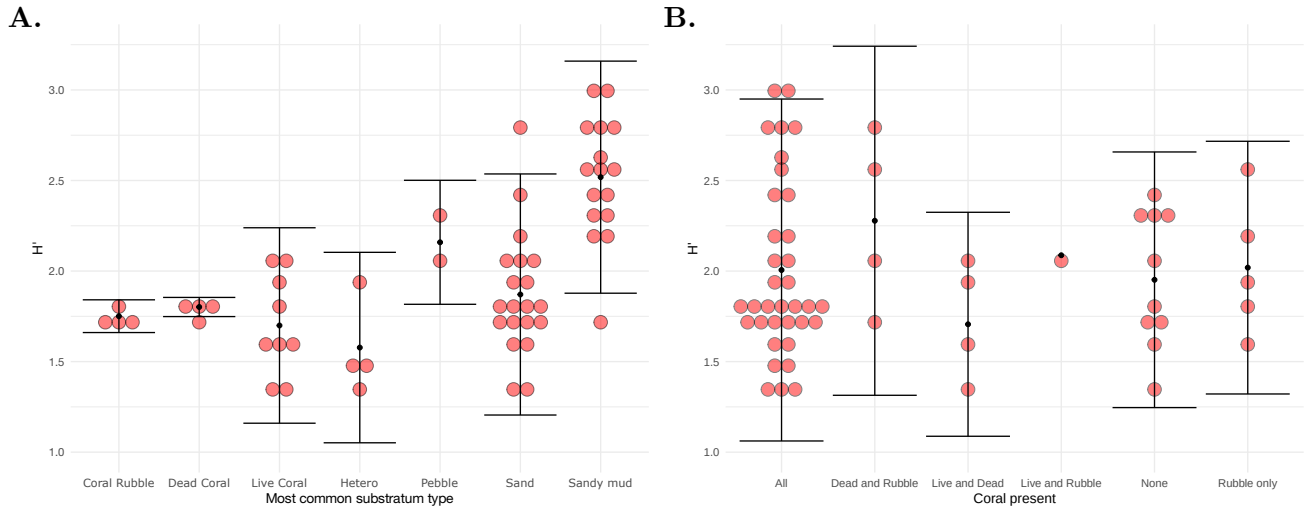


Figure 2.2: The mean Shannon index (H') of the 100m video sequences, based on their A) most common substratum type and B) type of coral substrata present. The black point represents the mean Shannon index with the error bars representing the 95% confidence interval. Orange dots represent the observed H' of each of the 59 video sequences, grouped in 0.1 wide bins.

2.3.1 Environmental data

2.3.1.1 Depth and gradient

The mean depth of each site, as described by the mean depth of each video sequence, significantly differed (ANOVA: $df = 8, 50$, $F = 644.3$, $p < 2 \times 10^{-16}$). A Tukey posthoc test indicated that the mean depth did not differ significantly between the following reef pairs; R0994 and R0948 ($p \approx 1$), R0948 and R0968 ($p > 0.1$), R0948 and R1243 ($p > 0.8$), R0968 and R1243 ($p \approx 1$), R1108 and R1562 ($p > 0.9$), and R1562 and R1130 ($p \approx 1$) (figure 2.3A). There was no significant difference in the mean gradient between the reefs (ANOVA: $df = 8, 50$, $F = 1.641$, $p = 0.137$) (figure 2.3B). Reefs R1243 and R1353 contain video sequences whose mean gradients are much larger than the overall mean for the reef; these outliers are retained as there is no clear error in measurement to justify their removal.

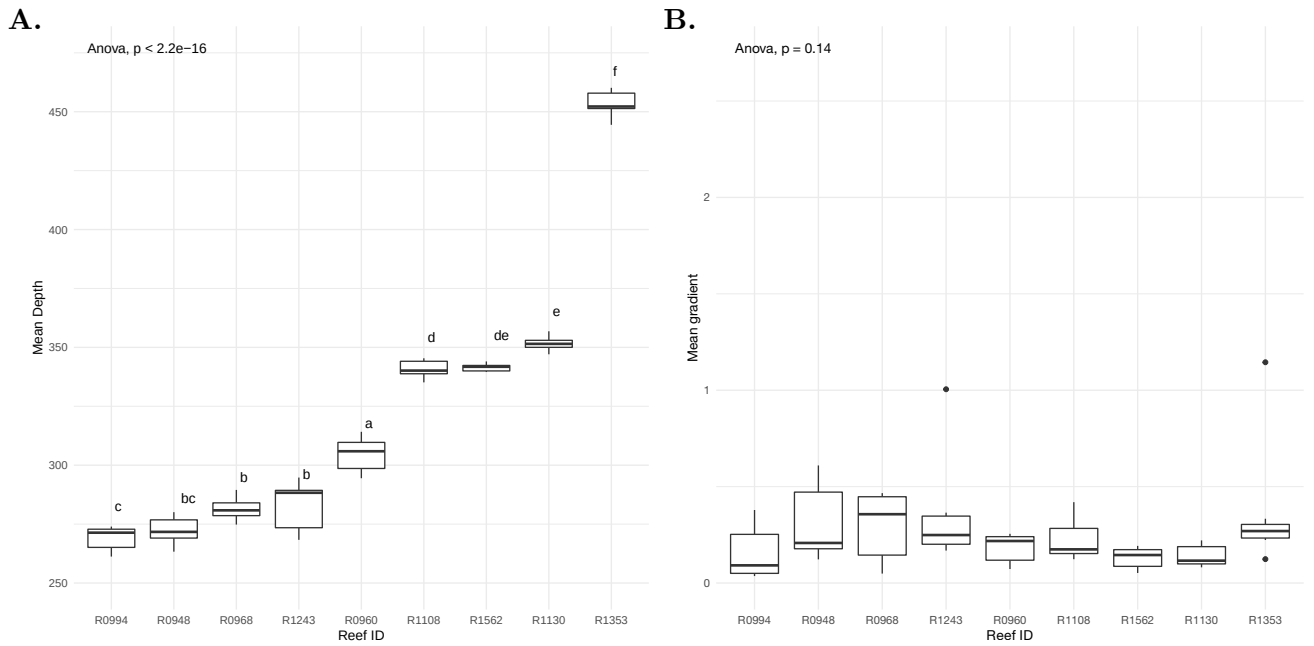


Figure 2.3: Summary of the A) depths and B) gradients of the reef sites. Depth and gradient represent the mean values across each of the 59 100m video sequences. The p-value of an ANOVA is represented in the top left corner of each graph. Letters represent groups of reefs between which A) mean depth and B) gradient significantly differed. The reefs are labelled on the x-axis in order of increasing median depth across the 100m video sequences taken on the reef, letters compare means, bars represent the median, boxes represent the interquartile range, while the whiskers represent the largest observation within 1.58 times the interquartile range.

2.3.1.2 Substrata distribution

The substratum composition was not equally spread out between the reefs ($\chi^2 = 888.06$, $p = 4.998 \times 10^{-4}$). Some substratum types showed greater variation between the sites than others (figure 2.4). The most notable is the substratum type **sandy mud**, which is very low at most of the reef sites; however, it is the most abundant substratum on reefs 0994, 1108 and 1130. The substratum coverage of **boulder** and **cobble** were relatively consistent and low across all the reef sites. The substratum **clay** and **sponge spicules** is essentially absent from the dataset, being absent at 98.3% of sites. At the two sites where **clay** and **sponge spicules** is present it represents less than 1.4% of the substratum type.

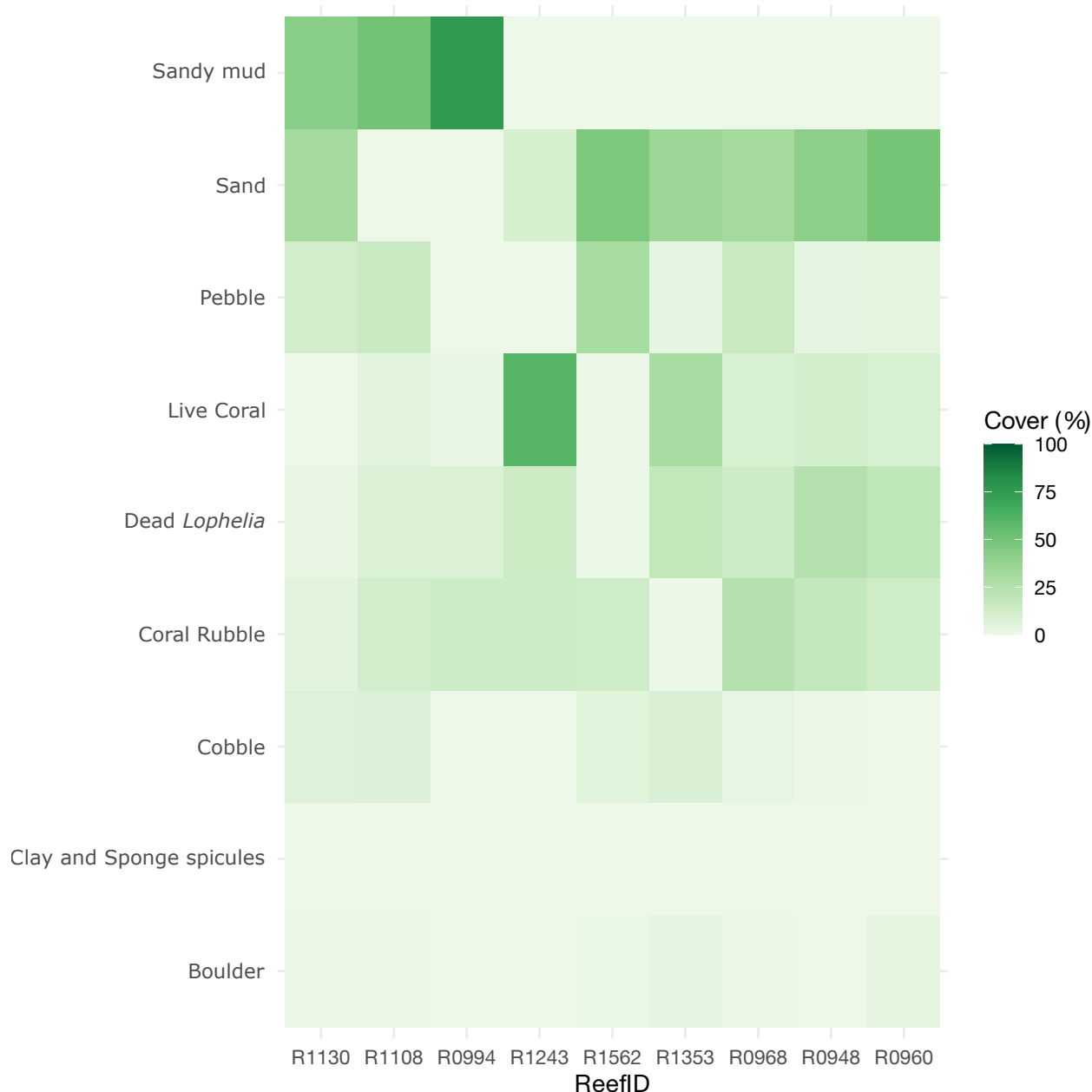


Figure 2.4: Comparison of the percentage cover of each of the substrata at each reef. Reefs are presented in order of similarities between substratum profiles, based on hierarchical clustering.

2.3.1.3 Correlations

The three different measures of depth were correlated with each other (figure 2.5), thus the mean depth is representative of both the maximum and minimum depths of the 100m video sequences. Mean depth was retained as the depth variable for all future analysis.

The correlation test indicated a significant positive correlation between latitude and longitude of the video sequences. There were no overlaps in the latitude and longitude of different reefs. Linear regression indicated that the relationship between latitude and longitude accounts for a low proportion of the variance ($R^2 = 0.3095$, figure 2.6A). The relationship between latitude and longitude was not sufficiently strong enough to justify removing one from the analyses.

A positive correlation was found between the latitude of the video sequences and the percentage cover of **pebble** (figure 2.5). Percentage pebble cover was arcsin transformed in order to reduce heteroscedasticity in the linear regression. The results of the regression on the transformed data indicated that this relationship accounted for around half of the variance unexplained by the two variables ($R^2 = 0.53$, figure 2.6B). Figure 2.4 indicated that the amount of pebble at each site varies between 0 and 57%. The number of observations that fell outside of the 95% confidence intervals and the relatively low R^2 value did not justify the removal of either variable from the analysis prior to forward selection.

Cobble was found to have a significant positive correlation with depth (figure 2.5). Plotting this relationship highlighted a large number of video sequences with no cobble at depths less than 350m. Since the range of percentage coverage of **cobble** increases with increasing depth, the percentage data were arcsin transformed to reduce heteroscedasticity during linear regression. The results of a linear regression indicate that the relationship between these two variables explains around half of the variance ($R^2 = 0.5321$ figure 2.6C). The relationship between **cobble** and mean depth visually suggests that the maximum **cobble** coverage increases with depth. However, there are more video sequences with at least 10% **cobble** coverage at around 250m than at around 450m. A large number of the video sequences fall outside the 95% confidence interval of the linear regression; this is particularly true at near the 350m mark. None of these findings support removing either variable from the analysis due to correlation prior to forward selection.

Pearson's correlation coefficient indicated a relatively strong, significant negative relationship between **sand** and **sandy mud** (figure 2.5). Plotting these variables indicated that, in this dataset, these two substrata were mutually exclusive in all but two video sequences. The mutually exclusive nature of these two variables makes linear regression uninformative. Figure 2.6D indicates that, in this dataset, **sand** or **sandy mud** were present across almost all percentages in the absence of each other, thus they do not covary and both are retained.

Sand was found to have a significant positive correlation with median longitude (figure 2.5). The variance in percentage coverage of **sand** is lower at the lowest longitude reef; however, the variance is relatively consistent across all other observations. Thus, the data were not transformed prior to linear regression. The results of the linear regression indicate that the relationship between percentage cover of **sand** and median longitude does not account for a large proportion of the variance ($R^2 = 0.2803$, figure 2.6E).

Pearson's correlation coefficient indicated that **live coral** had significant negative correlations with both median latitude and longitude. Percentage coverage of **live coral** did not have equal variance with either longitude or latitude. In the case of longitude, an arcsine transformation was applied; however, a log transformation was required to reduce the variance for the relationship between **live coral** and median latitude. Linear regression indicates that the relationship between the arcsine transformed **live coral** and longitude did not account for much of the observed variance ($R^2 = 0.2157$, figure 2.6F). A similarly low proportion of variance was explained by the relationship between the log transformed **live coral** and latitude ($R^2 = 0.2367$, figure 2.6G). The linear regression did not support removing either variable from the analysis due to correlation.

The relationship between percentage cover of *dead Lophelia* and *pebble* presented similar statistical issues as the relationship between *sand* and *sandy mud*. While this pair was not mutually exclusive to the extent of *sand* and *sandy mud*, there are 14 video sequences that contain no *dead Lophelia* but do contain *pebble*. Likewise, there are 15 video sequences where the inverse is true. This suggests that the variables do not covary, and should be retained until model selection.

	mean depth	min depth	max depth	grad2	Med lat	Med long	Boulder	Cobble	Sand	Sandy mud	Pebble	Dead <i>Lophelia</i>	Live Coral
min depth	1.00 ***												
max depth	1.00 ***	0.99 ***											
grad2	0.03		0.05										
Med lat	0.23	0.25	0.22	-0.22									
Med long	-0.18	-0.17	-0.19	-0.12	0.57 ***								
Boulder	0.30 *	0.32 *	0.29 *	-0.21	0.05	0.12							
Cobble	0.65 ***	0.66 ***	0.64 ***	-0.25	0.41 **	-0.06	0.17						
Sand	0.18	0.20	0.17	-0.17	0.33 **	0.54 ***	0.43 ***	0.17					
Sandy mud	-0.11	-0.10	-0.12	-0.24	-0.09	-0.30 *	-0.16	0.05	-0.66 ***				
Pebble	0.14	0.16	0.12	-0.36 **	0.64 ***	0.27 *	0.14	0.45 ***	0.32 *	-0.08			
Dead <i>Lophelia</i>	-0.10	-0.13	-0.08	0.45 ***	-0.25	0.16	-0.20	-0.38 **	-0.16	-0.33 *	-0.53 ***		
Live Coral	0.03		0.04	0.51 ***	-0.54 ***	-0.55 ***	-0.17	-0.29 *	-0.28 *	-0.35 **	-0.45 ***	0.38 **	
Coral Rubble	-0.40 **	-0.42 ***	-0.37 **	0.09	-0.03	0.19	-0.31 *	-0.36 **	-0.10	-0.18	-0.27 *	0.14	-0.09

Figure 2.5: The correlations between the environmental variables. Mean depth represents the mean depth of each video sequence; minimum and maximum depth represent the shallowest and deepest depth recorded during each video sequence. Grad2 refers to the mean gradient as an indicator of steepness, calculated as an average of the absolute values of gradients between each observation point during the video sequences. Med lat and Med long refer to the median co-ordinate values of latitude and longitude of each video sequence. The variables below Med long refer to the names of the substrata types, reported as the percentage composition for each video sequence. Numbers represent the Pearson correlation coefficient coloured based on values (highly positive in blue, highly negative in orange, both converging on white for zero values). The significance of the correlation is represented by stars below the numbers (***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$).

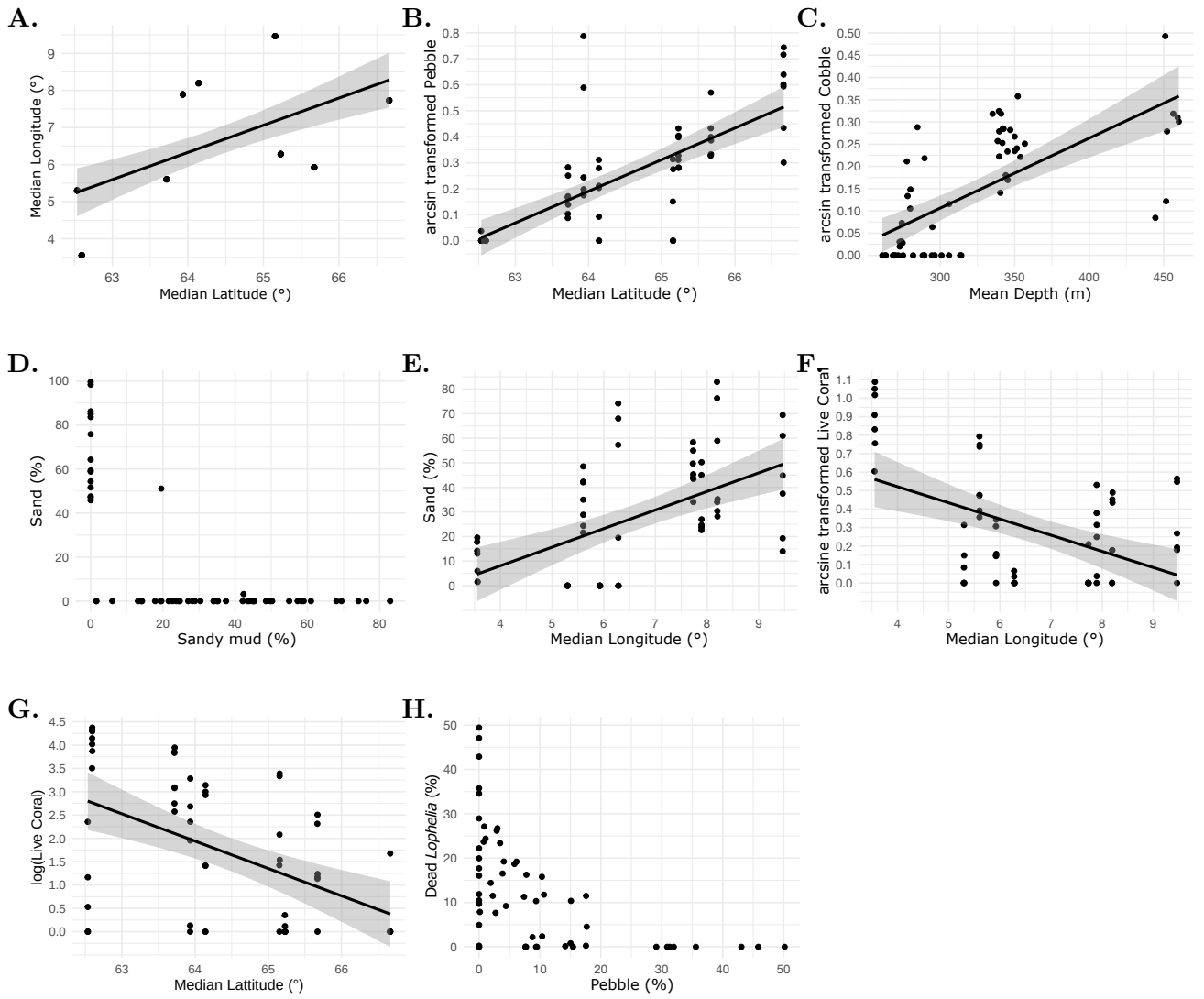


Figure 2.6: Graphs displaying the relationship between environmental variables that had significant positive or negative correlations of more than 0.5 and less than the automatic cut-off for highly correlated value of 0.7. The graphs show the relationship between A) median latitude and longitude, with latitude plotted as the x-axis for continuity with graph B, B) latitude and arcsine transformed proportion of **pebble** coverage, C) mean depth and arcsine transformed proportion of **cobble** coverage, D) **Sandy mud** and **Sand** cover, E) median longitude and **sand**, F) median longitude and arcsine transformed proportion of **live coral**, G) median latitude and log transformed percentage cover of **live coral**, and H). the percentage coverage of **pebble** and the percentage coverage of **dead Lophelia**. The black line represents the line of best fit from linear regression, while the grey area represents the standard error of the plot fit.

2.3.2 Community composition and drivers

2.3.2.1 Multipattern analysis

Two fish taxa were found to have significant associations with the most common substratum types (figure 2.7). The first was the genus *Sebastes* which was associated with video sequences where the most common substratum type was **dead coral**. *Gadiculus argenteus* was found to be more common on video sequences that were defined by the **sandy mud** substratum. Colonial green tunicata were associated with video sequences where the most common substratum type was **pebble**.

The heterogeneous video sequences in this study were made up of no more than 33% coverage of a single substratum type (figure 2.7). However, when the coral-related substrata are considered together, all four of these video sequences contained more than 50% coverage of coral-related substrata. Thus, all but one member of the phylum Cnidaria that were associated with video sequences based on their most common substratum types, were associated with coral-related substrata. The only exception was observations of Actiniaria that were buried and reddish in colour (Taxa and morphotypes listed in appendix A). These Actiniaria were more common on video sequences where the most common substratum type was **pebble**. Two different colour morphotypes of *Paragorgia* (red and white) associated with video sequences where **dead coral** was the most common substratum. The white morphotype also associated with video sequences where the most common substratum type was **coral rubble**. The two Cnidaria that were associated with video sequences where **live coral** was the most common substratum type were the *Clavularia borealis* and bush-shaped hydrozoa.

Like the members of Cnidaria, members of the phylum Echinodermata were more commonly associated with video sequences where the most common substratum type was related to coral (figure 2.7). Of the four members of this phylum that were significantly associated with video sequences based on the most common substratum type, only Poraniidae were associated with the non-coral substratum of **pebble**. *Porania*, *Echinus*, and *Cidaris cidaris* were associated with **coral rubble**, **dead coral**, and **live coral** respectively.

The porifera showed wider diversity in their associations than the Cnidaria and Echinodermata. Five of the nine members of this phylum that had significant associations with video sequences based on the most common substratum type were associated with **pebble**. These five included three morphotypical descriptions of porifera (encrusting, white and medium, and small). The species *Mycale lingua*, *Geodia barreti* and the genus *Plakortis* associated with video sequences where the most common substratum was **live coral**. The genus *Plakortis* was also associated with video sequences where the most common substratum was **coral rubble**.

Burrows, both big (around 2-5cm) and small (around 0.2-2cm), were associated with the non-coral substrata. Small burrows were associated with **pebble**, **sand**, and **sandy mud**. Big burrows were only associated with the **pebble** substratum, which likely relates to the physical properties of the different sized particles that make up the substratum.

Taxa	Coral				Non Coral			p
	Rubble	Dead	Live	Hetro	Pebble	Sand	Sandy mud	
Echiuroidea								0.012 *
<i>Munida</i>								0.025 *
Chordata	<i>Sebastes</i>							0.012 *
	<i>Gadiculus argenteus</i>							0.038 *
	Tunicata colonial green							0.042 *
	<i>Protanthea simplex</i>							0.008 **
Cnidaria	Paragorgia red							0.021 *
	Actiniaria buried redish							0.031 *
	Paragorgia white							0.037 *
	<i>Clavularia borealis</i>							0.016 *
	Hydrozoa bush							0.021 *
Echinodermata	<i>Porania</i>							0.040 *
	Poraniidae							0.025 *
	<i>Echinus</i>							0.034 *
	<i>Cidaris cidaris</i>							0.01 *
Porifera	<i>Phakellia</i>							0.036 *
	<i>Mycale lingua</i>							0.013 *
	<i>Geodia barreti</i>							0.021 *
	<i>Plakortis</i>							0.035 *
	Porifera encrusting							0.008 **
	Porifera white medium							0.004 **
	Porifera small							0.042 *
	Burrow big							0.016 *
	Burrows small							0.024 *

Figure 2.7: Results of multi-level pattern analysis between taxa and the most common substratum type at each of the video sequences. The list appears short as only taxa with a significant ($p < 0.05$) most common substratum type preference were included in the figure. Taxa are represented on the left of the figure, grouped and ordered by phylum. Phyla are separated by grey lines. Substratum types are represented by the columns; they are grouped based on coral or non coral-related substrata. The heterogeneous (Hetro) substratum type appears between the coral and non-coral groups, as although these video sequences contained no more than 33% of a single substratum type, in all cases coral-related substrata were more common ($> 50\%$) than non-coral related substrata. Green filled-in dots represent an association between the corresponding taxon and the substratum. The p-value indicated on the right of the graph represents the significance of the relationship described in the line. Thus, when more than one dot is coloured, it represents the relationship between the abundance of the taxon and all indicated substratum types.

2.3.2.2 Multidimensional scaling and cluster analysis

Multidimensional scaling (MDS) indicated that there was an overlap in the community assemblage found on the reef sites (figures 2.8 and 2.9). The video sequences from reef R1353 are slightly more separate from the other reef sites. Notably, the video sequences from reef R1353 are more tightly “clumped” together compared to the other reefs, followed by the video sequences from reef R1243. There is no clear separation between video sequences that contained cold-water coral substratum types and those that did not. This is expected as all the video sequences represent areas in close proximity (<400m) to cold-water coral reefs. The majority of video sequences that did not contain cold-water coral related substrata were adjacent to video sequences that did. The largest distance between a video sequence that contained coral and that did not was 400m.

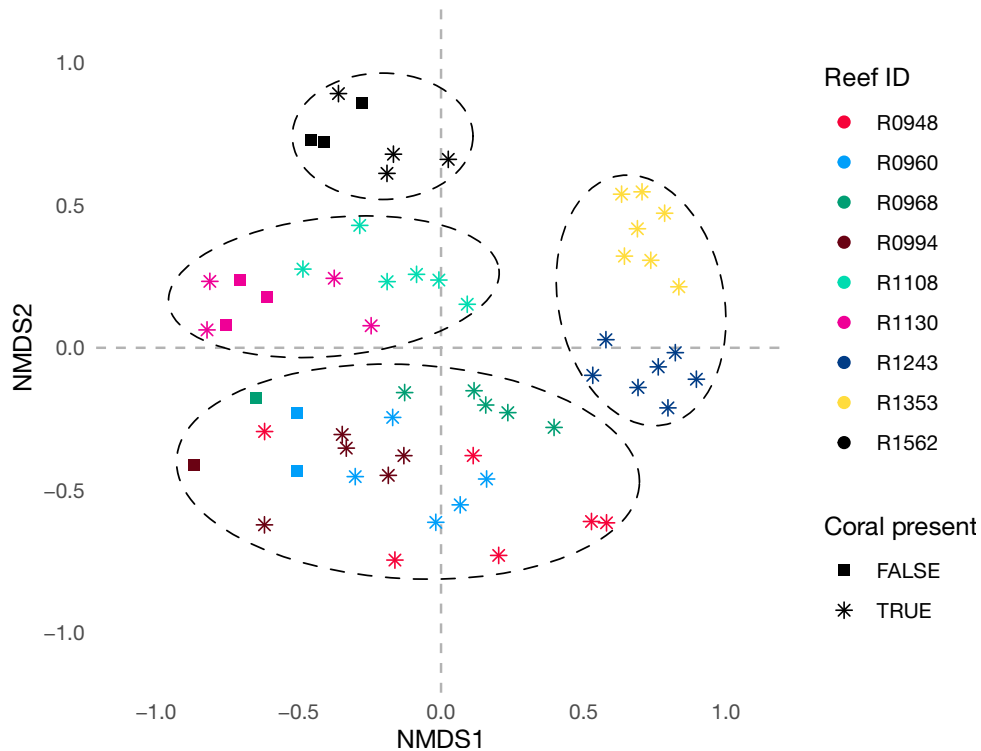


Figure 2.8: Non-metric multidimensional scaling results for the taxa found at each of the video sequences (stress ≈ 0.225), coloured by the reef from which the samples were obtained. Subsamples with solid points represent video sequences where no coral zones were present. Dashed ellipsoids represent video sequences that are indicated as being at least 40% similar by hierarchy clustering. These lines are purely a graphical representation of a separate analysis and do not represent any statistical values on the graph.

The sea urchin *Cidaris cidaris*, and the corals *Primnoa resedaeformis* and *Lophelia pertusa*, are associated with reef R1353 (figure 2.9). It should be noted that the observation of *Lophelia pertusa* represents individual corals that are not associated with a reef since, when they were associated with a cold-water coral reef, they were recorded as a substratum type instead. This reef was the deepest reef sampled (figure: 2.3A).

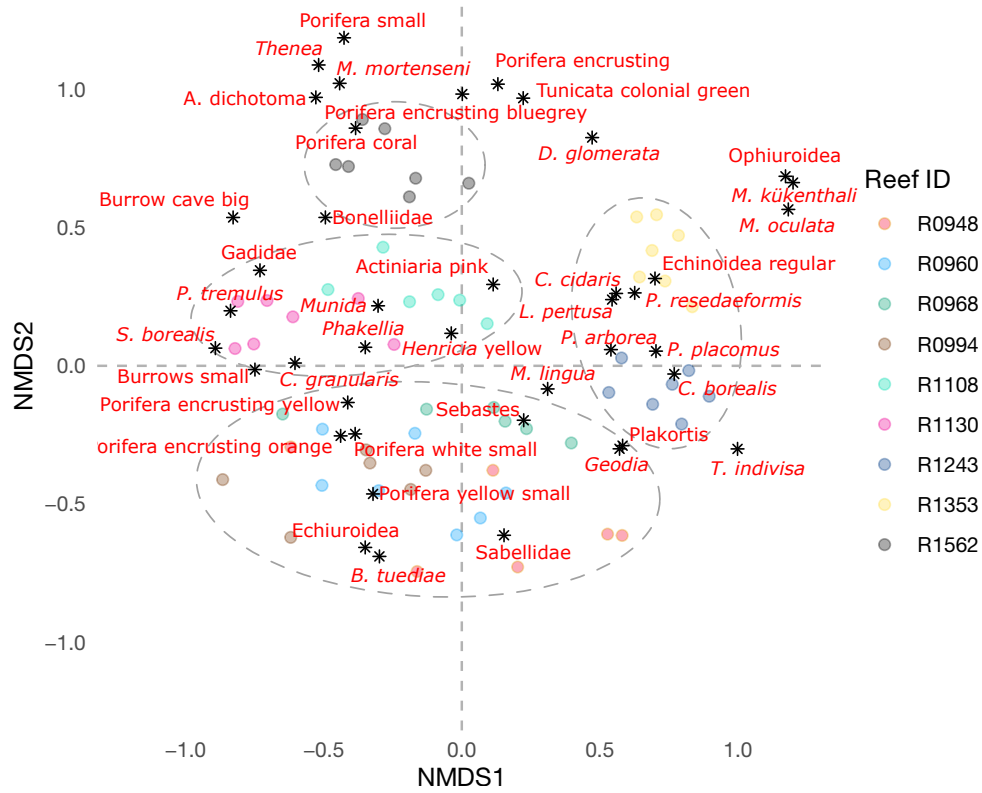


Figure 2.9: Non-metric multidimensional scaling results for the taxa found at each of the video sequences (stress ≈ 0.225), coloured by the reef from which the samples were obtained. Taxa that are indicated as significant by environmental fitting are represented by the black stars plotted over the video sequences. The taxon names are plotted in red, as near to their corresponding position while minimising overlaps. Dashed ellipsoids represent video sequences that are indicated as being at least 40% similar by hierarchy clustering. These lines are purely a graphical representation of a separate analysis and do not represent any statistical values on the graph. The full species names are *Asconema setubalense*, *Ceramaster granularis*, *Cidaris cidaris*, *Clavularia borealis*, *Drifa glomerata*, *Lophelia pertusa*, *Mellonympha mortenseni*, *Mycale lingua*, *Paragorgia arborea*, *Paramuricea placomus*, *Primnoa resedaeformis*, *Parastichopus tremulus*, *Stylocordyla borealis*, *Bolocera tuediae*, *Madrepora oculata*, *Tubularia indivisa*, *Muriceides kükenethali*, and *Antho dichotoma*.

Hierarchical clustering indicates three major groups between which video sequences are less than 20% similar. Reefs R1353 and R1243 are very dissimilar to the rest of the reef sites (figure 2.10), while reefs R0994, R0968, R0960, and R0948 form a group that is separate from reefs R1108, R1130, and R1562. Using the 40% cut-off represented in the diagrams places reef R1562 separate from R1108 and R1130. These results are evident in the non-metric multidimensional scaling (figure 2.8). Video sequences from the same reefs clustered together, with the exception of reef R0948. Three video sequences from reef R0948 are more similar to the video sequences from reef R0968 than the remaining videos sequences from reef R0948. These three video sequences along with a single video sequence from reef R0948 form a group together being around 75% similar. These represent the only video sequences that less than 70% similar to all the other video sequences from the same reef.

Reef R1562 was further north than all other reef sites, while R1108 and R1130 were relatively close together. These reefs also have similar depths, at approximately 350m. Statistically, reefs R1108 and R1130 had different depths; however, reef R1562 is considered to be statistically similar to both reefs (figure 2.3A). Substrata type differed between these reefs, particularly with regards to sand and sandy

mud (figure 2.4). The greater presence of **sand** on reef R1562 may suggest a reason for its separation from reefs R1108 and R1130.

Reefs R1353 and R1243 are significantly different in depth (figure 2.3A). Reef R1353 is significantly deeper than all the other reef sites, at more than 450m (figure 2.3A), while reef R1243 is around 280m deep, similar to the depth of both R0968 and R0948. Likewise, reefs R1353 and R1243 are not particularly close compared to the grouping of some other reef pairs (around 162km apart). However, both reefs R1243 and R1353 had relatively high percentages of **live coral** (figure 2.4), averaging 63% and 27% across their video sequences respectively, compared to the other reefs that averaged less than 12%.

The remaining reefs (R0948, R0960, R0968, and R0994) formed the single biggest cluster. These reefs were all between 310m and 277m in depth, although their depths did significantly differ between some reef pairs. Geographically, while reefs R0960 and R0968 were within 28km of each other, reefs R0948 and R0994 were around 128km NNE and 230km SSW from reef R0960. Reef R0948 was dominated by **sandy mud**, whereas the other reefs tended towards **sand**. This provides a possible driver for the less than 50% similarity between reef R0994 and (apart from a single video sequence on reef R0968) the other reefs in this cluster.

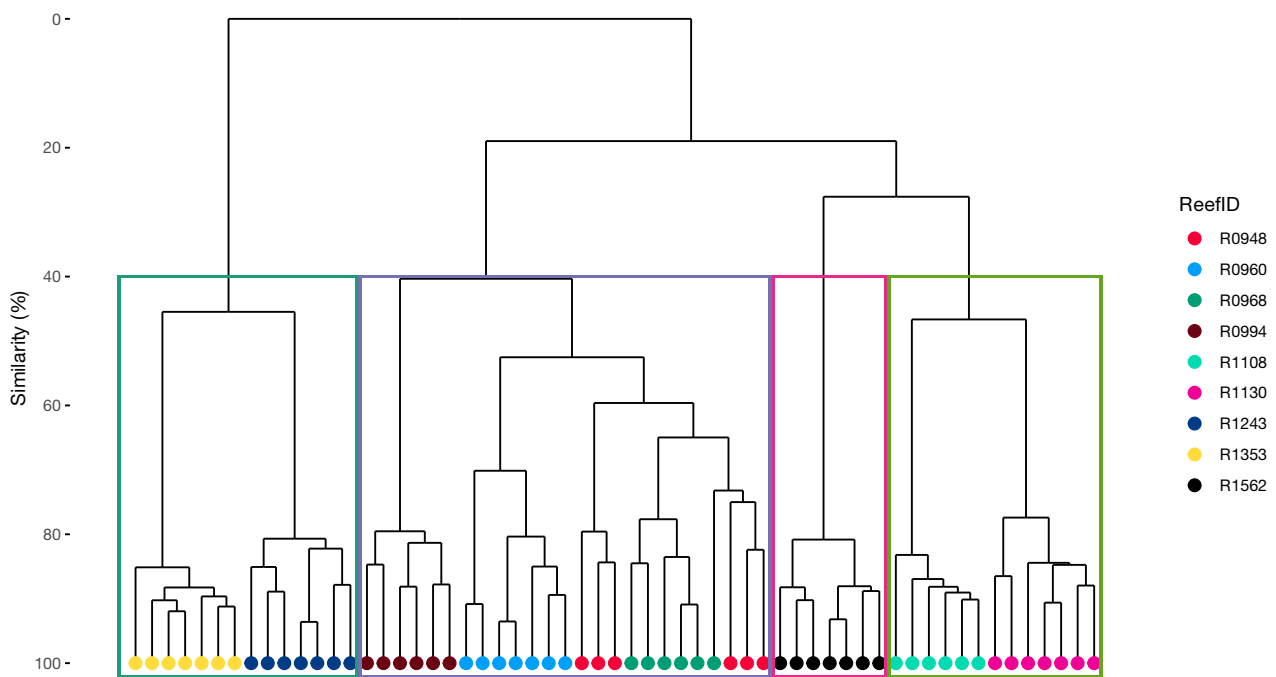


Figure 2.10: Hierarchical clustering based on the taxa found at each video sequence, coloured by the reef from which the samples were obtained. Coloured rectangles represent groups that are more than 50% similar.

2.3.2.3 Distance-based redundancy analysis

The constrained components from the db-RDA accounted for 59.98% of the observed variance, with 33.76% of the total variance accounted for by the first two axes (figure 2.11). The percentage cover of **live coral** explained the most variance in the dataset, acting along the first axis ($R^2 = 0.19$, $p < 0.001$),

followed by mean depth, latitude, and longitude ($R^2 = 0.11, 0.09, 0.08, p < 0.001$) (table 2.4). The sponge *Mycale (mycale) lingua* was associated with video sequences that contained **live coral** (figure 2.11). The gorgonian corals *Paragorgia arborea* and *Primnoa resedaeformis* were associated with **live coral**.

The encrusting sponge genus *Plakortis* was associated with the positive CAP1 and CAP2 axes, along which **live coral** and **coral rubble** act, respectively. Members of the phylum porifera that are encrusting were associated with both directions of both db-RDA axes (figure 2.11). Encrusting sponges that are orange or yellow were associated with greater median latitudes, while bluegrey encrusting sponges associated more with increased depth.

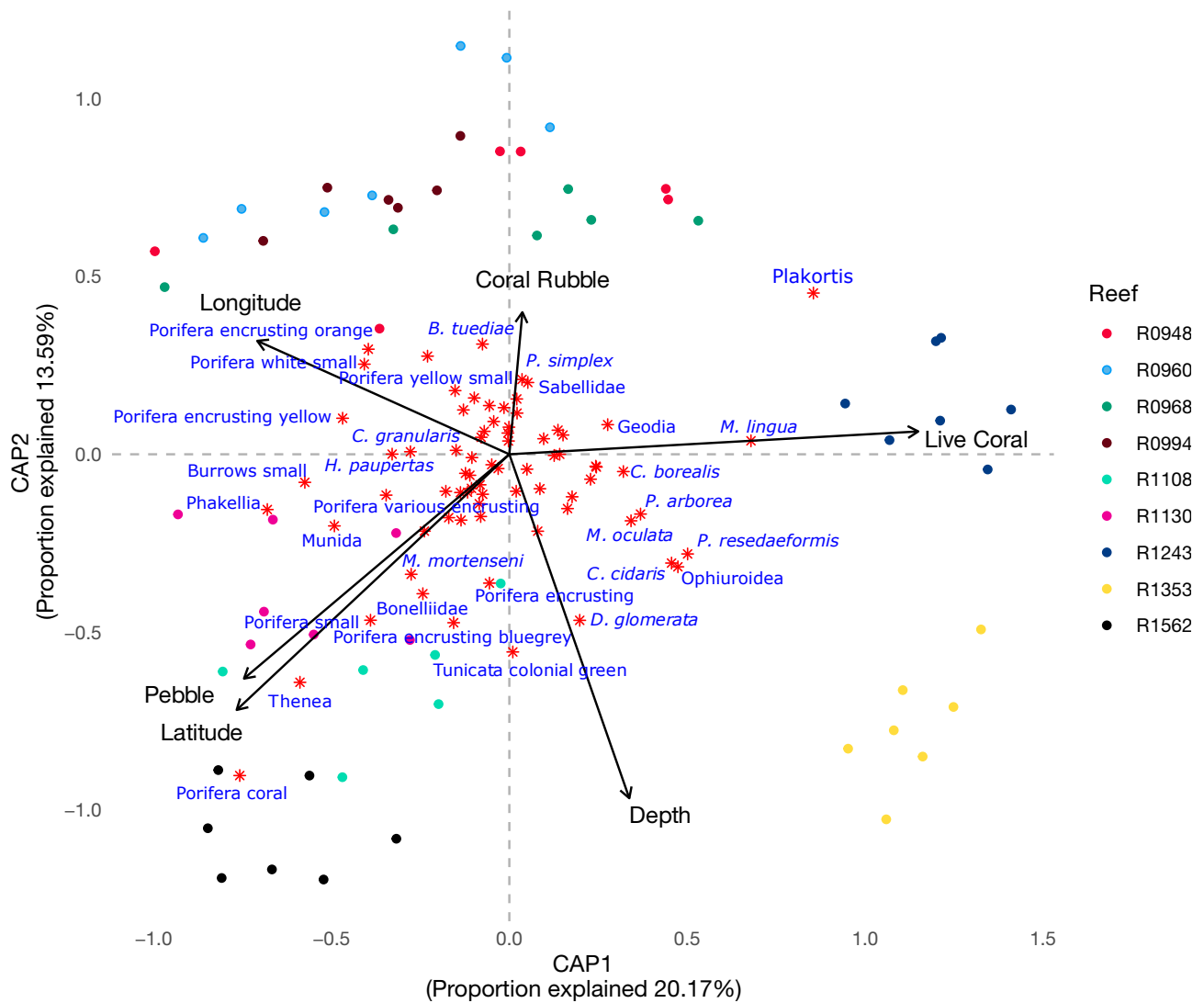


Figure 2.11: Distance-based redundancy analysis tri-plot. The red stars indicate taxa, arrows represent the environmental variables, and points represent the samples, coloured by reef. Taxa that are not clumped about the origin are labelled in blue. The full species names are *Ceramaster granularis*, *Cidaris cidaris*, *Drifa glomerata*, *Hymedesmia paupertas*, *Mellonympa mortenseni*, *Mycale lingua*, *Paragorgia arborea*, *Paramuricea placomus*, *Primnoa resedaeformis*, *Protanthea simplex*, *Bolocera tuediae*, and *Clavularia borealis*.

Table 2.4: Permutational Multivariate Analysis of Variance Using Distance Matrices output for the environmental factors included in the db-RDA model. Columns display the variable name, degrees of freedom (df), sum of squares (SumOfSqs), R-squared (R2), F statistic (F), the p-value (Pr(>F)), and an indicator of significance (***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$)

	Df	SumOfSqs	R2	F	Pr(>F)	
Live Coral	1	2.55	0.19	21.27	0.0010	***
Depth	1	1.60	0.12	13.33	0.0010	***
Latitude	1	1.25	0.09	10.39	0.0010	***
Longitude	1	1.07	0.08	8.92	0.0010	***
Coral Rubble	1	0.35	0.03	2.94	0.01	*
Pebble	1	0.32	0.03	3.21	0.0030	**
Residual	52	6.24	0.46			
Total	58	13.45	1.00			

2.4 Discussion

The species patterns observed in the indirect analysis were best explained by differences in substratum composition. The effect of depth and geographical position of the reef offer less of an explanation for the patterns observed in these analyses. Notably, reefs that differed significantly in depth but with similar proportions of **live coral** were grouped together. However, direct gradient analysis indicated depth to be the second most powerful explanatory variable. Both depth and substratum type are known to be drivers of community composition on cold-water coral reefs (Milligan et al., 2016; Corbera et al., 2019) and benthic habitats in general (Zajac et al., 2000; Santín et al., 2018).

The results of the indirect gradient analysis indicated several species that were associated with the deepest reef (R1353). The direct gradient analysis placed these species between the gradients for depth and **live coral** (figure 2.9). Thus, while depth was a significant driver of species composition, no individual taxa were associated with the upper end of the depth range. Longitude and latitude were also found to be significant drivers of species composition, this is supported by previous findings (Buhl-Mortensen, 2017).

The four reefs closer to the shore had similar taxonomic compositions, while the five reefs closer to the shelf edge formed three distinctive groups (figures 2.1 and 2.10). There are two water masses off the coast of Norway; the Norwegian Coast Water (NCW) and the North Atlantic Drift (NAD) (Juva et al., 2020). Differences in water masses and distance from the coast alone do not explain the results. The two reefs that had where the least similar to the others are located nearer the coast than the other “off-shore” reefs. However, they are also located near steeper parts of the shelf edge (reefs R1243 and R1353, figure 2.1). Local hydrographic and biochemical play a secondary role in cold-water coral reef health (Juva et al., 2020). The results of this study suggest that both the different water masses and hydrodynamics influenced the taxonomic composition of associated reef species on these reefs.

The amount of **live coral** present was the single greatest driver of differences in taxonomic compositions between video sequences. This finding was statistically supported by the results of the db-RDA and by previous indirect gradient analysis (Buhl-Mortensen, 2017). Increased **live coral** coverage, was not correlated with increased **dead coral** or **live coral** coverage. Furthermore, being a strong driver of taxonomic composition should not be confused with driving diversity. The live coral zone has previ-

ously been found to have a relatively low biodiversity compared to the dead and coral rubble zones (Jensen, 2014; Buhl-Mortensen, 2017). None of the video sequences in this study consisted of only living or dead coral. Thus, a direct comparison between the biodiversities of the different reef zones was not possible. However, the Shannon indices for video sequences where the most common substratum was live coral covered a relatively large range, on par with those for the non-coral related substrata. In both cases, this was likely due to different microhabitats present in these video sequences. The presence of dead coral sections within the living coral zone has been observed to influence biodiversity (Mortensen and Fosså, 2006; Buhl-Mortensen, 2017).

The findings of this study support previous observations that *Paragorgia arborea*, *Primnoa resedaeformis*, and *Mycale lingua* are associated with the live coral zone (Buhl-Mortensen et al., 1995; Buhl-Mortensen et al., 2017b). Likewise, in line with Buhl-Mortensen et al. (2017b), two species of anemones and the filter feeding family of polychaetes Sabellidae were associated with coral rubble. However, the dead coral substratum was not found to be significant in the db-RDA model. This does not necessarily mean that the dead coral substratum did not have species associated with it. An example of one such species association are *Sebastes*; this genus was significantly associated with video sequences where dead coral was the most common bottom type. Previous studies have shown *Sebastes* species to associate with both the dead and live coral zones (Buhl-Mortensen et al., 1995; Buhl-Mortensen, 2017).

Organisms that could not be identified to a finer taxonomic level than Teleostei, *Sebastes* species, *Brosme brosme*, *Pollachius virens*, *Gadidae* species, and *Molva molva* were observed in five or more video sequences. These species have been observed in previous reef studies (Buhl-Mortensen et al., 1995; Fosså et al., 2002; Husebø et al., 2002; Buhl-Mortensen et al., 2017a; Buhl-Mortensen, 2017; Buhl-Mortensen et al., 2017b). Fishing methods such as gillnets or line fishing were utilised by some past studies. Shrimp, on gorgonian corals, have been noted to not move away from lights associated with ROVs (Buhl-Mortensen and Mortensen, 2004). While the impact on mobile fauna of light can not be fully discounted, numerous cold-water coral reef studies have identified mobile fauna using video methods including light sources (Buhl-Mortensen and Mortensen, 2004; Purser et al., 2013; Buhl-Mortensen, 2017; Buhl-Mortensen et al., 2017b).

The Cnidaria *P. simplex* was found to be associated with video sequences where dead coral was the most common substratum type; however, the results of the db-RDA places it close to the coral rubble, which highlights the gradient nature of the video sequences.

The mutually exclusive nature of the two “sandy” substrata, sand and sandy mud warrants further discussion. These substrata are defined as follows. Sandy mud is a sediment type consisting of more than 50% silt and mud sized particles and less than 50% sand, provided the ratio of silt to mud particles is between 1:2 and 2:1 (table 2.2). By contrast, for a sediment to be classified as sand, it needed to consist of more than 90% sand-sized particles (table 2.2). While both substrata represent soft bottoms, the large percentage of mud and silt particles in sandy mud makes it clear that this is actually a mud-based bottom type. The environmental conditions that allow for high silt or mud sediments differ fairly substantially to those that support larger grains, such as sand. Thus, the mutually exclusive nature of these two substrata is not as unexpected as the names alone might suggest.

2.4.1 Limitations

Species level identifications based on video footage are not always possible, because many species require high resolution analysis for identification. In particular, the identifying feature for many members of the phylum Porifera are their spicules, which require microscopic analysis (e.g. descriptions in van Soest et al., 2000; van Soest et al., 2007). In lieu of species identification, morphotypes can be used. In this dataset, colour and the encrusting body form morphotypes were used extensively. When listing the shape, size or colour of an organism, consistency is critical. For example, when using human observations, what constitutes blue enough to be listed as blue can differ from person to person. A second problem presented by the use of morphotypes is overlap between species. For example, the genus *Plakortis* includes encrusting sponges. Some of the other unidentified sponges might logically fall into this genus. The separation of these groups could thus produce artificial variability. The use of traits removes some of the uncertainty introduced by problems with fine level identification.

The polychaete *Eunice norvegica* is a known cold-water coral symbiote that is present in Norwegian waters (Mueller et al., 2013). In general, it is known to be associated with the living part of the reef (Freiwald et al., 2004). However, *E. norvegica* is notably absent from this dataset. In general, very few polychaetes were observed in the dataset. This likely represents low levels of detection for infauna, based on the surveying method. Although, it should be noted that *E. norvegica* has been observed on cold-water coral reefs using video footage from a static camera (Buhl-Mortensen et al., 2015c). The absence of *E. norvegica* was notable, given the well-documented nature of its interactions with *L. pertusa* (Buhl-Mortensen, 2001; Mueller et al., 2013; van Oevelen et al., 2018a, e.g.). Many other small and cryptic species were undetectable by the sampling method. Given the nature of these reef and interactions between taxa, the megafauna that were detected would likely act indicator species for the under sampled taxa.

2.4.2 Conclusion

The findings of this chapter support the hypothesis that geographical locations of cold-water coral reefs influence the species found on the reef. Forward selection retained both longitude and latitude in the final model; however, their negative correlation with **live coral** cannot be disregarded. Likewise, **pebble** and latitude, while both retained in the final db-RDA model, appear to be similar drivers of community composition.

While longitude and latitude influenced species composition, they were likely proxies for other unmeasured factors such as local hydrodynamic factors and water temperatures. These local framing factors likely determine fine-scale species distributions or preferences. At larger scales, species ranges would have to be considered as a potential factor.

Chapter 3

Biological Trait Information:

Descriptions of the biological traits of select species, genera, and families from the dataset

Abstract

Biological trait analyses require that taxa be described in terms of their biological traits. Trait databases tend to be populated as needed, often stemming from biological trait or environmental sensitivity analysis that their authors have performed. This method is efficient; however, it leaves gaps in the documentation of traits. This chapter aimed to address these gaps, for the taxa observed on the reef sites that were not present or were under-described in existing trait databases. Biological traits were assigned to these taxa from literature sources. There was good trait coverage in the literature for many of these taxa. Body form, living habit and adult movement were the most commonly reported traits in the literature, while larval development was the least. The majority of taxa were found to be sessile and attached. Hierarchical clustering indicated that the expressed traits among these taxa generally grouped phyla, classes and orders correctly. In assigning traits, the continued relevance of encyclopedias, text books and other citable sources of general information became clear. Digital resources have been revolutionary; however, freely editable pages and websites lacking proper citations have made it challenging to find verified modern sources for general facts such as “starfish crawl”.

3.1 Introduction

Biological trait analysis requires that the relevant biological traits of the observed species be defined (Clare et al., 2022). A complete resource for this would be impossible to compile, as not every species has been discovered. The qualifier of relevant biological traits would make such an endeavour even more challenging, as trait selection is based on expert knowledge (de Juan et al., 2022). Biological trait information can be found by literature review for the species in question. Several authors who have performed such reviews have made their findings available in the form of databases. Examples of such databases include The Arctic Traits Database (Degen and Faulwetter, 2019), PolyTraits (Faulwetter et al., 2014), and BIOTIC (MarLIN, 2006). The existence of a similar endeavour by Clare et al. (2022) must be noted. This databased was published after this chapter had been compiled, thus, information from it was not used.

This chapter aims to supplement the existing information on species and higher taxonomic levels

recorded in existing databases, by presenting information for the species found in the dataset described in chapter 2. Since the trait descriptions are text and formatted in a manner more akin to a text book, they will be presented at the end of this chapter. Thus this introduction will be followed by a description of the dataset, the methods used to assign traits, a summary of the trait patterns, and a discussion of these patterns, after which the text description of the traits assigned will be presented.

3.2 Description of the dataset

The dataset was obtained from MAREANO, and is described in detail in chapter 2. The group names were used as they appear in the sanitised data used in chapter 2. However, in chapter 2, it was accepted that taxa with different colours (e.g. Porifera white and Porifera red) potentially represented unique taxonomic observations. As traits are assigned at taxonomic levels and a red poriferan might represent any number of different species, the colour does not affect the lowest taxonomic level for which traits can be assigned. In this chapter, traits were assigned based only on the finest taxonomic resolution possible. However, physical descriptions that were trait-relevant were retained in the dataset for use in the biological trait analysis.

Organisms belonging to 11 different phyla are present in the data. These phyla are: Annelida, Arthropoda, Brachiopoda, Bryozoa, Chordata, Cnidaria, Echinodermata, Foraminifera, Mollusca, Nemertea, and Porifera. Descriptive observations such as “Porifera Small Yellow” were reassigned to their lowest observed taxonomic level. This resulted in the 106 unique observations, compared to the 167 in chapter 2. Of these, 53 were at species level, 19 at genus, 15 at family, one at superfamily, one at infraorder, four at order, one at subclass, seven at class, one at subphylum, and four at phylum. Classification at levels more resolved than family account for 82.1% of the classifications. Not all high level classifications present the same issue of being overly-broad; some orders and classes in the dataset have very distinct biological traits.

3.3 Methods

3.3.1 Taxonomy

The World Register of Marine Species (WoRMS) (WoRMS Editorial Board, 2021) was used as the authority for taxonomy in this thesis. Groups that belonged to known synonyms were changed to conform with the accepted groups at time of writing. The exception to this rule is *Lophelia pertusa* (Linnaeus, 1758), which has been accepted as *Desmophyllum pertusum* (Linnaeus, 1758). As of July 2021, the name *L. pertusa* remains more common in literature (SCOPUS results since 2019: *L. pertusa* 53, *D. pertusum* 13). This is especially true in relation to the study region.

3.3.2 Traits

None of the three databases used were complete; 53 of the 106 unique taxon names were present in the databases. Literature sources were used to assign trait values where possible, to the remaining taxa. The taxa that were present in the databases were not covered in this chapter, as their traits were not assigned by this literature search. Sixty eight of the 167 unique taxon names were descriptions of monotypes representing 11 different taxa, traits were not assigned in this chapter for the four groups

representing observations of burrows. Eleven of the remaining 53 taxa represented fish. Literature was used to assign traits to the remaining 42 taxa. Traits are presented for 59 taxa in this chapter, the additional 17 taxa come from the study region. However, they were present in video sequences that were excluded from the study (see chapter 2).

The Arctic Traits Database (Degen and Faulwetter, 2019) was used as the primary source for the traits in this chapter. A large number of the organisms observed in the study region were already present in the Arctic Traits Database. Therefore, this chapter made use of the trait definitions from the Arctic Traits Database with a few additional traits. The additional traits were added to address the inclusion of grazing organisms and fish, which were not common in the dataset used to populate the Arctic Traits Database. The use of established trait naming assists with standardising biological trait analysis, this was in line with recent recommendations for biological trait analyses (de Juan et al., 2022).

Both PolyTraits (Faulwetter et al., 2014) and BIOTIC (MarLIN, 2006) were used as secondary sources of biological trait information. In addition to trait databases, FishBase (Froese and Pauly, 2021) was used to obtain the traits of fishes observed in the dataset. The data contained within these databases were converted to cover the traits and trait definitions of the Arctic Traits Database.

The trait definitions used in this chapter are summarised, almost verbatim, from the Arctic Traits Database in table 3.1. Only traits present in the Arctic Traits Database were defined by the Arctic Traits Database. The dataset analysed in this chapter contained species that exhibited trait modalities that were not present in the Arctic Traits Database. New definitions were made to better represent these traits modalities. The trait definitions that have been added to the list are represented in bold in the table.

Table 3.1: Table of trait definitions used by The Arctic Traits Database, leaving out the example taxa, and showing the name of the trait. The first column represents the different classes each trait can have, and the definition used by the Arctic Traits Database. Text in italics represents the authors' expansion or clarification of definitions.

Trait name	Class	Definition	Description
Size	S1	small	$< 10mm$
	S2	small-medium	$10 - 50mm$
	S3	medium	$50 - 100mm$
	S4	medium-large	$100 - 300mm$
	S5	large	$300mm - 500mm$
	S6	extra-large	$> 500mm$
Body Form	BF1	globulose	Round or oval
	BF2	vermiform, elongate	Worm-like or thin, elongate body form
	BF3	dorso-ventral compressed	Species that are flat, or encrusting
	BF4	laterally compressed	Thin
	BF5	upright	<i>More upright than globulose</i>
	BF6	Pisciform	Fish-shaped
	BF7	Branching	Forms branches, includes fan-like shapes
Fragility	F1	fragile	Likely to crush, break, or crack as a result of physical impact
	F2	intermediate	Liable to suffer minor damage, chips or cracks as a result of physical impacts
	F3	robust	Unlikely to be damaged as a result of physical impacts
Sociability	SO1	solitary	Single individual
	SO2	gregarious	Single individuals forming groups
	SO3	colonial	Living in permanent colonies
Skeleton	SK1	calcareous	Skeleton material aragonite or calcite
	SK2	siliceous	Skeleton material silicate
	SK3	chitinous	Skeleton material chitin
	SK4	cuticle	No skeleton but has a protective structure
	SK5	none	No form of protective structure
Reproduction	R1	asexual	Budding and fission
	R2	sexual - external	Fertilisation external, eggs and sperm deposited on substratum or released into the water (broadcast spawners)
	R3	sexual - internal	Fertilisation internal, but no brooding, eggs deposited on substrate, indirect or direct development
	R4	sexual - brooding	Fertilisation internal or external, eggs or larvae are brooded, indirect or direct development
Larval development	LD1	pelagic/planktotrophic	High fecundity, larvae feed and grow in water column, generally pelagic for several weeks
	LD2	pelagic/lecithotrophic	Medium fecundity, larvae with yolk sac, pelagic for short periods
	LD3	benthic/direct	Larvae have benthic or direct development
Life span	A1	short	< 2 years
	A2	medium	2-5 years
	A3	medium-long	5-20 years
	A4	long	> 20 years

Table 3.1: (Continued): Table of trait definitions used by The Arctic Traits Database, leaving out the example taxa, and showing the name of the trait. The first column represents the different classes each trait can have, and the definition used by the Arctic Traits Database. Text in italics represents the authors' expansion or clarification of definitions.

Trait name	Class	Definition	Description
Adult movement	MV1	sessile	No movement as an adult
	MV2	burrower	Movement in the sediment; includes tube dwellers
	MV3	crawler	An organism that moves along the substratum via movements of its legs, appendages or muscles
	MV4	swimmer	Movement above the substratum
Living habit	LH1	free living	No limit to any restrictive structure at any time. Able to move freely within and/or on the sediments
	LH2	crevice dwelling	Adults are typically cryptic, inhabiting spaces made available by coarse/rock substrata and or biological species or algal holdfasts
	LH3	tube dwelling	Tube may be lined with sand, mucus or calcium carbonate, tube can also be in a burrow
	LH4	burrowing	Species inhabiting permanent or temporary burrows in the sediment, or just burrowing in the sediment
	LH5	epi/endo zoic/phytic	Living on or in other organisms
	LH6	attached	Adherent to a substratum
Mobility	MO1	none	No movement as an adult
	MO2	low	Slow movement
	MO3	medium	Medium movement
	MO4	high	High movement, swimmer or fast crawler
Substratum	SA1	soft	Soft substrata, sand or mud
	SA2	hard	hard substrata, rock and gravel
	SA3	biological	Epizoid or epiphytic life style
	SA4	none	Species is hyper benthic
Feeding habit	FH1	deposit feeder	Removal of detrital matter from the sediment surface or from the sediment matrix, includes species which rake or scrape algal matter from surfaces
	FH3a	active filter feeder	Filter feeding by active pumping of water
	FH3p	passive filter feeding	Passive filter feeding or suspension feeding, relies on current to bring food particles to the organism
	FH4	opportunistic/scavenger	An organism that can use different types of food sources/an organism that feeds on dead organic material
	FH5	predator	An organism that feeds by preying on other organisms
	FH6	parasite, commensal or symbiotic	An organism that lives in or on another living organism (the host), from which it obtains food and other requirements; or an organism containing symbionts
	FH8	grazer	An organism that feeds on part of other organisms, without consuming the whole organism. Typically feeds on algae, kelp, or coral.
Bioturbation	B1	diffusive mixing	Surficial movement of sediment and/or particles, resulting from movement or feeding activities on the surface
	B2	surface deposition	Deposition of particles at the sediment surface resulting from e.g. defaecation or egestion (pseudo faeces) by, for example, surface deposit feeding organisms (e.g. holothuroids, bivalves, tubicolous polychaetes)
	B3	conveyor belt transport (upward)	Translocation of sediment and/or particulates from depth within the sediment to the surface during subsurface deposit feeding or burrow excavation.
	B4	downward (reverse) conveyor	The subduction of particles from the surface to some depth by feeding or defaecation.
	B5	none	No bioturbation (e.g. sessile animals on rocky ground)

Table 3.1: (Continued): Table of trait definitions used by The Arctic Traits Database, leaving out the example taxa, and showing the name of the trait, the first column represents the different classes each trait can have, and the definition used by the Arctic Traits Database. Text in *italics* represent the authors expansion or clarification of definitions.

Trait name	Class	Definition	Description
Trophic Level	TL1	1	Primary producer
	TL2	2	Primary consumers
	TL3	3	Secondary consumers
	TL4	4	Tertiary consumers
	TL5	5	Quaternary consumers
Tolerance	T1	low	Species are sensitive to changes in the environment like organic enrichment, pollution, temperature or salinity changes
	T2	intermediate	Species are indifferent or no information available
	T3	high	Species tolerates organic enrichments, pollution, temperature or salinity changes
Environmental position	EP1	infauna	Lives in the sediment
	EP2	epibenthic	Lives on the surface of the seabed
	EP3	hyper-benthic	Lives in the water column, but (primarily/occasionally) feeds on the bottom; benthopelagic
Depth Range	DR1	shallow	0-20m
	DR2	shelf	20-200m
	DR3	shelf-slope	200-1000m
	DR4	slope-basin	>1000m
Zoogeography	Z1	arctic	Confined to Arctic regions
	Z2	arctic-boreal	Arctic, sub-Arctic and North Atlantic/North Pacific distribution
	Z3	boreal	North Atlantic and/or North Pacific distribution; potentially sub-Arctic regions such as Southern Barents Sea or Bering Sea
	Z4	cosmopolite	Cosmopolitan

Some of the traits in the table are described differently in other sources; for example, the terms branched and massive are used frequently by van Soest et al. (2000) in articles on The Marine Species Identification Portal (<http://species-identification.org>). These terms would be upright and globulose (respectively) on the Arctic Traits Database. Additionally, some of the trait descriptions in table 3.1 require further clarification. Organisms would be described as deposit feeders under the Arctic Traits Databases definitions were assigned the feeding habit of grazing (FH6) if they consumed algae, coral or kelp (Degen 2021/09/21, personal communication). Unless explicitly mentioned otherwise in the literature, carnivorous species were considered as predators.

Taxa observed in the dataset that also occurred south of approximately 45°N were considered to be cosmopolite (Z3). This definition was used in order to avoid redefining the zoogeography trait for species already in the database. In practice, cosmopolitan species had distributions much further south than the defined cut-off longitude. Zoogeography is not technically speaking a trait, as it's not inherent to the organisms. Rather, range limitations are the result of traits such as salinity and temperature tolerance. It was assigned in this chapter for consistency with the Arctic Traits Databases format.

Fuzzy coding (Chevenet et al., 1994) allows for more detailed coding of traits than binary coding. This is very useful when observations are at taxonomic levels higher than species. Each value a trait

can have is referred to as a trait modality (e.g. small is a modality of the trait size). Fuzzy coding assigns a numerical value based on the prevalence of each modality for a taxon. Fuzzy coding was done using a zero to three scale; where zero, represents the trait modality never being displayed; one, represents a modality that is sometimes present; two, represents a modality that is often present; and three, a modality that is the only one present. This fuzzy coding scale was used by previous studies in the North Atlantic (Bolam et al., 2014; Degen and Faulwetter, 2019; Sutton et al., 2021). Hence, a species that only swims would be given a three for swimming, while a species like a shrimp that swims and crawls would be assigned values of two for both modalities.

3.3.3 Summary of assigned traits

All summary figures and statistics were produced using R (R Core Team, 2022). The assigned trait modalities were summarised as a heatmap, with the taxa ordered based on heretical clustering of traits. Statistically each modality was considered separately in this heatmap, rather than as part of a trait. The assigned traits were further summarised as a table representing the percentage of taxa for which information related to each trait could be found in the literature. Additionally, the expression of each modality-affinity pair (EI Total affinity (3) for the modality FH6) were calculated as a percentage of taxa for which trait information was available. This was calculated by calculating the number of taxa for which a trait was assigned, and then calculating the number of times each modality-affinity pair was assigned. For example, trait information for feeding habit was present for 56 taxa, of which 3 taxa exhibited a low affinity to the feeding method FH1. This was expressed as 5.4%.

3.4 Results

The most commonly described traits for the taxa in this chapter were body form, living habit, adult movement, feeding habit, and environmental position. Descriptions of all of these traits were present in the literature for 55 out of the 59 taxa described in this chapter (93.2%). Of the three taxa for which all of these traits could not be assigned, three were missing information for a single trait, and one for two of the traits. The taxa described in this chapter had relatively well defined traits with most containing only a few missing values.

Since most descriptions of species either describe their shape or include photographs from which shape can be inferred, it was surprising that body form could not be assigned to all of the taxa in this chapter. The only taxa for which body forms could not be defined was the genus *Oceanapia*. This genus contains 104 species, no citable description of body form found in the literature. The traits of fishes present were well-defined in FishBase; as such, they were not described in this chapter. The absence of the pisciform body shape from this list was therefore expected. The most common body form was upright (39.7% of taxa for which body size was described expressed at least low affinity (table 3.2)), highlighting the prevalence of erect sponges and corals described in this chapter.

Living habit and adult movement are dependent on each other for some modality pairs; attached organisms (LH6) are by definition sessile (MV1). Assigning both living habit, adult movement, and mobility to species in the phyla Porifera, Bryozoa, and the subclass Octocorallia was trivial, This was because, it is well documented that all species in these taxonomic ranks are attached and sessile. In figure 3.1, the main split in the clustering of taxa was between those that move (the bottom 11

taxa) and those that do not. The vast majority of taxa described in this chapter had total affinity for the attached living habit, representing 75.9% of taxa for which living habit was described. The most common adult movement trait in the dataset was sessile, with 77.6% of taxa for which adult movement was described as having total affinity for MV1. Note that this indicated that there was at least one taxon described in this chapter that was sessile, but not attached.

Given the nature of the sampling method used to gather the data, it is unsurprising that 100% of the taxa for which the trait environmental position was described had at least medium affinity for being epibenthic. The only taxa that exhibited medium, rather than total, affinity represent the genus *Munida*, which included swimming species.

Size range is a useful identifying feature; however, its measurement requires physical interaction with the organism or imagery from which scale can be calculated. Additionally, while the size of many species in a family or genus might be known, if there is a large size range, assigning fuzzy codes to the group as a whole is challenging. As a result, size was described for 83.1% of the taxa in this chapter, with the majority of missing data belonging to taxonomic ranks of genus or higher.

The hierarchical clustering of the taxa, based on their fuzzy coded trait modalities grouped the taxa similarly to their taxonomic hierarchy (figure 3.1). This result is expected since traits are often conserved within a taxa, and can be viewed as an indicator of sufficient trait coverage.

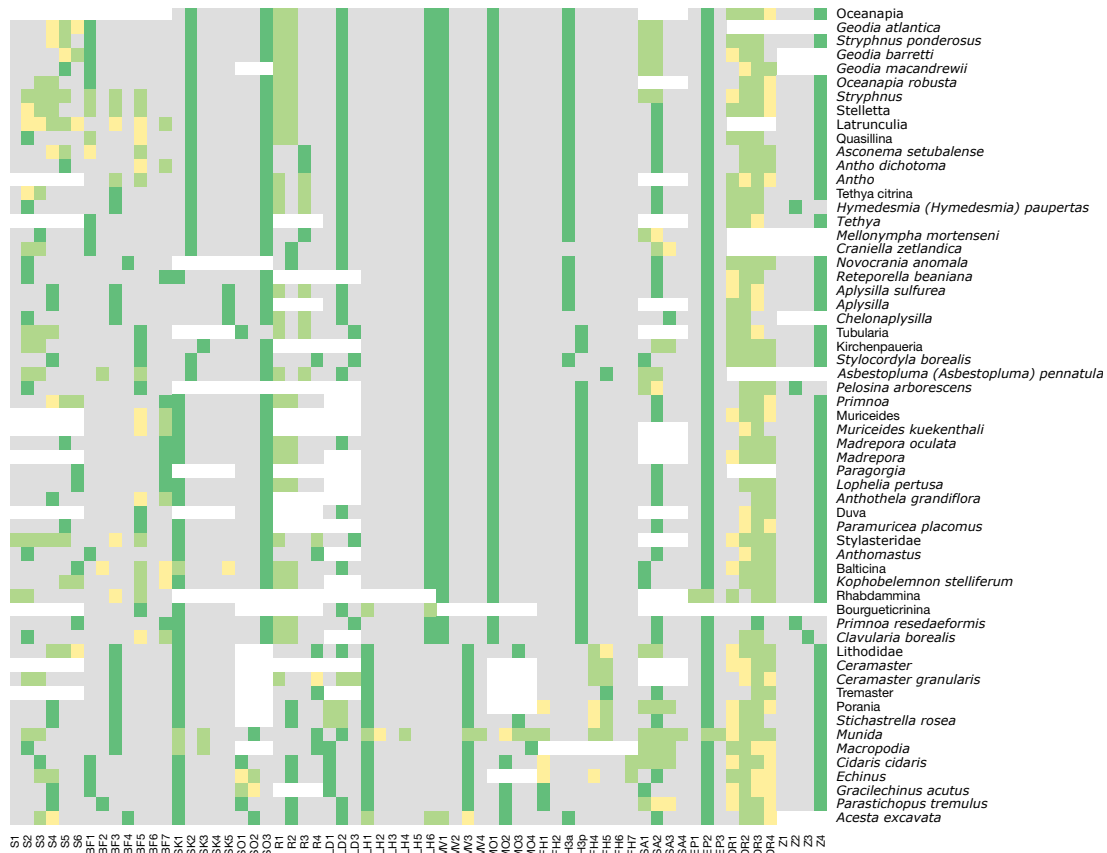


Figure 3.1: Heatmap of the traits described in this chapter for each taxon. Colours represent fuzzy coded trait values: total affinity is dark green, some affinity is light green, low affinity is yellow, no affinity is grey, unassigned modalities are white. The taxa are ordered based on cluster analysis of the trait modalities, while the trait modalities are ordered as in table 3.1.

Table 3.2: Summary of the percentage presences for the most commonly assigned traits. Trait, indicates the name of the trait. Percentage, displays the percentage of taxa described in this chapter for which trait data were available in the literature. Trait value, represents the fuzzy coded values, from trait modality not exhibited (0) to total affinity for the trait modality (3). Possible modalities are represented by the columns 1 through 8, blank and grey cells indicate modalities that were not used. The cell values of the modality columns represent the percentage of taxa (in which the trait was present) that expressed each modality at the corresponding Trait Value (EI of the 83.1% of taxa for which size was assigned 95.9% were assigned the fuzzy coded value of 0 for the modality S1).

Trait	Percentage	Trait Value	Modality Code							
			1	2	3	4	5	6	7	8
Size	83.1	0	95.9	57.1	67.3	57.1	71.4	79.6		
		1	0	6.1	2	10.2	2	6.1		
		2	4.1	18.4	26.5	16.3	18.4	6.1		
		3	0	18.4	4.1	16.3	8.2	8.2		
Body form	98.3	0	72.4	94.8	67.2	96.6	60.3	100	74.1	
		1	1.7	1.7	5.2	0	12.1	0	3.4	
		2	5.2	1.7	5.2	0	15.5	0	10.3	
		3	20.7	1.7	22.4	3.4	12.1	0	12.1	
Skeleton	89.8	0	45.3	62.3	94.3	100	92.5			
		1	0	0	0	0	1.9			
		2	5.7	0	3.8	0	0			
		3	49.1	37.7	1.9	0	5.7			
Social	79.7	0	89.4	91.5	14.9					
		1	2.1	2.1	0					
		2	2.1	2.1	0					
		3	6.4	4.3	85.1					
Laval development	71.2	0	85.7	19	88.1					
		1	0	0	0					
		2	4.8	7.1	2.4					
		3	9.5	73.8	9.5					
Living habit	98.3	0	75.9	98.3	100	98.3	100	20.7		
		1	0	1.7	0	0	0	0		
		2	5.2	0	0	1.7	0	3.4		
		3	19	0	0	0	0	75.9		
Adult movement	98.3	0	20.7	100	77.6	98.3				
		1	0	0	1.7	0				
		2	1.7	0	1.7	1.7				
		3	77.6	0	19	0				
Feeding habit	94.9	0	89.3	100	58.9	62.5	87.5	85.7	100	96.4
		1	5.4	0	0	0	5.4	1.8	0	0
		2	1.8	0	0	0	7.1	8.9	0	3.6
		3	3.6	0	41.1	37.5	0	3.6	0	0
Substrata	74.6	0	59.1	11.4	81.8	97.7				
		1	0	6.8	4.5	0				
		2	31.8	29.5	11.4	2.3				
		3	9.1	52.3	2.3	0				
Environmental position	98.3	0	98.3	0	98.3					
		1	0	0	0					
		2	1.7	3.4	1.7					
		3	0	96.6	0					
Depth range	88.1	0	36.5	7.7	1.9	28.8				
		1	30.8	15.4	13.5	30.8				
		2	32.7	76.9	82.7	40.4				
		3	0	0	1.9	0				
Zoogeography	84.7	0	100	94	98	8				
		1	0	0	0	0				
		2	0	0	0	0				
		3	0	6	2	92				

3.5 Discussion

The species for which traits were assigned in this chapter were observed using a tow camera (chapter 2). Tow cameras are known to be biased against certain traits. Specifically, species level identifications of smaller taxa would be more challenging than for larger taxa. Additionally, smaller taxa and hidden taxa, such as those with living habits of burrowing or crevice dwelling, would have been undersampled or missed. This should be considered when interpreting these results.

Even with an in-depth literature search, it was impossible to assign trait values to every trait of each species. This is indicative of gaps in the collective knowledge of these taxa. Trait information being absent in the literature differs from under-expression of a trait. The differences between these two factors are highlighted in figure 3.1 and table 3.2. Blank rows in figure 3.1 represent gaps in the literature, where high percentages for trait values of zero for certain modalities in table 3.2 represents low expression.

In discussing sparse traits and under-represented modalities, it must be reiterated that fish were excluded from this chapter. The fish taxa present in the dataset were well-represented in FishBase (Froese and Pauly, 2021). This accounts for the absence of the pisciform (BF6) from the traits modalities assigned here. Additionally, it explains, in part, why hyper-benthic taxa were uncommon.

Low trait expression could be the result of two factors: either high coverage of taxa with that trait in the already established trait databases, or restrictions based on sampling method or location. Only two of the nine reef sites in this study were north of the Arctic Circle (66°N), which accounts for the lack of taxa that were defined as confined to the arctic regions. Furthermore, The Arctic Traits Database focused on arctic taxa, making it less likely for a taxon that was not already in the database to have this trait modality.

Some traits are harder to observe in situ than others, while others require direct study. For example, trophic level was not assigned in this chapter due to lack of information for many of the taxa. This is because trophic level is often calculated based on gut contents, stable isotope analyses or a combination of both methods (e.g. Preti et al., 1999; Post, 2002; Weidner et al., 2017). Both methods require direct sampling and analysis, and results are normally assigned at a species level. This makes this trait challenging to assign to coarse taxonomic groups, unless the species are well-documented. Likewise, the challenges in observing reproductive method and larval development are highlighted by their relative sparseness in figure 3.1. Despite the need for direct observation, reproductive method was the second most described trait in the original version of The Arctic Traits Database (Degen and Faulwetter, 2019). This is likely the result of the fact that 48% of the observations in The Arctic Traits Database are described at species level; directly observed traits are easier to describe at a species level, since only one set of observations is required.

Skeleton was the most commonly described trait in The Arctic Traits Database; however, it was only assigned to less than 25% of Cnidaria and Porifera (Degen and Faulwetter, 2019). Both of these groups were uncommon in The Arctic Traits Database (Degen and Faulwetter, 2019). Cnidaria and Porifera represented the two most common phyla for which traits were assigned in this chapter.

Biological trait analysis requires resources that list relevant biological traits. Ideally, these lists should be prepared using a bottom-up approach, with species descriptions supporting statements about higher levels. In practice, however, top-down approaches are more commonly published. The issue with top-down approaches is that phylogenetics is an ever-evolving landscape. The ever-evolving nature of some taxonomic groups leads to changes in the species in the group. If these species introduce new traits to the group, any previous group-level trait description would be incorrect. Thus, it is better to, whenever possible, define traits for a taxonomic group based on its children. For this reason, wherever possible, species-based sources were used in this chapter. However, in many cases, this was not possible as the primary literature defined certain traits at higher levels to avoid repetition in the text.

The advent of digital resources has made information more readily accessible and searchable. However, it has relegated some general statements to the realms of unverifiable websites and freely editable pages of Wikipedia. These are valuable resources but, unlike published encyclopedias and textbooks, they are unsuited for scientific citation. Encyclopedias, textbooks, and reference books prove to be invaluable resources for compiling information on biological traits. Textbooks aimed at broader audiences represent a source of citable base facts, such as sizes and shapes of common organisms. More in-depth textbooks, such as Brusca et al.'s (2016) *Invertebrates* and Bouillon et al.'s (2006) *An Introduction to Hydrozoa*, provide detailed information that can be used in top-down approaches to assigning traits. Field guides such as Hayward and Ryland's (2017) *Handbook of the Marine Fauna of North-West Europe* and Atkinson and Sink's (2018) *Field Guide to the Offshore Marine Invertebrates of South Africa*, proved very useful for bottom-up approaches.

3.6 Conclusion

There are major gaps in both our knowledge of certain taxonomic groups and in the availability of authoritative sources of certain facts. Simple facts, such as the average size of some species, can be hard to come by. The literature reviewed in preparation for this chapter suggests that this is the result of a streamlined approach to species identification. For example, the nature of Porifera spicules at a microscopic level allows for species-level identification from samples. This results in species descriptions focusing on these factors. This makes complete logical sense; however, it does little to help with species identification during video surveys or in biological trait analyses. Future resources, like The Arctic Traits Database, on which this chapter is modelled, are required for biological trait-based approaches.

3.7 Traits

To avoid reproducing the work done by the authors of The Arctic Traits Database, PolyTraits, and BIOTIC, the descriptions below will focus only on the taxa that were not included in these databases. Descriptions of some of the traits presented in table 3.1 were unclear or not reported for the taxa observed in this study, hence, their absence in table 3.2. These traits are typically not relevant or hard to observe for megafauna from video observations. For example, bioturbation is more commonly associated with species sampled by grabs. Likewise, while fragility is a trait that is commonly assigned to sessile organisms the size range covered on video makes the definition of each group hard to apply.

The layouts of the trait descriptions are divided according to taxonomic hierarchy. Where applicable, traits that are consistent within phyla, families, genera or species are noted under these headings. Since the aim of this chapter is to document traits in a usable manner, these consistent traits will still be explicitly mentioned in the descriptions of lower levels. This repetition is necessary to produce a resource where each individual taxonomic ranking that has been assigned traits is clear, even when read in isolation.

In order to further clarify the trait assignment, each entry for which traits were assigned is summarised below the text in a table, and fuzzy code values of 0 to 3 are assigned to the traits. Traits that are unknown or not expressed are not reported in these tables to preserve readability. To distinguish between modalities within a trait, and between different traits, modalities that belong to different traits are separated by vertical lines. The tables make use of a consistent colour code to aid in quick interpretation, where high affinity is green, low affinity is yellow, and medium affinity the mid-point (pale green) of these two colours. Modalities that are not expressed are not shown.

Phylum: ARTHOPODA

All members of this phylum have a chitinous exoskeleton, which may be calcified to varying degrees (Brusca et al., 2016).

Class: Malacostraca

Order: Decapoda

Family: Lithodidae (Samouelle, 1819)

Species in the family Lithodidae are dorso-ventrally compressed (Hall and Thatje, 2009). They are large in size (Hayward and Ryland, 2017), with some species having carapaces exceeding 220mm (Powell and Nickerson, 1965), and with legs included the total size can reach up to 1.8m (Stevens and Lovrich, 2014). The main skeletal component in their exoskeleton is chitin (Donaldson and Byersdorfer, 2014); however, their carapaces are well calcified (Hayward and Ryland, 2017). As a result of this calcification this family is considered to have a calcium based skeleton during fuzzy coding. As members of the suborder Pleocyemata, reproduction is sexual with brooding of the eggs (Brusca et al., 2016). Species in this family produce pelagic larvae that are either lecithotrophic or planktotrophic, with the majority generally producing lecithotrophic larvae (Hall and Thatje, 2009, and the references therein). Species in this family are free-living crawlers (inferred from descriptions of species movements) (Collins et al., 2002; Starbatty, 2016), and they have medium (Collins et al., 2002; Jensen, 2014) mobility. Species in this family are predominately opportunistic scavengers, the diet of some species is supplemented by predation (Collins et al., 2002; Jørgensen and Primicerio, 2007; Falk-Petersen et al., 2011). Species in this family are associated with both soft and hard substrata (from species descriptions). This is an epibenthic family with a cosmopolitan distribution (OBIS, 2021). They are found at depths ranging from 0 to 400m (OBIS, 2021), with two noticeable peaks in observations between 200 and 700m and between 1000 and 2000m.

S4	S5	S6	BF3	SK1	R4	LD2	LH1	MV3	MO3	FH4	FH5	SA1	SA2	EP2	DR1	DR2	DR3	DR4	Z4
2	2	1	3	3	3	3	3	3	3	2	1	2	2	3	1	2	2	2	3

Family: Munididae

Munida (Leach, 1820)

Species of the genus *Munida* are dorso-ventrally compressed and range in size between 1 and 90mm (Baba et al., 2011). As members of the phylum Arthropoda, their exoskeleton consists mainly of chitin, with varying degrees of calcification. As members of the squat lobster superfamily Galatheoidea, reproduction is sexual with brooding of the eggs (Thiel and Lovrich, 2011; Brusca et al., 2016). The only observed larval development is planktotrophic (Pérez-Barros et al., 2007). Species in the genus *Munida* are typically burrowing (i.e. *M. rugosa*, *M. tenuimana*) (Hartnoll et al., 1992; Trenkel et al., 2007; Lovrich and Thiel, 2011); however, there are free living pelagic species (i.e. *M. gregaria*) (Diez et al., 2016). These differences in living habit result in a wide range of movements across the genus, with species burrowing, crawling, and swimming (Hessler, 1981; Hartnoll et al., 1992; Diez et al., 2016). Species in this genus have diverse feeding methods; they are scavengers, surface deposit feeders, and predators (Hudson and Wigham, 2003; Lovrich and Thiel, 2011). *Munida* is predominantly an epibenthic genus with at least one hypo-benthic species (Diez et al., 2016). This genus has a cosmopolitan distribution (Hartnoll et al., 1992; OBIS, 2021). Species are found at depths between 0 and 4000m (OBIS, 2021), with observational peaks at between 70 and 100m, 200 and 600m and a small peak between 1000 and 2000m.

S2	S3	BF3	SK1	SK3	SO2	R4	LD2	LH1	LH2	LH4	MV3	MV4	MO2	MO3	MO4	FH1	FH4	FH5
2	2	3	2	2	3	3	3	2	1	2	2	2	1	2	2	2	2	2

SA1	SA2	SA3	SA4	EP2	EP3	DR1	DR2	DR3	DR4	Z4
2	2	3	2	2	2	1	2	2	2	3

Family: Inachidae

Macropodia (Leach, 1814)

As members of the “true crab” infraorder Brachyura, species in the genus *Macropodia* are dorso-ventrally compressed (Brusca et al., 2016). They grow up to 33mm in length (from species descriptions). As members of the phylum Arthropoda, their exoskeleton consists mainly of chitin, with varying degrees of calcification. As members of the suborder Pleocyemata, reproduction is sexual with brooding of the eggs (Brusca et al., 2016). They have pelagic planktotrophic larvae (Lebour, 1927; Spiridonov et al., 2020). Species in the genus *Macropodia* are free living crawlers (Schäfer in Spiridonov et al., 2020) and are highly motile (Brusca et al., 2016). Different species in this genus show different affinities to substrata, with preferences for hard, soft and biological observed. *Macropodia* is an epibenthic genus with a cosmopolitan distribution. Some species, however, are restricted to relatively small areas (Queirós et al., 2013; OBIS, 2021). They are found at depths between 0 and 1500m (OBIS, 2021), with both OBIS observations and species descriptions indicating that the majority of species are found at depths less than 150m.

S2	BF3	SK1	SK3	R4	LD1	A1	LH1	MV3	MO4	SA1	SA2	SA3	EP2	DR1	DR2	DR3	DR4	Z4
3	3	2	2	3	3	3	3	3	3	2	2	2	3	2	2	1	1	3

Phylum: BRACHIOPODA

Class: Craniata

Order: Craniida

Family: Craniidae

Novocrania anomala (Müller, 1776)

Novocrania anomala are laterally-compressed bivalved brachiopods that range in size between 0.23 and 15mm (Jackson, 2000). They have a shell made of calcium carbonate (Jackson, 2000). Reproduction is sexual with external fertilisation (Jackson, 2000). They have short-lived lecithotrophic larvae (Jackson, 2000). These organisms have a life span of between 8 and 10 years (Jackson, 2000). *Novocrania anomala* are attached and sessile (Jackson, 2000). This species is an active suspension feeder (Jackson, 2000). They are found on hard substrata (Jackson, 2000). *Novocrania anomala* is an epibenthic species with a cosmopolitan distribution (Jackson, 2000; OBIS, 2021). They are found at depths between 15 and 1500m (Jackson, 2000).

S2	BF4	R2	LD2	A3	LH6	MV1	MO1	FH3a	SA2	EP2	DR1	DR2	DR3	DR4	Z4
3	3	3	3	3	3	3	3	3	3	3	2	2	2	2	3

Phylum: BRYOZOA

All Bryozoa are colonial (Fish and Fish, 2011; Brusca et al., 2016; Hayward and Ryland, 2017). The majority of species in this phylum are attached and sessile (Fish and Fish, 2011; Fuchs, 2011; Brusca et al., 2016; Hayward and Ryland, 2017). Bryozoa are active suspension feeders (Fuchs, 2011; Brusca et al., 2016).

Class: Gymnolaemata

Order: Cheilostomatida

The cuticle is calcareous in all species of this order; however, the degree of calcification varies between species (Brusca et al., 2016; Hayward and Ryland, 2017). Sexual reproduction typically involves brooding of the embryos (Brusca et al., 2016).

Family: Phidoloporidae

Reteporella beaniana (King, 1846)

Reteporella beaniana are upright branching Bryozoa (Kuklinski, 2009) that are between 40 and 50mm in size (Hayward and Ryland, 1996). As members of the order Cheilostomatida their cuticle is calcareous. Like all Bryozoa, *R. beaniana* are colonial. Like the majority of Bryozoa, *R. beaniana* are attached and sessile (Hayward and Ryland, 1996). As a member of the phylum Bryozoa, *R. beaniana* are suspension feeders. *Reteporella beaniana* are found on hard substrata. This is an epibenthic species with a cosmopolitan distribution (OBIS, 2021). They are found at depths between 0 and 500m (OBIS, 2021), with the majority of observations between 40 and 400m.

S2	BF7	SK1	SO3	LH6	MV1	MO1	FH3a	SA2	B5	EP2	DR1	DR2	DR3	Z4
3	3	3	3	3	3	3	3	3	3	3	1	2	2	3

Phylum: CNIDARIA

Class: Anthozoa

Subclass: Octocorallia

A subclass of Anthozoa. Members of this subclass are colonial (Fish and Fish, 2011). All species are attached and sessile (Moen and Svensen, 2004). Species are passive filter feeders (Ribes et al., 2003; Macdonald et al., 2010). Species of Octocorallia are found on hard substrata (Jones and Gates, 2010). All members are epibenthic (Macdonald et al., 2010).

Order: Alcyonacea

The main skeletal component of members of the order Alcyonacea (previously Gorgonacea) are calcite and gorgonin (Goldberg, 1976; Brusca et al., 2016).

Family: Alcyoniidae

Anthomastus (Verrill, 1878)

Species in the genus *Anthomastus* are mushroom-shaped octocorals that are around 10mm in height (Molodtsova, 2013). As members of the order Alcyonacea, they have a calcareous skeleton. As members of the subclass Octocorallia, species in the genus *Anthomastus* are colonial. At least one species, *A. ritteri* are brooders (Cordes et al., 2001). Likewise, species in this genus are attached and sessile. Additionally, they are passive filter feeders. Octocorallia are associated with hard substrata. *Anthomastus* is an epibenthic genus with a cosmopolitan distribution (OBIS, 2021). Species in this genus are found at depths between 140 and 3000m (OBIS, 2021).

S3	BF1	SK1	SO3	LH6	MV1	MO1	FH3p	SA2	B5	EP2	DR2	DR3	DR4	Z4
3	3	3	3	3	3	3	3	3	3	3	1	2	2	3

Anthothela grandiflora (Sars, 1857)

Anthothela grandiflora are upright branching octocorals that are around 11.2cm tall (Aran-tes and de Medeiros, 2006). As members of the order Alcyonacea, they have a calcareous skeleton. As members of the subclass Octocorallia, they are colonial. As members of the class Anthozoa, they have both asexual and sexual reproduction (Fairbairn, 2013); fertilisation type is not well defined in the literature. As members of the subclass Octocorallia, *A. grandiflora* is attached and sessile. Additionally, they are passive filter feeders. This genus is associated with hard substrata (Jones and Gates, 2010; Kutti and Husa, 2020). This is an epibenthic species with a cosmopolitan distribution (OBIS, 2021). It is found at depths between 300 and 3000m, with a few records at shallower depths (OBIS, 2021).

S4	BF5	BF7	SK1	SO3	LH6	MV1	MO1	FH3p	SA2	B5	EP2	DR3	DR4	Z4
3	1	2	3	3	3	3	3	3	3	3	3	2	2	3

Family: Clavulariidae

Clavularia borealis (Koren and Danielssen, 1883)

Clavularia borealis are upright branching octocorals (Koren and Danielssen, 1883). While published sizes were not found, photographs suggest they are between 1 and 5cm. They have a soft calcareous skeleton (Koren and Danielssen, 1883). As members of the subclass Octocorallia, they are colonial. As members of the class Anthozoa, they have both asexual and sexual reproduction (Fairbairn, 2013); fertilisation type is not well defined in the literature.

As members of the subclass Octocorallia, *C. borealis* is attached and sessile. Additionally, they are passive filter feeders. They are found on hard substrata (Kutti and Husa, 2020). This is an epibenthic species with a boreal distribution (Kutti and Husa, 2020). It is found at depths between 100 and 500m (Kutti and Husa, 2020).

S2	BF5	BF7	SK1	SO3	R1	R2	LH6	MV1	MO1	FH3p	SA2	B5	EP2	DR2	DR3	Z3
3	1	2	3	3	2	2	3	3	3	3	3	3	3	2	2	3

Family: Nephtheidae

Species in this family are upright (Jørgensen et al., 2015). Members of this family have pelagic lecithotrophic larvae (Sun et al., 2011).

Duva (Koren and Danielssen, 1883)

As members of the family Nephtheidae, species in the genus *Duva* are upright. As members of the subclass Octocorallia, they are colonial. As members of the class Anthozoa, they have both asexual and sexual reproduction (Fairbairn, 2013). One species, *D. florida*, is a brooder, while the fertilisation methods of the other two known species are unknown (Sun et al., 2011). As members of the family Nephtheidae, they have lecithotrophic larvae. As members of the subclass Octocorallia, species in the genus *Duva* are attached and sessile. Additionally, they are passive filter feeders. Species in this genus are associated with hard substrata. *Duva* is an epibenthic genus with a cosmopolitan distribution (OBIS, 2021). *Duva* species are found at depths between 200 and 2000m, with the majority of observations between 200 and 600m and a few shallower observations at depths between 60 and 200m (OBIS, 2021).

BF5	SO3	LD2	LH6	MV1	MO1	FH3p	EP2	DR2	DR3	DR4	Z4
3	3	3	3	3	3	3	3	1	2	2	3

Family: Paragorgiidae

Paragorgia (Milne Edwards and Haime, 1857)

Species in the genus *Paragorgia* are upright branching octocorals that grow to sizes in excess of 10m (Smith, 2001). As members of the subclass Octocorallia, they are colonial. As members of the class Anthozoa, they have both asexual and sexual reproduction (Fairbairn, 2013). As members of the subclass Octocorallia, species in the genus *Paragorgia* are attached and sessile. Additionally, they are passive filter feeders. Octocorallia are associated with hard substrata (Li et al., 2017). *Paragorgia* is an epibenthic genus with a cosmopolitan distribution (OBIS, 2021).

S6	BF7	SO3	LH6	MV1	MO1	FH3p	SA2	EP2	Z4
3	3	3	3	3	3	3	3	3	3

Paragorgia arborea (Linnaeus, 1758)

Paragorgia arborea are upright branching octocorals that range in size between 5 and 180cm, averaging around 53cm (Mortensen and Buhl-Mortensen, 2005b). They have a calcareous skeleton (Mortensen and Buhl-Mortensen, 2005b). As members of the subclass Octocorallia, they are colonial. As members of the class Anthozoa, they have both asexual and sexual reproduction (Fairbairn, 2013). Lacharité and Metaxas (2013), hypothesises that *P. arborea* is a brooder. These organisms are long lived with a life span of around 400 years (Mortensen and

Buhl-Mortensen, 2005b). As members of the subclass Octocorallia, *P. arborea* is attached and sessile. Additionally, they are passive filter feeders (Mortensen and Buhl-Mortensen, 2005b). They are found on hard substrata (Mortensen and Buhl-Mortensen, 2005b). *Paragorgia arborea* is an epibenthic species with a cosmopolitan distribution (OBIS, 2021). They are found at depths between 40 and 3000m, with the majority of observations between 200 and 2000m (OBIS, 2021).

S6	BF7	SK1	SO3	R1	R4	A4	LH6	MV1	MO1	FH3p	SA2	B5	EP2	DR2	DR3	DR4	Z4
3	3	3	3	2	2	3	3	3	3	3	3	3	3	1	2	2	3

Family: Plexauridae

Muriceides (Wright and Studer, 1889)

As members of the suborder Holaxonia, *Muriceides* are upright branching octocorals (Brusca et al., 2016). Species in the genus *Muriceides* have calcareous skeletons (Wing and Barnard, 2004). As members of the subclass Octocorallia, they are colonial. As members of the class Anthozoa, they have both asexual and sexual reproduction (Fairbairn, 2013). As members of the subclass Octocorallia, species in the genus *Muriceides* are attached and sessile. Additionally, they are passive filter feeders. They are found on hard substrata. *Muriceides* is an epibenthic genus with a cosmopolitan distribution (OBIS, 2021). They are found at depths between 0 and 6000m, with the majority of observations between 200 and 600m (OBIS, 2021).

BF5	BF7	SK1	SO3	LH6	MV1	MO1	FH3p	SA2	B5	EP2	DR1	DR2	DR3	DR4	Z4
1	2	3	3	3	3	3	3	3	3	3	1	2	2	1	3

Muriceides kuekenthali (Broch, 1912)

Muriceides kuekenthali is an upright branching octocoral (Brusca et al., 2016). This species has a calcareous skeleton (Wing and Barnard, 2004). As members of the subclass Octocorallia, they are colonial. As members of the class Anthozoa, they have both asexual and sexual reproduction (Fairbairn, 2013). As members of the subclass Octocorallia, *M. kuekenthali* is attached and sessile. Additionally, they are passive filter feeders. They are found on hard substrata. *Muriceides kuekenthali* is epibenthic. Based on a small sample size, they are found at depths between 40 and 800m (OBIS, 2021).

BF5	BF7	SK1	SO3	LH6	MV1	MO1	FH3p	B5	EP2	DR2	DR3	Z4
1	2	3	3	3	3	3	3	3	3	1	2	3

Paramuricea (Kölliker, 1864)

Species in the genus *Paramuricea* are fan like octocorals that grow to sizes greater than 30cm (from species observations in Wareham and Edinger, 2007; and Linares et al., 2008). As members of the subclass Octocorallia, they are colonial. As members of the class Anthozoa, they have both asexual and sexual reproduction (Fairbairn, 2013). As members of the subclass Octocorallia, species in the genus *Paramuricea* are attached and sessile. Additionally, they are passive filter feeders. They are found on hard substrata. *Paramuricea* is an epibenthic genus with a cosmopolitan distribution (OBIS, 2021). They are found at depths between 0 and 3000m, with increased frequency of observations with depth, up to 2000m (there are a large number of observations at 200-300m) (OBIS, 2021).

Paramuricea placomus (Linnaeus, 1758)

Paramuricea placomus are upright, fan like octocorals that grow to sizes greater than 30cm (Wareham and Edinger, 2007). This species has a calcareous skeleton (Wing and Barnard, 2004). As members of the subclass Octocorallia, they are colonial. As members of the class Anthozoa, they have both asexual and sexual reproduction (Fairbairn, 2013). As members of the subclass Octocorallia, *P. placomus* is attached and sessile. Additionally, they are passive filter feeders. They are found on hard substrata. *Paramuricea placomus* is epibenthic with a cosmopolitan distribution (OBIS, 2021). They are found at depths between 150 and 2000m, with the vast majority of observations between 200 and 300m (OBIS, 2021).

S5	BF5	SK1	SO3	LH6	MV1	MO1	FH3p	SA2	EP2	DR2	DR3	DR4	Z4
3	3	3	3	3	3	3	3	3	3	1	2	1	3

Family: Primnoidae

Primnoa (Lamouroux, 1812)

Primnoa species are upright branching corals that range in size from 15cm to larger than 1m (Risk et al., 2002; Cairns and Bayer, 2005; Taylor and Rogers, 2017). As members of the order Alyconacea, their skeletons are calcareous. As members of the subclass Octocorallia, they are colonial. As members of the class Anthozoa, they have both asexual and sexual reproduction (Fairbairn, 2013). Species level studies for *Primnoa notialis*, *Primnoa pacifica* and *Primnoa resedaeformis* indicated that sexual reproduction in this genus involves external fertilisation (Mercier and Hamel, 2011; Waller et al., 2014; Feehan and Waller, 2015). Species in this genus are long lived with life spans estimated to be in excess of 100 years (Risk et al., 2002; Sherwood et al., 2005). As members of the subclass Octocorallia, this genus is attached and sessile. Additionally, they are passive filter feeders. *Primnoa* is an epibenthic genus with a cosmopolitan distribution (Taylor and Rogers, 2017; OBIS, 2021). They are found at depths between 0 and 3186m (Risk et al., 2002; Sherwood et al., 2005; Taylor and Rogers, 2017; OBIS, 2021).

S4	S5	S6	BF7	SK1	SO3	R1	R2	A4	LH6	MV1	MO1	FH3p	SA2	EP2	DR2	DR3	DR4	Z4
1	2	2	3	3	3	2	2	3	3	3	3	3	3	3	2	2	1	3

Primnoa resedaeformis (Gunnerus, 1763)

Primnoa resedaeformis are upright branching corals that grow to around 1m (Broch, 1912; Madsen, 1944; Risk et al., 2002; Mortensen and Buhl-Mortensen, 2005b). They have a calcareous and gorgonin skeleton (Risk et al., 2002). As members of the subclass Octocorallia, they are colonial. As members of the class Anthozoa, they have both asexual and sexual reproduction (Fairbairn, 2013). Sexual reproduction involves external fertilisation in *P. resedaeformis* (Mercier and Hamel, 2011). Despite observing no larvae, Mercier and Hamel (2011) presumed the larvae to be lecithotrophic. This is a long lived species with a predicted lifespan in excess of 300 years (Risk et al., 2002). Mortensen and Buhl-Mortensen (2005b) observed 65 year old colonies. Like other octocorallia, *P. resedaeformis* are attached and sessile. This species is a passive filter feeder (Mortensen and Buhl-Mortensen, 2005b); they have a trophic level of 3.6 (Sherwood et al., 2005). *Primnoa resedaeformis* are found on hard substrata (Mortensen and Buhl-Mortensen, 2005b). This is an epibenthic species with

an arctic-boreal distribution (in both the Atlantic and Pacific Oceans) (OBIS, 2021). They are found at depths between 200 and 600m (Risk et al., 2002; OBIS, 2021).

S6	BF7	SK1	SO3	R1	R2	LD3	A4	LH6	MV1	MO1	FH3p	TL3	TL4	SA2	EP2	DR3	Z2
3	3	3	3	2	2	3	3	3	3	3	3	2	2	3	3	3	3

Order: Pennatulacea

Species for which larval development is known or hypothesised by oocyte size have short-lived lecithotrophic larvae (Servetto et al., 2013). Members of this order are found on soft bottoms (Williams, 1998; Brusca et al., 2016).

Family: Balticinidae

Balticina (Gray, 1870)

Synonymous with *Halipterus*, which is used by the Arctic Traits Database and some of the primary sources.

Species in the genus *Balticina* are upright slender feather-like sea pens that grow up to lengths greater than 1m (Brodeur, 2001; López-González et al., 2001; Neves et al., 2015). In species that have a skeleton, the main component is calcium (Moen and Svensen, 2004; Hayward and Ryland, 2017). As members of the subclass Octocorallia, they are colonial. As members of the class Anthozoa, they have both asexual and sexual reproduction (Fairbairn, 2013). During sexual reproduction fertilisation is external (Moen and Svensen, 2004). This genus likely has short-lived lecithotrophic larvae, supported by species level oocyte size (Baillon et al., 2014) and all known larval development in Pennatulacea species (Servetto et al., 2013). This is a long lived genus, with a life span of more than 20 years (Wilson et al., 2002; Neves et al., 2015). As members of the subclass Octocorallia, this genus is attached and sessile. Species in this genus are passive filter feeders (Lundsten et al., 2010). As a member of the order Pennatulacea, species in this genus are found on soft bottoms. *Balticina* is an epibenthic genus with a cosmopolitan distribution (under both names, OBIS, 2021). Species in this genus are found at depths between 0 and 4000m (under both names, OBIS, 2021), with peaks in most observations between 70 and 2000m.

S6	BF1	BF5	BF6	SK1	SK5	SO3	R1	R2	LD2	A4	LH6	MV1	MO1	FH3p	SA1	EP2	DR1	DR2	DR3	DR4	Z4
3	1	2	1	2	1	3	2	2	3	3	3	3	3	3	3	3	1	2	2	2	3

Family: Kophobelelemnidae

Kophobelemnion stelliferum (Müller, 1776)

Kophobelemnion stelliferum are upright feather-like sea pens that grow up to 70cm (Rice et al., 1992). They have a skeleton containing calcium (Greeley, 2022). As members of the subclass Octocorallia, they are colonial. As members of the class Anthozoa, they have both asexual and sexual reproduction (Fairbairn, 2013). Rice et al. (1992) suggest that *K. stelliferum* has external fertilization. Likewise, Rice et al. (1992) infer that their larvae are short-lived and lecithotrophic. *Kophobelemnion stelliferum* are attached and sessile (Rice et al., 1992). This species is a passive filter feeder (Rice et al., 1992). They are commonly found on soft bottoms (Rice et al., 1992; Mastrototaro et al., 2013). *Kophobelemnion stelliferum* is an epibenthic species with a cosmopolitan distribution (Mastrototaro et al., 2013; OBIS, 2021). They are found at depths between 0 and 6000m (López-González et al., 2001; OBIS, 2021).

S5	S6	BF5	BF7	SK1	SO3	R1	R2	LH6	MV1	MO1	FH3p	SA1	EP2	DR2	DR3	DR4	Z4
2	2	2	1	3	3	2	2	3	3	3	3	3	3	2	2	2	3

Subclass: **Hexacorallia**

A subclass of Anthozoa. This subclass contains both the sea anemones and the so-called true corals. Unlike the Octocorallia, there are both solitary and colonial species in this subclass (Brusca et al., 2016).

Order: **Scleractinia**

The main skeletal component of species in the order Scleractinia is calcium (Brusca et al., 2016; Hayward and Ryland, 2017). Species in this order are attached and sessile (Hayward and Ryland, 2017).

Family: **Caryophylliidae**

Lophelia pertusa (Linnaeus, 1758)

Accepted as *Demophyllum pertusa* in the same family.

Lophelia pertusa are large upright branching corals that can grow to heights on the order of meters (Freiwald et al., 2004). They have calcareous skeletons (Oppelt et al., 2017). *Lophelia pertusa* are colonial (Freiwald et al., 2004). As members of the class Anthozoa, they have both asexual and sexual reproduction (Fairbairn, 2013). During sexual reproduction fertilisation is external (Brooke and Järnegren, 2013; Pires et al., 2014). They have planktotrophic larvae (Strömberg and Larsson, 2017). These organisms are extremely long lived with lifespans in excess of 1000 years (Mortensen and Fosså, 2001). Like other Scleractinia, species in this genus are attached and sessile. *Lophelia pertusa* is a passive filter feeder (Duineveld et al., 2007; van Oevelen et al., 2018b). They require hard substratum for attachment (Roberts et al., 2006). *Lophelia pertusa* is an epibenthic species with a cosmopolitan distribution (Zibrowius, 1980; Freiwald et al., 2017; OBIS, 2021). They are found at depths between 39m (Svensen et al., 1998) and more than 3000m (Squires, 1959).

S6	BF7	SK1	SO3	R1	R2	A4	LH6	MV1	MO1	FH3p	SA2	EP2	DR2	DR3	DR4	Z4
3	3	3	3	2	2	3	3	3	3	3	3	3	2	2	2	3

Family: **Oculinidae**

Madrepora (Linnaeus, 1758)

Species in the genus *Madrepora* are upright branching corals that grow to sizes larger than 20cm (Cairns and Zibrowius, 1997; Tsounis et al., 2010). They have calcareous skeletons (Oppelt et al., 2017). As members of the class Anthozoa, they have both asexual and sexual reproduction (Fairbairn, 2013). Fertilisation mode has only been observed for *M. oculata*, which has external fertilisation (Pires et al., 2014). Like other Scleractinia, species in this genus are attached and sessile. *M. oculata* is confirmed to be a filter feeder (Duineveld et al., 2007); there is no evidence suggesting the remaining five species are not. As members of the phylum Cnidaria, all species are likely passive filter feeders. *Madrepora* species are commonly associated with hard substrata. This is an epibenthic genus with a cosmopolitan distribution (Freiwald et al., 2004; Roberts et al., 2009; OBIS, 2021). They are found at depths between 200 and 3000m (OBIS, 2021).

BF7	SK1	SO3	R1	R2	LH6	MV1	MO1	FH3p	SA2	EP2	DR1	DR2	DR3	DR4	Z4
3	3	3	2	2	3	3	3	3	3	3	1	2	2	2	3

Madrepora oculata (Linnaeus, 1758)

Madrepora oculata are upright branching corals that grow to sizes of 30 to 50cm (Tsounis et al., 2010). They have a calcareous skeleton (Oppelt et al., 2017). *Madrepora oculata* are colonial (Tursi et al., 2004). As members of the class Anthozoa, they have both asexual and sexual reproduction (Fairbairn, 2013). During sexual reproduction fertilisation is external (Pires et al., 2014). The large oocyte size suggests that this species has lecithotrophic larvae (Pires et al., 2014). These organisms are relatively long lived with observations of a colony estimated to be 200 ± 68 years old (Orejas et al., 2021), while isotopic confirmed ages indicate colonies of around 50 years (Montero-Serrano et al., 2013). Like other Scleractinia, *M. oculata* are attached and sessile. This species is a filter feeder (Duineveld et al., 2007), likely feeding passively. *Madrepora oculata* is typically found on hard substrata (Orejas et al., 2009). This is an epibenthic species with cosmopolitan distribution (Hayward and Ryland, 2017; OBIS, 2021; Orejas et al., 2021). They are found at depths between 200 and 3000m (Tsounis et al., 2010; OBIS, 2021; Orejas et al., 2021).

S5	BF7	SK1	SO3	R1	R2	LD2	A4	LH6	MV1	MO1	FH3p	SA2	EP2	DR2	DR3	DR4	Z4
3	3	3	3	2	2	3	3	3	3	3	3	3	3	2	2	2	3

Class: Hydrozoa

Members of the class Hydrozoa can be challenging for assigning traits, as most of them have both a pelagic medusoid and sessile polyp stage to their life-cycles (Fish and Fish, 2011; Brusca et al., 2016; Hayward and Ryland, 2017). The polyp stage of the hydrozoan life-cycle is typically benthic, attached, and sessile, with asexual reproduction. The medusa stage is typically the opposite; thus free-living, pelagic, and sexually reproducing (Brusca et al., 2016; Hayward and Ryland, 2017). During their polyp life-stage, Hydrozoa may have a chitinous or calcareous exoskeleton (Brusca et al., 2016; Hayward and Ryland, 2017). Hydrozoa are generally considered to be passive filter feeders; however, some such as *Aglaophenia octodonta* exhibit tentacles movements more commonly associated with active filter feeders (Puce et al., 2002).

Order: Anthoathecata

Family: Stylasteridae (Gray, 1847)

Species in this family lack a free medusa stage (Brusca et al., 2016).

Species in the family Stylasteridae are typically upright or, more rarely, encrusting corals (Bouillon et al., 2006). Species are diverse in size, ranging from 7mm to in excess of 1m (Cairns and Zibrowius, 1997; Cairns, 2011). They have a calcareous skeleton (Cairns, 1992; Bouillon et al., 2006). Species in this family are colonial (Bouillon et al., 2006). As members of the phylum Hydrozoa, reproduction is both asexual and sexual. Fertilisation is internal during sexual reproduction, and the larvae are brooded (Cairns, 2011). They have benthic larvae (Cairns, 2011). As they lack a free medusa stage, species in the family Stylasteridae are attached and sessile. As members of the class Hydrozoa, species in this family are passive filter feeders. Stylasteridae is an epibenthic family with a cosmopolitan distribution (Cairns, 2011; OBIS, 2021). They are found at depths between 0 and 2789m (Cairns, 2011; OBIS, 2021). OBIS (2021) indicates that

most observations are between 200 and 2000m, with 80% of observations at depths greater than 50m (Cairns, 2007).

S1	S2	S3	S4	S5	BF3	BF5	SK1	SO3	R1	R4	LD3	LH6	MV1	MO1	FH3	EP2	DR1	DR2	DR3	DR4	Z4
2	2	2	2	2	1	2	3	3	2	2	3	3	3	3	3	3	1	2	2	2	3

Family: Tubulariidae

Tubularia (Linnaeus, 1758)

Species in this genus lack a free medusa stage (Fish and Fish, 2011; Brusca et al., 2016).

During their polyp life-stage:

Species of the genus *Tubularia* are upright. Species range in size from 50 to 300mm (averaged from species observations). The species of this genus are solitary (Bouillon et al., 2006). As members of the phylum Hydrozoa, reproduction is both asexual and sexual. Fertilisation is internal during sexual reproduction (Miller, 1976). *Tubularia* produce an actinula larvae, which is benthic (Fish and Fish, 2011). As they lack a free medusa stage, species of *Tubularia* are attached and sessile. As members of the class Hydrozoa, species in this genus are passive filter feeders. *Tubularia* is an epibenthic genus with a cosmopolitan distribution (OBIS, 2021). They are found at depths between 0 and 800m (OBIS, 2021), with most observations at depths less than 50m.

S2	S3	S4	BF5	SO1	R1	R3	LD3	LH3	LH6	MV1	MO1	B5	EP2	DR1	DR2	DR3	Z4
2	2	2	3	3	2	2	3	3	3	3	3	3	3	2	2	1	3

Order: Leptothecata

Many species in this class lack free living medusae (Brusca et al., 2016, as Thecata (synonym)). All species in this order are colonial during their polyp life-stage (Brusca et al., 2016).

Family: Kirchenpaueriidae

During the polyp life-stage, species in the family Kirchenpaueriidae have chitinous skeletons (Bouillon et al., 2006).

Kirchenpaueria (Jickeli, 1883)

Species in this genus lack a free medusa stage (Fish and Fish, 2011). During their polyp life-stage:

Species in the genus *Kirchenpaueria* are upright hydroids (Hayward and Ryland, 2017; Genzano and Meretta, 2021). Species reach sizes between 30 and 100mm (Ramil et al., 1998; Schuchert, 2000; Hayward and Ryland, 2017; Genzano and Meretta, 2021). As members of the family Kirchenpaueriidae, they have chitinous skeletons. Like other members of the order Leptothecata, polyps are colonial. As members of the phylum Hydrozoa, reproduction is sexual. Likewise, during this life stage they are attached and sessile. As members of the class Hydrozoa, species in this genus are passive filter feeders. During this life stage, *K. haleciods*, *K. pinnata*, *K. similis* and *K. bonneviease* were found on hard or biological substrata (Hayward and Ryland, 2017; Genzano and Meretta, 2021); there is no reason to assume that this is not a trait of the genus. This is an epibenthic life-stage and the genus has a cosmopolitan distribution (OBIS, 2021). Polyp colonies are found at depths between 0 and 4000m (OBIS, 2021).

S2	S3	BF5	SK3	SO3	LH6	MV1	MO1	FH3p	SA2	SA3	EP2	DR1	DR2	DR3	DR4	Z4
2	2	3	3	3	3	3	3	3	2	2	3	2	2	2	2	3

Phylum: ECHINODERMATA

This exclusively marine phylum (Fish and Fish, 2011; Hayward and Ryland, 2017) contains the commonly named starfish, sea urchins, sea cucumbers, sea lilies, brittle stars and feather stars. The members of the phylum are characterised by pentamerous radial symmetry.

The main skeletal component of members of this phylum is calcium, in the form of calcite (Fish and Fish, 2011; Brusca et al., 2016; Hayward and Ryland, 2017). The prominence of the calcite skeleton varies greatly between groups in this phylum, but even the relatively “squishy” sea cucumbers (class: Holothuroidea) have scattered ossicles (Brusca et al., 2016).

Class: Asteroidea

Order: Forcipulatida

Family: Stichasteridae

Stichastrella rosea (Müller, 1776)

Stichastrella rosea are dorso-ventrally compressed starfish that grow up to sizes between 15 and 30cm in diameter (Hayward and Ryland, 2017). As members of the phylum Echinodermata, their skeleton is calcareous. Reproduction is sexual with external fertilisation (Marshall et al., 2012). They produce a planktonic larva, feeding nature of which has not been described (Marshall et al., 2013). *Stichastrella rosea* are free living crawlers (Lambert, 2000), as a result they are considered to have medium mobility. This species is both a predator and scavenger (Dean et al., 2020). They are commonly found on hard substrata (Picton and Morrow, 2016). This is an epibenthic species, with a cosmopolitan distribution (OBIS, 2021). They are found at depths up to 700m (OBIS, 2021)

S4	BF3	SK1	R2	LD1	LD2	LH1	MV3	MO3	FH4	FH5	SA2	EP2	DR1	DR2	DR3	Z4
3	3	3	3	2	2	3	3	3	1	2	3	3	1	2	2	3

Order: Valvatida

All members of this order have tube feet with suckers (Brusca et al., 2016).

Family: Asterinidae

Tremaster (Verrill, 1880)

This genus is represented by a single extant species *Tremaster mirabilis* (Gale, 2018; WoRMS Editorial Board, 2021).

Tremaster mirabilis (Verrill, 1880)

Tremaster mirabilis is a dorso-ventrally compressed starfish (Hayward and Ryland, 2017). As members of the phylum Echinodermata, their skeleton is calcareous. Reproduction is sexual, with brooding of the young (Jangoux, 1982). This species is a predator (Gale et al., 2013). *Tremaster mirabilis* are found on hard substrata (Gale, 2018). This is an epibenthic species with a cosmopolitan distribution (OBIS, 2021). They are found at depths between

150 and 1060m (Ringvold, 1999; OBIS, 2021), with the majority of observations at depths between 200 and 700m (OBIS, 2021). Birk et al. (2018) report a depth range of 400 to 600m, which is consistent with the majority of OBIS observations.

BF3	SK1	F3	R4	LH1	MV3	FH5	SA2	EP2	DR3	DR4	Z4
3	3	3	3	3	3	3	3	3	2	2	3

Family: Goniasteridae

Members of the family Goniasteridae are dorso-ventrally compressed (Lambert, 2000).

Ceramaster (Verrill, 1899)

As members of the family Goniasteridae, species of the genus *Ceramaster* are dorso-ventrally compressed starfish. As members of the phylum Echinodermata, their skeleton is calcareous. Species in this genus are both predators and scavengers (Yeh and Drazen, 2009; Jewett et al., 2012; Gale et al., 2013). This is an epibenthic species with a cosmopolitan distribution (OBIS, 2021). They are found at depths between 0 and 6000m (OBIS, 2021), with the majority of observations between 200 and 300m.

BF3	SK1	LH1	MV3	FH4	FH5	EP2	DR1	DR2	DR3	DR4	Z4
3	3	3	3	2	2	3	1	1	2	2	3

Ceramaster granularis (Retzius, 1783)

As members of the family Goniasteridae, *Ceramaster granularis* are dorso-ventrally compressed starfish that grow up to around 20mm. As members of the phylum Echinodermata, their shell is calcareous. Reproduction is sexual, likely external or brooding (Lambert, 2000). Yolk size is indicative of direct or lecithotrophic larval development (Mortensen, 1927). This species is both a predator and scavenger; they have a trophic level of 4.4 (tertiary consumer) (Gale et al., 2013). This is an epibenthic species with a cosmopolitan distribution (OBIS, 2021). They are found at depths between 50 and 3000m (OBIS, 2021), with the majority of observations between 200 and 700m.

S2	S3	BF3	SK1	R2	R4	LD2	LD3	LH1	MV3	FH4	FH5	TL4	EP2	DR2	DR3	DR4
2	2	3	3	2	1	2	2	3	3	2	2	3	3	1	2	1

Family: Poraniidae

Porania (Gray, 1840)

Species in the genus *Porania* are dorso-ventrally compressed starfish (Hayward and Ryland, 2017), species descriptions suggests a size range of 10 to 30cm. As members of the phylum Echinodermata, their shell is calcareous. Reproduction is sexual with external fertilisation (Marshall et al., 2013). Species in this genus produce either short-lived lecithotrophic larvae (e.g. *P. hispidia*) or longer-lived planktotrophic larvae (e.g. *P. antarctica*) (Marshall et al., 2013). At least one species in the genus, *P. pulvillus*, obtains nutrients through predation, scavenging, and surface deposit feeding (Ericsson and Hansson, 1973). Based on species descriptions, this genus contains species that associate with hard, soft and biological substrata. *Porania* is a cosmopolitan genus (OBIS, 2021). Species in this genus are found at depths between 0 and 2000m (OBIS, 2021); there are peaks in observations between 60 and 170m and 200 and 700m (OBIS, 2021).

S4	BF3	SK1	R2	LD1	LD2	LH1	MV3	FH1	FH4	FH5	SA1	SA2	SA3	EP2	DR1	DR2	DR3	DR4	Z4
3	3	3	3	2	2	3	3	1	1	2	2	2	2	3	1	2	2	1	3

Class: Crinoidea

Order: Comatulida

Traits are present in the Arctic Traits Database, included here since Bourgueticrinia is not present in the database.

Members of the order Comatulida are upright (Hayward and Ryland, 2017). The main skeletal component of members of this order is calcium (Hayward and Ryland, 2017). Species in this order produce short-lived lecithotrophic larvae (Lambert and Austin, 2007). Members are either attached or free living (UMORF, [n.d.]). Species in this order are passive filter feeders (Lambert and Austin, 2007)

Bourgueticrinina

All traits mentioned here are defined at the order level.

BF5	SK1	LD2	LH1	LH6	FH3p
3	3	3	2	2	3

Class: Echinoidea

This class contains the sea urchins, which are globulose or dorso-ventrally compressed in shape (Fish and Fish, 2011; Brusca et al., 2016; Hayward and Ryland, 2017). The main component of their exoskeleton is calcium (Alexander, 1990; Fish and Fish, 2011; Hayward and Ryland, 2017). Species of this class are typically free living crawlers (Brusca et al., 2016).

Order: Camarodonta

Family: Echinidae

Echinus (Linnaeus, 1758)

Species in the genus *Echinus* are globulose (Fish and Fish, 2011). Species range in size between 84 and 200mm (averaged from species: Fish and Fish, 2011; Minin, 2012; Filander, 2014). As members of the class Echinoidea, they have a calcareous exoskeleton. Species in this genus are either solitary or found in groups. Reproduction is sexual with external fertilisation (Tyler et al., 1995). The relatively large size of the otocysts indicate planktotrophic larvae (Tyler et al., 1995). The larvae of *E. esculentus* are known to be planktotrophic. Like most other Echinoidea, species in the genus *Echinus* are free living crawlers. *Echinus* are surface deposit feeders (Tyler et al., 1995), but some species graze on algae and seaweeds or scavenge. Species in this genus are associated with hard substrata. This is an epibenthic genus with a cosmopolitan distribution (OBIS, 2021). They are found at depths between 0 and 4000m (Minin, 2012; OBIS, 2021).

S3	S4	BF1	SK1	SO1	SO2	R2	LD1	LH1	MV3	FH1	FH4	FH7	SA2	EP2	DR1	DR2	DR3	DR4	Z4
2	2	3	3	1	2	3	3	3	3	1	1	2	3	3	2	2	1	1	3

Gracilechinus acutus (Lamarck, 1816)

Gracilechinus acutus are globulose sea urchins that grow up to 15cm (Bay-Nouailhat, 2008).

As members of the class Echinoidea, they have a calcareous exoskeleton. This species is either solitary or found in groups. They have pelagic planktotrophic larvae (White et al., 2017). These organisms are long lived (González-Irusta et al., 2014). *Gracilechinus acutus* are free living crawlers (Zühlke et al., 2001). As a result, they can be considered slow moving (by Arctic Traits Database definition). This species is a surface deposit feeder (inherited for old classification in Echinus), as well as being grazers. Unlike many other urchins, *G. acutus* is typically associated with unconsolidated to soft substrata (Bay-Nouailhat, 2008). *Gracilechinus acutus* is an epibenthic species with a cosmopolitan distribution (González-Irusta et al., 2014; OBIS, 2021). They are found at depths between 0 and 400m (González-Irusta et al., 2014; OBIS, 2021), with most observations between 71 and 200m.

S4	BF1	SK1	SO1	SO2	LD1	A3	A4	LH1	MV3	MO2	FH1	FH7	SA1	EP2	DR1	DR2	DR3	DR4	Z4
3	3	3	2	1	3	2	2	3	3	3	2	2	3	3	1	2	1	1	3

Family: Cidaridae

Cidaris cidaris (Linnaeus, 1758)

Cidaris cidaris are globulose sea urchins that grow to around 65mm (Mortensen, 1927). As members of the class Echinoidea, they have a calcareous exoskeleton. They are either found as solitary organisms or in pairs (Stevenson et al., 2015). They have pelagic planktotrophic larvae (Mortensen, 1927), this suggests that *C. cidaris* do not brood their young. Thus implying, sexual reproduction with external fertilisation, as internal fertilisation is not present in the Echinoidea. *Cidaris cidaris* are free living crawlers. As a result, they can be considered slow moving (by Arctic Traits Database definition). This species is both a surface deposit feeder and a grazer, as it feeds both on detrital plant material as well as on living algae, sponges and seaweeds (Gage and Tyler, 1991). While they are associated with cold-water coral reefs and fine sandy-mud bottoms in Malta (Terribile and Patrick, 2013), this species can be found on all substratum types (Mortensen, 1927). *Cidaris cidaris* is an epibenthic species with a cosmopolitan distribution (OBIS, 2021). They are found at depths between 0 and 3000m (OBIS, 2021), with the majority of observations at depths between 50 and 600m. The core depth range reported on OBIS agrees with Terribile and Patrick's (2013) observations from Malta: depths between 50 and more than 550m.

S3	BF1	SK1	SO1	R2	LD1	LH1	MV3	MO2	FH1	FH7	SA1	SA2	SA3	EP2	DR1	DR2	DR3	DR4	Z4
3	3	3	3	3	3	3	3	3	1	2	2	2	2	3	1	2	2	1	3

Class: Holothuroidea

This class contains the sea cucumbers. All species are vermiform and elongated (Fish and Fish, 2011; Brusca et al., 2016). The main skeletal component of members of this class is calcium; however, the skeleton is greatly reduced in most species (Fish and Fish, 2011; Brusca et al., 2016).

Order: Synallactida

Brusca et al. (2016) include this order under its older name, Aspidochirotida, which is listed as uncertain by WoRMS Editorial Board (2021) due to being polyphyletic. It should be noted that all the members of Synallactida were previously in Aspidochirotida, but due to the polyphyletic nature of Aspidochirotida the inverse is not true.

Family: Stichopodidae

Parastichopus tremulus (Gunnerus, 1767)

Parastichopus tremulus are vermiform elongated sea cucumbers, that can reach up to 500mm in length and 100mm in diameter (Barnes, 2008). Christophersen et al. (2020) report an observed range of between 77 and 302mm. As members of the order holothuroidea, they have a much reduced calcareous skeleton. This is a solitary species. Reproduction is sexual with external fertilisation (Schagerström and Sundell, 2021). They most likely have short-lived lecithotrophic larvae (Billett, 1989). *Parastichopus tremulus* are free living crawlers (Schagerström and Sundell, 2021). They are considered to be slow moving (Brusca et al., 2016). This species is a surface deposit feeder (Hudson et al., 2004; Gates and Jones, 2012; Schagerström and Sundell, 2021). They are found various substrata including silt-covered rocks and pebble bottoms (Schagerström and Sundell, 2021); however, they are most common on soft substrata (Hudson et al., 2004; Christophersen et al., 2021). This is an epibenthic species with a cosmopolitan distribution (restricted to the North Atlantic) (OBIS, 2021). They are found at depths between 18 and 4000m, but are most common between 150 and 300m (OBIS, 2021; Schagerström and Sundell, 2021).

S4	S5	BF2	SK1	SO1	R2	LD2	LH1	MV3	MO2	FH1	SA1	SA2	SA3	EP2	DR1	DR2	DR3	DR4	Z4
2	1	3	3	3	3	3	3	3	3	3	2	1	1	3	1	2	2	1	3

Phylum: FORAMINIFERA

This is a phylum of single cell organisms that can reach sizes on the order of centimetres (Murray, 2006; Jones, 2013). Brusca et al. (2016) place foraminifera in the phylum Granuloreticulosa. While this phylum is not accepted by WoRMS Editorial Board (2021), the Foraminifera referred to by Brusca et al. (2016) appear to be synonymous with the current placement of Foraminifera. Foraminifera range from benthic attached organisms to floating planktonic forms (Jones, 2013). Despite their single cell nature, Foraminifera utilise phagocytotic feeding methods (Brusca et al., 2016) ranging from suspension-feeding through to parasitic and mutualistic methods (Jones, 2013).

Class: Monothalamea

Order: Astrorhizida

Family: Astrorhizidae

Pelosina arborescens (Pearcey, 1914)

Pelosina arborescens are upright, giant, single cell organisms (Cedhagen, 1993; Jones, 2013) that range in size between 30 and 48mm (Pearcey, 1914). *Pelosina arborescens* are attached by root like projections, and are functionally sessile; Cedhagen (1993) notes that when up-rooted they return to their “natural” position within a fortnight. This species is a passive filter feeder (Cedhagen, 1993; Jones, 2013). They require soft sediment for root attachment. However, given their size, they are sometimes observed on hard substrata, provided their small crevices are filled with soft sediment (Cedhagen, 1993). *Pelosina arborescens* is an epibenthic species with a boreal distribution (Cedhagen, 1993; Jones, 2013). Most known samples come from depths greater than 25m (Cedhagen, 1993).

S2	BF5	LH6	MV1	MO1	FH3p	SA1	SA2	B5	EP2	DR2	DR3	DR4	Z2
3	3	3	3	3	3	2	1	3	3	2	2	2	3

Family: Rhabdamminidae

Rhabdammina (Sars in Carpenter, 1870)

Species in the genus *Rhabdammina* are upright (Murray, 2006) or encrusting (Hoffmann, 2009). They grow to around 20mm (Goody, 1986; Murray, 2006). Species in this genus are filter feeders (Kaminski and Wetzel, 2004), they are likely passive filter feeders. *Rhabdamminidae* is an epibenthic genus with a cosmopolitan distribution (Kaminski and Wetzel, 2004; Lee and Lee, 2020; OBIS, 2021). They are found at depths between 40 and 4000m (*R. neglecta* 3000-4000m; Goody, 1986; *R. abyssorum* 48-3220m; Lee and Lee, 2020).

S1	S2	BF3	BF5	MV1	MO1	FH3	EP2	DR1	DR3	DR4	Z4
2	2	1	2	3	3	3	3	2	2	2	3

Phylum: MOLLUSCA

The Mollusca include both terrestrial and aquatic members, with a wide range of body forms and life histories.

Class: Bivalvia

Members of the class Bivalvia are made up of two shell parts, joined together by a dorsal hinge (Fish and Fish, 2011). They therefore have a body form that is laterally compressed (Brusca et al., 2016). The main skeletal component of their shells is calcium (Gosling, 2015). Reproduction of species in this class is sexual (Fairbairn, 2013), with external fertilisation being the most common form (Fish and Fish, 2011).

Order: Limida

Family: Limidae

Acesta excavata (Fabricius, 1779)

Acesta excavata are laterally-compressed and can grow up to 20cm tall (López Correa et al., 2005). As members of the class Bivalvia they have a shell made of calcium. They are typically found in groups. *Acesta excavata* are free living, but typical remain temporarily attached to the substrate and thus sessile; when relocating they move by crawling (Järnegren, 1999, in; López Correa et al., 2005). This species is an active filter feeder (López Correa et al., 2005; Järnegren et al., 2007). They are found on hard substrata (López Correa et al., 2005). This is an epibenthic species with insufficient data to obtain a zoogeographical range (Järnegren et al., 2007). They are found at depths between 40 and 3200m (López Correa et al., 2005).

S3	S4	BF4	SK1	F1	SO2	LD2	LH1	LH6	MV1	MV3	MO2	FH3a	SA2	B5	EP2	DR2	DR3	DR4
2	1	3	3	3	3	3	2	2	2	1	3	3	3	3	3	2	2	1

Phylum: PORIFERA

Commonly known as the sponges, the phylum Porifera contains four classes of widely recognisable marine organisms. It should be noted that the classification of Porifera is relatively in-depth, with

three of the four classes containing subclasses and many orders including suborders. The classifications used here are overly simplified and the reader should bear that in mind when utilising these data.

Asexual reproduction is present in most sponges, in addition to sexual reproduction (Ereskovsky, 2018). Sponges exhibit both viviparity in the form of brooding, and oviparity. As a general rule oviparous sponges have external fertilisation (Ereskovsky, 2018). The following exceptions are listed by Ereskovsky (2018): *Cliona celata* and *Chondrosia reniformis*, which have internal fertilisation; thus, the generalisation should be used with caution. Sponges lack planktotrophic larvae (Ereskovsky, 2010), having short-lived lecithotrophic larvae (Ereskovsky, 2018).

Porifera have a range of different body forms; however, they are all colonial, sessile, attached and epibenthic (Fish and Fish, 2011; Brusca et al., 2016). It should be noted that, in addition to being attached, species in the family Clionidae are considered to burrow (Hayward and Ryland, 2017). Typically, they are active filter feeders; however, some deep-water sponges have evolved carnivory in areas where food is in short supply (Fish and Fish, 2011).

Class: Demospongiae

Subclass: Keratosa

With the exception of the calcified genus *Vacelelia*, sponges in this subclass have skeletons made of spongin fibres (Brusca et al., 2016).

Order: Dendroceratida

Members of this order are viviparous, reproducing sexually with internal fertilisation. In addition, some members reproduce asexually via budding (Ereskovsky, 2018).

Family: Darwineliidae

Aplysilla (Schulze, 1878)

Species of the genus *Aplysilla* are encrusting (Bergquist and de Cook, 2002). They have a skeleton made up of fibrous spongin (Bergquist and de Cook, 2002). Like all members of the phylum Porifera, species in the genus *Aplysilla* are colonial. As members of the order Dendroceratida, reproduction is both asexual and sexual, with internal fertilisation. Likewise, as members of the order Dendroceratida, they have short-lived pelagic lecithotrophic larvae. Like other Porifera, species in the genus *Aplysilla* are attached and sessile. Species in this genus are active filter feeders. This is an epibenthic genus with a cosmopolitan distribution (OBIS, 2021). They are found at depths between 0 and 450m, with the majority of observations at depths up to 40m (OBIS, 2021).

S4	BF3	SK5	SO3	LD2	LH6	MV1	MO1	FH3a	EP2	DR1	DR2	DR3	Z4
3	3	3	3	3	3	3	3	3	3	2	2	1	3

Aplysilla sulfurea (Schulze, 1878)

Aplysilla sulfurea are encrusting sponges that grow up to 40m wide and 5mm thick (Picton et al., 2011). They have no spicules; rather, the skeleton is made up of spongin (Picton et al., 2011). Like all members of the phylum Porifera, *A. sulfurea* are colonial. Reproduction is sexual with external fertilisation (Ereskovsky, 2018). They have short-lived pelagic lecithotrophic larvae (Ereskovsky, 2018). Like other Porifera, *A. sulfurea* are attached and sessile. This species is an active filter feeder (Fish and Fish, 2011). They are commonly found on

hard substrata such as rocks, and tend to avoid bright light (Picton et al., 2011). This is an epibenthic species with a cosmopolitan distribution (Picton et al., 2011; OBIS, 2021). They are found at depths between 0 and 320m (Picton et al., 2011); recorded depths on OBIS (2021) are all less than 170m.

S4	BF3	SK5	SO3	R1	R3	LD2	LH6	MV1	MO1	FH3a	SA2	EP2	DR1	DR2	DR3	Z4
3	3	3	3	2	2	3	3	3	3	3	3	3	1	2	1	3

Chelonaplysilla noevus (Carter, 1876)

Chelonaplysilla noevus are encrusting sponges that while only several milometers thick can grow indefinitely laterally (van Soest et al., 2000). They have a skeleton made up of fibrous spongin (van Soest et al., 2000). Like all members of the phylum Porifera, *C. noevus* are colonial. As members of the order Dendroceratida, reproduction both asexual and sexual with internal fertilisation. Likewise, as members of the order Dendroceratida, they have short-lived pelagic lecithotrophic larvae. Like other Porifera, *C. noevus* are attached and sessile. This species is an active filter feeder (Fish and Fish, 2011). They are commonly found on hard substrata (van Soest et al., 2000). This is an epibenthic species (van Soest et al., 2000). They are found at depths between 15 and 115m (van Soest et al., 2000).

S2	BF3	SK5	SO3	R1	R3	LD2	LH6	MV1	MO1	FH3	SA3	EP2	DR1	DR2
3	3	3	3	2	2	3	3	3	3	3	3	3	2	2

Subclass: Heteroscleromorpha

The skeleton is made up of siliceous spicules (Brusca et al., 2016; Goodwin et al., 2017; Hayward and Ryland, 2017).

Order: Haplosclerida

The majority of species in this order reproduce sexually, with external fertilisation. However, two genera, *Haliclona* and *Xestospongia*, are viviparous and thus have internal fertilisation. In addition, members reproduce asexually (Ereskovsky, 2018). Species in this order produce short-lived pelagic lecithotrophic larvae (Ereskovsky, 2018).

Family: Phloeodictyidae

Oceanapia (Norman, 1869)

As members of the subclass Heteroscleromorpha, species in this genus have siliceous spicules. Like all members of the phylum Porifera, species in the genus *Oceanapia* are colonial. As a “non-exception” genus of the order Haplosclerida, reproduction is both asexual and sexual, with external fertilisation. Likewise, as members of this order, they have short-lived pelagic lecithotrophic larvae. Like other sponges, species in the genus *Oceanapia* are attached and sessile. Like most other sponges, species in this genus are active filter feeders. Species in this genus are epibenthic and have a cosmopolitan distribution (Fish and Fish, 2011; OBIS, 2021). They are found at depths between 0 and 6000m, with the majority of observations at depths less than 400m (OBIS, 2021).

SK2	SO3	R1	R2	LD2	LH6	MV1	MO1	FH3a	EP2	DR1	DR2	DR3	DR4	Z4
3	3	2	2	3	3	3	3	3	3	2	2	2	1	3

Oceanapia robusta (Norman, 1869)

Oceanapia robusta are globulose sponges that are between 5 and 20cm in diameter (van Soest et al., 2000). As members of the subclass Heteroscleromorpha, species in this genus have siliceous spicules. Like all members of the phylum Porifera, *O. robusta* are colonial. As a member of the genus *Oceanapia*, reproduction is both asexual and sexual, with external fertilisation. Likewise, they have short-lived pelagic lecithotrophic larvae. Like other sponges, *Oceanapia robusta* are attached and sessile. Like most other sponges this species is an active filter feeders. This species is epibenthic with a cosmopolitan distribution (Fish and Fish, 2011; OBIS, 2021). OBIS (2021) indicates observations between 20 and 2000m; this depth range is marginally wider than the 70 to 1700m range reported by van Soest et al. (2000).

S3	S4	BF1	SK2	SO3	R1	R2	LD2	LH6	MV1	MO1	FH3a	EP2	DR2	DR3	DR4	Z4
2	2	3	3	3	2	2	3	3	3	3	3	3	2	2	1	3

Order: Tetractinellida

Family: Tetillidae

Members of this family are viviparous, reproducing sexually with internal fertilisation (Ereskovsky, 2018). In addition, all members reproduce asexually (Ereskovsky, 2018).

Craniella zetlandica (Carter, 1872)

Craniella zetlandica are globulose sponges that range in size and shape from a “large pea” to a “golf ball” (Picton and Morrow, 2016; Busch et al., 2020). As members of the subclass Heteroscleromorpha, species in this genus have siliceous spicules. Like all members of the phylum Porifera, *C. zetlandica* are colonial. As members of the family Tetillidae, reproduction is both asexual and sexual, with internal fertilisation. Likewise, as members of this family, they exhibit direct development. Like other sponges, *C. zetlandica* are attached and sessile. Like most other sponges this species is an active filter feeders. *Craniella zetlandica* are typically found on hard substrata or inside cup-shaped sponges (Picton and Morrow, 2016). This species is epibenthic.

S2	S3	BF1	SK2	SO3	R1	R3	LD2	LH6	MV1	MO1	FH3	SA2	SA3	EP2
2	2	3	3	3	2	2	3	3	3	3	3	2	1	3

Order: Poecilosclerida

As an order of the subclass Heteroscleromorpha, species in this order contain skeletons made up of siliceous spicules. Reproduction of species in this order is both asexual and sexual, with internal fertilisation (Ereskovsky, 2018). Species in this order produce short-lived pelagic lecithotrophic larvae (Maldonado, 2006; Ereskovsky, 2018).

Family: Cladorhizidae

Unlike the majority of other families in the phylum Porifera, the species of Cladorhizidae are carnivorous (Watling, 2007).

Asbestopluma (asbestopluma) pennatula (Schmidt, 1875)

Alternatively represented as *Asbestopluma pennatula*, this shorter representation will be used in the text.

Asbestopluma pennatula are slender upright sponges (Schmidt, 1875) that range in size

between 22 and 60mm (Hestetun et al., 2015). As members of the subclass Heteroscleromorpha, they have siliceous spicules. Like all members of the phylum Porifera, *A. pennatula* are colonial. As members of the order Poecilosclerida, reproduction is both asexual and sexual, with internal fertilisation. Likewise, as members of this order, they have short-lived pelagic lecithotrophic larvae. Like other sponges, *Asbestopluma pennatula* is attached and sessile. Their root structure allows them to be present on soft substrata (Hestetun et al., 2015). This species is a predator. *Asbestopluma pennatula* are epibenthic (Fish and Fish, 2011). This species is found at depths between 150 and 1800m (Hestetun et al., 2017).

S2	S3	BF2	BF5	SK2	SO3	R1	R3	LD2	LH6	MV1	MO1	FH5	SA1	SA2	EP2	DR2	DR3	DR4
2	2	2	2	3	3	2	2	3	3	3	3	3	2	2	3	1	2	2

Family: Latrunculiidae

Members of this family have several different body forms: encrusting, globulose or upright (van Soest et al., 2000).

Latrunculia (Barboza du Bocage, 1870)

Species of the genus *Latrunculia* have several different body forms, these can be: encrusting, globulose or upright and branching (van Soest et al., 2000), that grow to sizes ranging from 1cm to around 70cm. As members of the subclass Heteroscleromorpha, they have siliceous spicules. Like all members of the phylum Porifera, species in the genus *Latrunculia* are colonial. As members of the order Poecilosclerida, reproduction is both asexual and sexual, with internal fertilisation. Likewise, as members of this order, they have short-lived pelagic lecithotrophic larvae. Like other sponges, species in the genus *Latrunculia* are attached and sessile. Like most other sponges species in this genus are active filter feeders. They are commonly found on hard substrata. Species in this genus are epibenthic and have a cosmopolitan distribution (Fish and Fish, 2011; OBIS, 2021).

S2	S3	S4	S5	S6	BF3	BF5	BF7	SK2	SO3	R1	R3	LD2	LH6	MV1	MO1	FH3a	EP2	Z4
1	1	2	2	1	1	1	2	3	3	2	2	3	3	3	3	3	3	3

Family: Microcionidae

Antho (Gray, 1867)

Species of the genus *Antho* are more commonly encrusting than upright (species observations). As members of the subclass Heteroscleromorpha, they have siliceous spicules. Like all members of the phylum Porifera, species in the genus *Antho* are colonial. As members of the order Poecilosclerida, reproduction is both asexual and sexual, with internal fertilisation. Likewise, as members of this order, they have short-lived pelagic lecithotrophic larvae. Like other sponges, species in the genus *Antho* are attached and sessile. Like most other sponges, species in this genus are active filter feeders. Species in the genus *Antho* are epibenthic and have a cosmopolitan distribution (Fish and Fish, 2011; OBIS, 2021). Species in this genus are found at depths between 0 and 4000m (OBIS, 2021).

BF3	BF5	SK2	SO3	R1	R3	LD2	LH6	MV1	MO1	FH3a	EP2	DR1	DR2	DR3	DR4	Z4
2	2	3	3	2	2	3	3	3	3	3	3	2	1	2	1	3

Antho (antho) dichotoma (Linnaeus, 1767)

Antho (antho) dichotoma are upright branching sponges that grow up to 30cm (van Soest et al., 2000). As members of the subclass Heteroscleromorpha, they have siliceous spicules. Like all members of the phylum Porifera, *A. dichotoma* are colonial. As members of the order Poecilosclerida, reproduction is both asexual and sexual, with internal fertilisation. Likewise, as members of this order, they have short-lived pelagic lecithotrophic larvae. Like other sponges, this species is attached and sessile. *Antho dichotoma* are active filter feeders. They are commonly found on hard substrata. This species is epibenthic and has a cosmopolitan distribution (Fish and Fish, 2011; OBIS, 2021). They are found at depths between 20 and 900m (OBIS, 2021), and are considered to be a deepwater species, with most observations below 100m (Picton et al., 2011).

S4	BF5	BF7	SK2	SO3	R1	R3	LD2	LH6	MV1	MO1	FH3a	SA2	EP2	DR2	DR3	DR4	Z2
3	1	2	3	3	2	2	3	3	3	3	3	3	3	2	2	2	3

Family: Hymedesmiidae

Hymedesmia (hymedesmia) paupertas (Bowerbank, 1866)

Alternatively represented as *Hymedesmia paupertas*, this shorter representation will be used in the text.

Hymedesmia paupertas are encrusting sponges that form patches between 1cm and 2cm in diameter (van Soest et al., 2000). As members of the order Poecilosclerida, they have siliceous spicules. Like all members of the phylum Porifera, *H. paupertas* are colonial. Additionally, this means that reproduction is both asexual and sexual, with internal fertilisation. Likewise, as members of this order, they have short-lived pelagic lecithotrophic larvae. Like other sponges, *H. paupertas* are attached and sessile. Like most other sponges, this species is an active filter feeders. *Hymedesmia paupertas* are found on hard substrata (van Soest et al., 2000). This is an epibenthic species with an arctic-boreal distribution (van Soest et al., 2000; Fish and Fish, 2011). They are found at depths up to 400m (van Soest et al., 2000).

S2	BF3	SK2	SO3	R1	R3	LD2	LH6	MV1	MO1	FH3a	SA2	EP2	DR1	DR2	DR3	Z2
3	3	3	3	2	2	3	3	3	3	3	3	3	2	2	2	3

Order: Polymastiida

As an order of the subclass Heteroscleromorpha, species in this order contain skeletons made up of siliceous spicules. Reproduction of species in this order is both asexual and sexual, with internal fertilisation (Ereskovsky, 2018). Species in this order produce short-lived pelagic lecithotrophic larvae (Ereskovsky, 2018).

Family: Polymastiidae

Quasillina (Norman, 1869)

Species of the genus *Quasillina* are erect globulose sponges (species level observations (Plotkin, 2003; Picton et al., 2011)), that grow to between 1 and 5cm in height. As members of the order Polymastiida, they have siliceous spicules. Like all members of the phylum Porifera, species in the genus *Quasillina* are colonial. As members of the order Polymastiida, their reproduction is both asexual and sexual, with internal fertilisation. Additionally, they have short-lived pelagic lecithotrophic larvae. Like other sponges, species in the genus *Quasillina*

are attached and sessile. Like most other sponges, species in this genus are active filter feeders. The substratum affinity of individual species indicates that the genus is associated with hard substrata (Plotkin, 2003). This is an epibenthic species with a cosmopolitan distribution (Fish and Fish, 2011; Picton et al., 2011). They are found at depths up to 400m (averaged from species data (Picton et al., 2011; OBIS, 2021)).

S3	BF1	BF5	SK2	SO3	R1	R2	LD2	LH6	MV1	MO1	FH3a	SA2	B5	EP2	DR1	DR2	DR3	Z4
3	2	1	3	3	2	2	3	3	3	3	3	3	3	3	2	2	2	3

Order: Suberitida

As an order of the subclass Heteroscleromorpha, species in this order contain skeletons made up of siliceous spicules.

Family: Stylocordylidae

Reproduction is sexual, with either external or internal fertilisation. This is one of only two families in the class Demospongiae that has direct development of the young (Ereskovsky, 2018).

Stylocordyla borealis (Lovén, 1868)

Stylocordyla borealis are upright sponges and grow to 20cm height (*The SCAR Antarctic Field Guides*, [n.d.]). As members of the order Suberitida, they have siliceous spicules. Like all members of the phylum Porifera, *S. borealis* are colonial. Reproduction is sexual, with the young being brooded (Sarà et al., 2002). They have direct development of the young (Sarà et al., 2002). Like other sponges, *Stylocordyla borealis* are attached and sessile. Like most other sponges, they are active filter feeders. This is an epibenthic species with a bipolar distribution (cosmopolitan, by the definitions (table 3.1)) (Fish and Fish, 2011; *The SCAR Antarctic Field Guides*, [n.d.]). They are found at depths between 13 and 2300m (*The SCAR Antarctic Field Guides*, [n.d.]).

S4	BF5	SK2	SO3	R4	LD3	LH6	MV1	MO1	FH3a	SA1	EP2	DR1	DR2	DR3	DR4	Z4
3	3	3	3	3	3	3	3	3	3	3	3	2	2	2	2	3

Order: Tethyida

Members of this order are oviparous, reproducing sexually with external fertilisation. In addition, some members reproduce asexually via budding (Ereskovsky, 2018).

Family: Tethyidae

The spicules of members of this family are siliceous (Hayward and Ryland, 2017).

Tethya (Lamarck, 1815)

Species in the genus *Tethya* are globulose (Sarà and Sarà, 2002). As a genus of the family Tethyidae, they have siliceous spicules. Like all members of the phylum Porifera, species in the genus *Tethya* are colonial. As members of the order Tethyida, reproduction is both asexual and sexual, with external fertilisation. They have short-lived pelagic lecithotrophic larvae. Like other Porifera, *Tethya* species are attached and sessile. This genus contains active filter feeding species. Species in the genus *Tethya* are epibenthic and the genus has a cosmopolitan distribution (OBIS, 2021).

BF1	SK2	SO3	LD2	LH6	MV1	MO1	FH3a	EP2	DR1	DR2	DR3	Z4
3	3	3	3	3	3	3	3	3	2	2	1	3

Tethya citrina (Sarà and Melone, 1965)

Tethya citrina are globulose sponges that grow up to 6cm in diameter (van Soest et al., 2000; Hayward and Ryland, 2017). As members of the family Tethyidae, they have siliceous spicules. Like all members of the phylum Porifera, *T. citrina* are colonial. As members of the order Tethyida, reproduction is both asexual and sexual, with external fertilisation. They have short-lived pelagic lecithotrophic larvae. Like other Porifera, *T. citrina* are attached and sessile. This species is an active filter feeder. *Tethya citrina* is found on hard substrata (van Soest et al., 2000). This is an epibenthic species with a cosmopolitan distribution (van Soest et al., 2000; Fish and Fish, 2011). They are found at depths up to 930m (van Soest et al., 2000).

S2	S3	BF3	SK2	SO3	R1	R3	LD2	LH6	MV1	MO1	FH3a	SA2	EP2	DR1	DR2	DR3	Z4
1	2	3	3	3	2	2	3	3	3	3	3	3	3	2	2	2	3

Order: Tetractinellida

Sponges in this order reproduce sexually with external fertilisation. In addition to sexual reproduction, they reproduce asexually via budding or fragmentation (Ereskovsky, 2018).

Family: Ancorinidae

Stelletta (Carter, 1886)

Species of the genus *Stelletta* are either encrusting, globulose, or upright. These forms range in size from 1cm to more than 20cm (van Soest et al., 2000; Samaai and Gibbons, 2005; Picton et al., 2011). As an order of the subclass Heteroscleromorpha, they have siliceous skeletons. Like all members of the phylum Porifera, species in the genus *Tethya* are colonial. As members of the order Tetractinellida, reproduction is sexual, with external fertilisation. They have short-lived pelagic lecithotrophic larvae. Like other Porifera, *Stelletta* are attached and sessile. This is an active filter feeding genus. Species descriptions suggest this genus is associated with hard substrata (van Soest et al., 2000; Picton et al., 2011). This is an epibenthic genus with a cosmopolitan distribution (van Soest et al., 2000; Samaai and Gibbons, 2005; Fish and Fish, 2011; Picton et al., 2011; OBIS, 2021). They are found at depths from 0 to 4000m, with frequency peaks between 0 and 110m, 200 and 600m, and 1000 and 2000m (OBIS, 2021).

S2	S3	S4	BF1	BF3	BF5	SK2	SO3	R1	R2	LD2	LH6	MV1	MO1	FH3a	SA2	EP2	DR1	DR2	DR3	DR4	Z4
1	2	2	2	2	2	3	3	2	2	3	3	3	3	3	3	3	2	2	2	1	3

Stryphnus (Sollas, 1886)

Species of the genus *Stryphnus* are either encrusting, upright or globulose. Their size ranges from about 4cm wide and 3cm thick encrusting species to 40cm encrusting species (*S. ponderous*), to species such as *S. fortis* which is 15cm high (van Soest et al., 2000; Kelly and Sim-Smith, 2012). As an order of the subclass Heteroscleromorpha, they have siliceous skeletons. Like all members of the phylum Porifera, species in the genus *Stryphnus* are colonial. As members of the order Tetractinellida, reproduction is both sexual, with external fertilisation, and asexual via fragmentation. They have short-lived pelagic lecithotrophic larvae. Like other Porifera, species of this genus are attached and sessile. Species in this genus are

active filter feeders. They are found on both hard and soft substrata (Holte et al., 2016). This is an epibenthic genus with a cosmopolitan distribution (OBIS, 2021). They are found at depths between 0 and 700m (OBIS, 2021).

S2	S3	S4	S5	BF1	BF3	BF5	SK2	SO3	R1	R2	LD2	LH6	MV1	MO1	FH3a	SA1	SA2	EP2	DR1	DR2	DR3	DR4	Z4
2	2	2	2	2	2	2	3	3	2	2	3	3	3	3	3	2	2	3	1	2	2	1	3

Stryphnus ponderosus (Bowerbank, 1866)

Stryphnus ponderosus are encrusting sponges that grow up to 40cm wide (van Soest et al., 2000; Picton et al., 2011). As an order of the subclass Heteroscleromorpha, they have siliceous skeletons. Like all members of the phylum Porifera, *S. ponderosus* are colonial. As members of the order Tetractinellida, reproduction is both asexual and sexual, with external fertilisation. As members of the family Ancorinidae, they have short-lived pelagic lecithotrophic larvae. Like other Porifera, *S. ponderosus* are attached and sessile. This species is an active filter feeder (Fish and Fish, 2011). They are found on both hard and soft substrata (Holte et al., 2016). *Stryphnus ponderosus* are epibenthic with a cosmopolitan distribution Picton et al. (2011). They are found between 1 and 740m (Picton et al., 2011).

S4	S5	BF1	SK2	SO3	R1	R2	LD2	A4	LH6	MV1	MO1	FH3a	SA1	SA2	EP2	DR1	DR2	DR3	Z4
1	2	3	3	3	2	2	3	3	3	3	3	3	2	2	3	2	2	2	3

Family: Geodiidae

Trait definitions for this family can be found in the Arctic Traits Database (Degen and Faulwetter, 2019).

Geodia atlantica (Stephens, 1915)

Geodia atlantica are globulose sponges that range in size between 12cm and 128cm, with an observed mean of 51cm (Kutti et al., 2013; Koutsouveli et al., 2020). As members of the family Geodiidae, they have siliceous spicules (Hayward and Ryland, 2017). Like all members of the phylum Porifera, *G. atlantica* are colonial. As a species in the genus *Geodia*, reproduction is both asexual and sexual, with external fertilisation (Ereskovsky, 2018; Koutsouveli et al., 2020). As members of the class Demospongiae, they have short-lived pelagic lecithotrophic larvae. Klitgaard and Tendal (2004) suggest their study species, which includes *Geodia atlantica*, would likely take decades to reach the sizes that are commonly encountered. Like other sponges, *G. atlantica* are attached and sessile. This species is an active filter feeder (Last et al., 2020). They are found on hard substrata (Holte et al., 2016). *Geodia atlantica* are epibenthic (Fish and Fish, 2011). Based on a relatively small sample, OBIS (2021), suggests that this species has an arctic-boreal distribution and is found at depths between 200 and 1000m. These data are comparable to the known distribution of other *Geodia* in this study.

S4	S5	S6	BF1	SK2	SO3	R1	R2	LD2	A4	LH6	MV1	MO1	FH3a	SA1	SA2	B5	EP2	DR3	Z2
1	2	1	3	3	3	2	2	3	3	3	3	3	3	2	2	3	3	3	3

Geodia barretti (Bowerbank, 1858)

Geodia barretti are globulose sponges that can grow up to 50cm (van Soest et al., 2000). As members of the family Geodiidae, they have siliceous spicules (Hayward and Ryland, 2017).

Like all members of the phylum Porifera, *G. barretti* are colonial. As a species in the genus *Geodia*, reproduction is both asexual and sexual, with external fertilisation (Ereskovsky, 2018; Koutsouveli et al., 2020). As members of the class Demospongiae, they have short-lived pelagic lecithotrophic larvae. These organisms are long-lived, with a life span of around 440 years (Hoffmann et al., 2003). Like other sponges, *G. barretti* are attached and sessile. This species is an active filter feeder (Leys et al., 2018). They are found on hard substrata (van Soest et al., 2000; Holte et al., 2016). *Geodia barretti* are epibenthic with an arctic-boreal distribution (van Soest et al., 2000; Fish and Fish, 2011). They are found at depths between 15 and 329m (van Soest et al., 2000)

S5	S6	BF1	SK2	SO3	R1	R2	LD2	A4	LH6	MV1	MO1	FH3a	SA2	B5	EP2	DR1	DR2	DR3	Z2
1	2	3	3	3	2	2	3	3	3	3	3	3	3	3	3	1	2	2	3

Geodia macandrewii (Bowerbank, 1858)

Geodia macandrewii are globulose sponges that can grow larger than 1m (van Soest et al., 2000). As members of the family Geodiidae, they have siliceous spicules (Hayward and Ryland, 2017). Like all members of the phylum Porifera, *G. macandrewii* are colonial. As a species in the genus *Geodia*, reproduction is both asexual and sexual, with external fertilisation (Ereskovsky, 2018; Koutsouveli et al., 2020). As members of the class Demospongiae, they have short-lived pelagic lecithotrophic larvae. Like other sponges, *G. macandrewii* are attached and sessile. This species is an active filter feeder (Last et al., 2020). They are found on hard substrata and cold-water coral reefs (van Soest et al., 2000; Holte et al., 2016). *Geodia macandrewii* are epibenthic (Fish and Fish, 2011). They are found at depths greater than 180m (van Soest et al., 2000). Descriptions by van Soest et al. (2000) suggest the species is found as far south as France, indicating a more cosmopolitan distribution, based on the definitions used in this study.

S6	BF1	SK2	SO3	R1	R2	LD2	A4	LH6	MV1	MO1	FH3a	SA2	SA3	B5	EP2	DR2	DR3	DR4	Z4
3	3	3	3	2	2	3	3	3	3	3	3	2	1	3	3	1	2	2	3

Class: Hexactinellida

Species in this class have siliceous spicules (Fish and Fish, 2011; Brusca et al., 2016).

Order: Lyssacinosa

Members of this order are viviparous, reproducing sexually with internal fertilisation. There is no asexual reproduction in this order (Ereskovsky, 2018). Species in this order have short-lived lecithotrophic larvae (Ereskovsky, 2018).

Family: Rossellidae

Asconema setubalense (Kent, 1870)

Asconema setubalense are globulose sponges (Rodríguez-Basalo et al., 2021) that grow up to 95cm in diameter and 110cm high (Prado et al., 2021). As members of the class Hexactinella, they have siliceous spicules. Like all members of the phylum Porifera, *A. setubalense* are colonial. As members of the order Lyssacinosa, reproduction is sexual with internal fertilisation. Likewise, they have short-lived lecithotrophic larvae. These organisms are long lived, with a lifespan between 60 and 120 years (Prado et al., 2021). Like other sponges, *A. setubalense* are attached and sessile. This species is an active filter feeder. *Asconema*

setubalense is found on hard substrata (Rodríguez-Basalo et al., 2021). This is an epibenthic species (Gage and Tyler, 1991) and they have a cosmopolitan distribution (Tabachnick and Menshenina, 2007). They are at depths between 93 and 4270m (Tabachnick and Menshenina, 2007).

S4	S5	BF1	BF5	SK2	SO3	R3	LD2	A4	LH6	MV1	MO1	FH3a	SA2	B5	EP2	DR2	DR3	DR4	Z4
1	2	1	2	3	3	3	3	3	3	3	3	3	3	3	3	2	2	2	3

Mellonympa mortenseni (Burton, 1928)

Mellonympa mortenseni are globulose sponges that grow to around 5cm in diameter (Burton, 1928). As members of the class Hexactinella they have siliceous spicules. Like all members of the phylum Porifera, *M. mortenseni* are colonial. As members of the order Lysacinosa, reproduction is sexual with internal fertilisation. Likewise, they have short-lived lecithotrophic larvae. Like other sponges, *M. mortenseni* are attached and sessile. This species is an active filter feeder. *Mellonympa mortenseni* is considered a soft bottom sponge. This is an epibenthic species.

S3	BF1	SK2	SO3	R3	LD2	LH6	MV1	MO1	FH3a	SA1	SA2	EP2
3	3	3	3	3	3	3	3	3	3	2	1	3

Class: Homoscleromorpha

Species in this class usually have neither spongin fibres nor a rigid skeleton. When a rigid skeleton is present it is made of siliceous spicules (Brusca et al., 2016). Reproduction is both asexual and sexual, with internal fertilisation (Ereskovsky, 2018). They have short-lived lecithotrophic larvae (Ereskovsky, 2018).

Order: Homosclerophorida

Family: Plakinidae

Species in this family are found on hard substrata (Muricy and Díaz, 2002).

Plakortis (Schulze, 1880)

Species of the genus *Plakortis* are encrusting (Muricy and Díaz, 2002). They have siliceous spicules (Muricy and Díaz, 2002). Like all members of the phylum Porifera, species in the genus *Plakortis* are colonial. As members of the class Homoscleromorpha, reproduction is both asexual and sexual, with internal fertilisation. Likewise, they have short-lived lecithotrophic larvae. Like other sponges, species in the genus *Plakortis* are attached and sessile. They are active filter feeders. As members of the family Plakinidae, they are found on hard substrata. This is an epibenthic genus with a cosmopolitan distribution (Muricy and Díaz, 2002). Species in this genus are found at depths up to 300m, with the majority of observations occurring either below 90m or between 180-300m (OBIS, 2021).

BF3	SK2	SO3	R1	R4	LD2	LH6	MV1	MO1	FH3a	SA2	EP2	DR1	DR2	DR3	Z4
3	3	3	2	2	3	3	3	3	3	3	3	2	2	1	3

Chapter 4

Biological Trait Analysis

Abstract

Biological traits can be used to understand and model ecosystems. There are different approaches to analysing and describing the biological traits found at different sites. In this chapter, the RLQ method, combined with the fourth corner approach, was used to investigate the link between trait and environmental conditions in a number of video sequences from nine different cold-water coral reefs along the coast of Norway. Trait relationships were also investigated using community weighted means to determine the role of longitude and latitude as a proxy for local environmental framing factors, or species range restrictions in driving different trait assemblages. The trait composition of the reef associated communities were compared as a whole to identify common trait trends across different cold-water coral reefs. The results indicated that burrow dwelling was negatively associated with the presence of cold-water coral related substrata. The results of biological trait analyses support the hypothesis that cold-water coral reefs have similar functioning. While there was variability within trait modalities, in general the reefs had similar overall trait profiles. The results of the community weighted redundancy analysis (CWM-RDA) indicated that, while location accounted for 19% of the variability in the trait assemblages found on the reefs, the presence of reef related substrata and depth accounted for 36%. The CWM-RDA resulted indicated that burrowing both as a living habit and movement type, as well as a preference for soft substrata negatively associated with the coral related substrata. While the an attached living habit and sessile “movement” were associated with the coral related substrata. The community weighted trait compositions for the different reefs indicated that the nine reefs all had greater expression of dorso-ventral compressed body forms, attached and sessile life styles. The community weight mean expression of passive and active filter feeding modalities where negatively related to each other. When considering the most common substratum present, passive filter feeding was associated with the presence of dead *Lophelia* and active with sand. These findings support the hypothesis that the community associated with cold-water coral reefs have similar traits regardless of their location.

4.1 Introduction

4.1.1 Biological Trait Analysis

Biological traits are related to the habitat in which the organisms are found (Southwood, 1977; Southwood, 1988). In many regards, this is a logical assertion, based on evolutionary theory. Selection pressure is environmentally driven, thus, traits are selected for based on both biotic and abiotic drivers present where an organism occurs. While traits are the result of evolutionary processes, they determine the environment in which an organism can survive. Hence, traits can be used to understand

and model ecosystems (e.g. Diaz and Cabido, 1997; Bell, 2007; Zakharova et al., 2019; Zhulay et al., 2021).

Strictly speaking, just about every feature of an organism could be considered a biological trait; Violle et al. (2007) defines a trait as anything that is measurable at the organism level. Given the practically undefinable number of traits that any given organism can have, it becomes evident that the traits chosen for biological trait analysis must be ecologically relevant (Beauchard et al., 2017). In chapter 1, the idea that traits can be used to describe ecosystem functioning is discussed. In this context, the traits used in a biological trait analysis should reflect the ability of a community to function (Sutton et al., 2020; de Juan et al., 2022).

By selecting relevant traits, biological trait analysis can be used as a proxy for ecosystem function (Bremner et al., 2006; Bremner, 2008; Sutton et al., 2020). By extension, biological trait analysis can thus relate function to environmental factors. Relating variability in biological traits to environmental conditions can provide insight into the impacts of nutrient loading (Dong et al., 2021), fishing pressures (Tillin et al., 2006; de Juan et al., 2007; Fleddum et al., 2013; Bolam et al., 2014), and climate change (Degen and Faulwetter, 2019). Beyond responses to change, traits can also be used to highlight the importance of different environmental conditions (Sutton et al., 2021). Using traits, the ecological impacts of disturbances, natural or anthropogenic, can be predicted. Current trends have been used to predict poleward shift of larger, longer-lived, piscivorous fish in response to climate warming (Frainer et al., 2017). Based on small-scale experiments, the loss of a key consumer and ocean warming on eelgrass communities were predicted to significantly alter the traits present in the community (Eklöf et al., 2015). The ability to predict changes in the ranges of traits, or the traits present in a specific area, makes trait-based modelling an incredibly useful tool for spatial management of marine resources.

Both Eklöf et al. (2015) and Frainer et al. (2017) are examples of extrapolation from small-scale experiments or observations of current trends. These examples provide support for the idea that trait-based modelling can be used for scenario-based hypothesis testing. As with species or functional group-based models, this allows for the testing of hypotheses that would be impractical or unethical to test in situ. A trait-based approach offers a chance to focus directly on trait changes and their impact on ecological functioning. For example, traits can be used to link environmental factors to ecological processes.

Biological trait analyses are inherently multivariate. This is because the analyses are based on the idea that biological traits represent survival strategies (Southwood, 1977; Southwood, 1988; Townsend and Hildrew, 1994). These strategies are related to a collection of traits. In multivariate statistics, multiple response variables are related to the explanatory variables. As with univariate statistics, there are a multitude of methods; however, the results typically focus on finding patterns and correlations between collections of response variables.

Over the past decade and a half, biological trait approaches and analyses have become more common in the marine environment (Törnroos, 2014; examples since 2014, Bolam et al., 2014; Costello et al., 2015; Tavares et al., 2019; Cano-Barbacil et al., 2020; Lam-Gordillo et al., 2020a; Lam-Gordillo et al., 2020b; Sutton et al., 2020; Dong et al., 2021; Sutton et al., 2021; Zhulay et al., 2021). A total

of 168 publications related to biological trait analysis the majority of which focus on benthic macrofauna, have been identified since 2006 (de Juan et al., 2022). The methods by which these analyses have been conducted have been updated continually and refined. Methods utilised in biological trait analyses, include fuzzy correspondence analysis (Bolam et al., 2014; Sutton et al., 2020; Dong et al., 2021; Zhulay et al., 2021), RLQ and fourth-corner approaches (Edegbene et al., 2021; Sutton et al., 2021), and community weighted redundancy analysis (CWM-RDA) (Sutton et al., 2021). In addition to these examples, Degen and Faulwetter (2019) highlighted several other multivariate approaches that can be used. Currently, the main applications are frequentist in nature; however, Sarker et al. (2021) described a Bayesian-based trait model that allows for forecasting.

4.1.2 Cold-Water Coral Reefs

Cold-water coral reefs are biological hotspots (Freiwald et al., 2004). Off the coast of Norway, these reefs are typically dominated by *Lophelia pertusa* or *Madrepora oculata* (Freiwald et al., 2004). While a cold-water coral reef can take on several shapes, relating to current flow and topography, they naturally consist of three distinct sections (Buhl-Mortensen et al., 2010), namely, the live coral zone, dead coral zone and coral rubble zone (See chapter 1). Each coral region can support different organisms. The coral rubble section is relatively exposed compared to the massive 3-dimensional structures of the living and dead regions. The implication of this is that the areas under the living and dead coral regions are not visible during video and photographic surveys.

A unique feature of cold-water coral reefs is the “sponge loop”. This is a process whereby coral derived dissolved organic matter (DOM) is utilised as a nutrient source by sponges living on the reef (Rix et al., 2016). Recently, it has been shown that this recycling is not restricted to sponges, rather it takes place across the whole community (Maier et al., 2021). The functional role, in nutrient retention and recycling, of species that can utilise DOM is thus well established on cold-water coral reefs. Cold-water coral reefs are hypothesised to be fish nurseries (Baillon et al., 2012; D’Onghia et al., 2012; Costello et al., 2015), this hypothesis is not supported by all studies (Biber et al., 2014). However, it is widely accepted that some fish abundances are increased in the vicinity of these reefs (Husebø et al., 2002; D’Onghia et al., 2012). These abundances have been attributed to increases in food and shelter on the reefs (Price et al., 2019), as well as enhanced feeding conditions on the reefs (Buhl-Mortensen et al., 1995). Biological trait analysis can be used to identify traits associated with these processes to better understand what parts of the reef they are associated with.

Given the distinct zonation of cold-water coral reefs, it stands that trait differences might exist between the different zones of the reef. Identifying the drivers of differences in the biological trait composition will help highlight how these drivers influence the functionality of the system. This applies both to within and beyond cold-water coral reefs, potentially indicating processes that impact benthic-pelagic coupling on the reefs. The primary aim of this chapter is to determine whether similar trait assemblages were present on the nine different cold-water coral reefs. Secondly, this chapter aims to identify both individual and trait groups that associate with the environmental factors, which include substratum type, on and around the cold-water coral reef sites. The methods will be discussed in detail below; however, the two methods used will be justified in terms of the aims. One of the aims of this thesis is to investigate whether geographical location (co-ordinate position) significantly influences the species and traits found in different habitats that occur as part of cold-water coral reefs.

The combined RLQ fourth-corner method (section 4.3.3) allows for the relationship between traits and the environment to be described. This method does not allow for the impact of longitude and latitude to be considered. However, the community weighted means, combined with redundancy analysis (CWM-RDA) (section 4.3.4), allows for the the co-ordinate positions of the reefs to be included (Sutton et al., 2021).

4.2 Introduction to Statistical Methods

In order to assess the relationship between biological traits and environmental gradients, three datasets are needed. The first dataset represents the organisms or operational taxonomic units present at each site (Taxa by Sites); this is referred to as the **L** matrix. The second dataset represents the environmental conditions at each site (Environment by Sites); this is referred to as the **R** matrix. The last dataset requires the traits of each observed taxonomic unit (Taxa by Traits); this is the **Q** matrix. The aim of all methods of biological trait analysis is to relate these three matrices into an interpretable representation of trait associations along the environmental gradients. While there are several methods for showing the relationships between these matrices, this introduction will focus on three specific methods: the co-inertia based RLQ method, the fourth-corner method, and community weighted means (CWM).

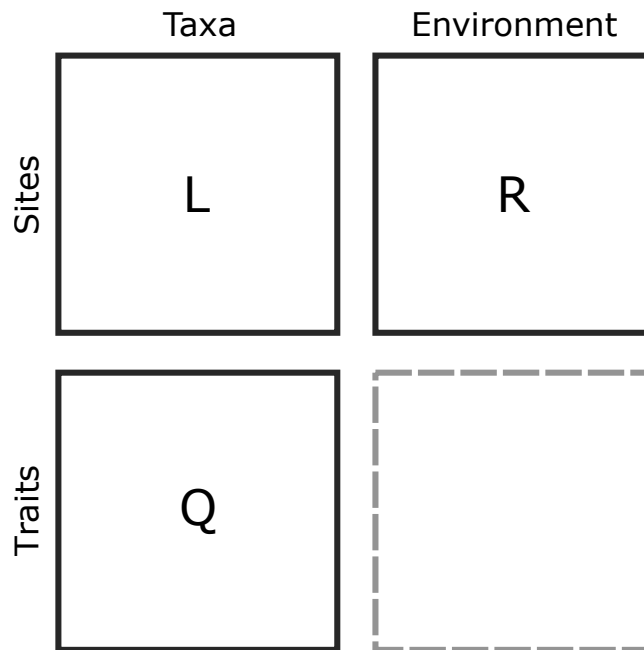


Figure 4.1: A visual representation of the **R**, **L**, and **Q** matrices. The **Q** matrix has been transposed to represent Traits by Taxa in order to highlight the shared axis. The dashed matrix represents the fourth-corner relationship between traits and the environment.

4.2.1 RLQ (co-inertia) method

The term, co-inertia is not mentioned in Dolédec et al.'s (1996) original description of the **RLQ** method. However, the method is technically an extension of Dolédec and Chessel's (1994) co-inertia analysis, applied to three tables (Dray et al., 2003).

The **R**, **L**, and **Q** tables can be analysed by themselves using single-table ordination techniques, such as principal component analysis (PCA) (originally, Pearson, 1901; updated and explained by Escoufier, 1987; Jolliffe, 2002) or correspondence analysis (CA) (Greenacre, 1984), while the links between tables sharing a common axis (**L** and **R** or **L** and **Q**) can be analysed using ordination techniques such as canonical correspondence analysis (CCA) or co-inertia analysis. The RLQ method can be described as a summary of five multivariate analyses, each single-table analysis on **L**, **R**, and **Q** and two-table analyses between **L-R** and **Q-L** (Dolédéc et al., 1996). The RLQ-analysis represents the relationship between the **R** and **Q** tables.

The **R** table is linked to **L** by shared row weights; likewise, **Q** is linked to **L** by shared column weights (figure 4.1 Dolédéc et al., 1996). Thus, rather than performing the analysis in triplicate, general singular value decomposition can be used to express this as a triplet. Dolédéc et al. (1996) described the resulting RLQ analysis as a compromise between the individual matrix ordinations.

In short, if **L** is analysed by CA, then the RLQ method maximises the covariances of **R** and **Q** (Dolédéc et al., 1996)

4.2.1.1 Fourth-corner Method

Inspired by the RLQ method, the fourth-corner method was first proposed a year later (Legendre et al., 1997). This method calculated the matrix that would occupy the fourth-corner in figure 4.1 using clockwise multiplication around the matrices:

$$\mathbf{D} = \mathbf{LR}'\mathbf{Q} \quad (4.1)$$

While **L** was restricted to binary presence or absence data (Legendre et al., 1997; Dray and Legendre, 2008), **R** and **Q** could contain either quantitative or nominal data. Equation 4.1 is still applicable to the data if **R** and **Q** both contain either quantitative or ordinal variables, provided that the scales used for the ordinal variables are similar (Legendre et al., 1997).

The result of equation 4.1 is a contingency table. While Pearson’s formula can be used to calculate a χ^2 test statistic, the significance of this statistic cannot be assessed traditionally. This is because there are multiple taxa observed at each site, thus the data contained in the contingency table are not independent (Legendre et al., 1997). To overcome this limitation, Legendre et al. (1997) proposed the use of a permutation test. Four permutation models were described in detail by Legendre et al. (1997), but the fourth model was not applicable to their data. Little guidance was provided on when each model should be used which, in hindsight, left many ecologists over the following decade unsure about which model to apply (Dray and Legendre, 2008).

Information is lost when abundances are converted to binary data. Since differences in abundances are no longer considered, the ability to detect gradients of habit preference is removed. The original fourth-corner framework’s lack of support for data more complex than binary observations limited its appeal (Dray and Legendre, 2008). The original method was thus extended by Dray and Legendre (2008) to include abundance data. Permutation tests are used to test for a relationship between bio-

logical traits (**Q**) and the environmental conditions (**R**), mediated through occurrences of species (**L**). The original permutation models tested the relationships between **L** and either **R** or **Q** by performing permutations of **L** in different ways. Since the permutations are performed on **L**, the relationship between **R** and **Q** is demonstrated if and only if **L** is linked to **Q** and **L** is linked **R** (iff $\mathbf{L} \leftrightarrow \mathbf{Q}$ and $\mathbf{L} \leftrightarrow \mathbf{R}$). When originally describing the models, Legendre et al. (1997) provided details relating to the premise of each model; these are summarised by the model names. Legendre et al. (1997) described these models in terms of **L** where columns represented sites and rows species, in this description as in Borcard et al. (2018) the matrices are discussed in the orientation presented in figure 4.1 (Rows are sites and columns are taxa). Model 1: Environmental control over individual species. In this model, the cell values along each column of **L** are switched randomly; this model rejects the NULL hypothesis if $\mathbf{L} \leftrightarrow \mathbf{R}$ and/or $\mathbf{L} \leftrightarrow \mathbf{Q}$. Model 2: Environmental control over species assemblages. In this model, the whole rows of **L** are switched randomly; this model rejects the NULL hypothesis if $\mathbf{L} \leftrightarrow \mathbf{Q}$ regardless of the relationship between **L** and **R**. Model 3: Lottery. In this model, the cell values along each row of **L** are randomly switched; this model rejects the NULL hypothesis if $\mathbf{L} \leftrightarrow \mathbf{R}$ and/or $\mathbf{L} \leftrightarrow \mathbf{Q}$. Model 4: Random species attributes. In this model, the whole columns of **L** are switched randomly; the NULL hypothesis is rejected if $\mathbf{L} \leftrightarrow \mathbf{R}$ regardless of the relationship between **L** and **Q**. By considering the number of type I errors in the following three scenarios: 1) $\mathbf{L} \leftrightarrow \mathbf{Q}$ and $\mathbf{L} \leftrightarrow \mathbf{R}$, 2) $\mathbf{L} \leftrightarrow \mathbf{Q}$ but $\mathbf{L} \nleftrightarrow \mathbf{R}$ and 3) $\mathbf{L} \nleftrightarrow \mathbf{Q}$ but $\mathbf{L} \leftrightarrow \mathbf{R}$, it was found that combining Model 2 and Model 4 produced the fewest errors (Dray and Legendre, 2008). This combined model has a NULL hypothesis that **R** and/or **Q** are related to **L** (Dray et al., 2014).

Dray and Legendre (2008) proposed that each of the two tests, Model 2 and Model 4, be evaluated at a significance level of $\sqrt{\alpha}$, as this would produce a global significance of α . However, the type I error can be further reduced by applying the tests sequentially (ter Braak et al., 2012). Under this sequential approach, both tests are considered to be separate, thus they are evaluated at the α significance level. Since the NULL hypothesis states that $\mathbf{L} \nleftrightarrow \mathbf{R}$ AND $\mathbf{L} \nleftrightarrow \mathbf{Q}$, the second test is only conducted if the first one rejects the NULL hypothesis. Likewise, significance is assumed if the largest of the two p-values obtained is less than α . This approach is applicable to the RLQ method as well (ter Braak et al., 2012).

This sequential approach is not given a specific name in either of the papers that described it; however, it is referred to as model 6 in the documentation for the ade4 package (Chessel et al., 2004; Dray and Dufour, 2007; Dray et al., 2007; Bougeard and Dray, 2018; Thioulouse et al., 2018) and in publications (Sutton et al., 2021). The NULL hypothesis of model 4 is that the species traits are not significantly different to random assignment (Legendre et al., 1997). Thus, the species matrix is not linked to the trait matrix. A system may contain many species with the same traits, such as areas that are dominated by different species of Porifera. Since model 6 requires both models 2 and 4 to be significant, overlaps in traits to the point that model 4 is not significant will result in the whole analysis being declared not significant.

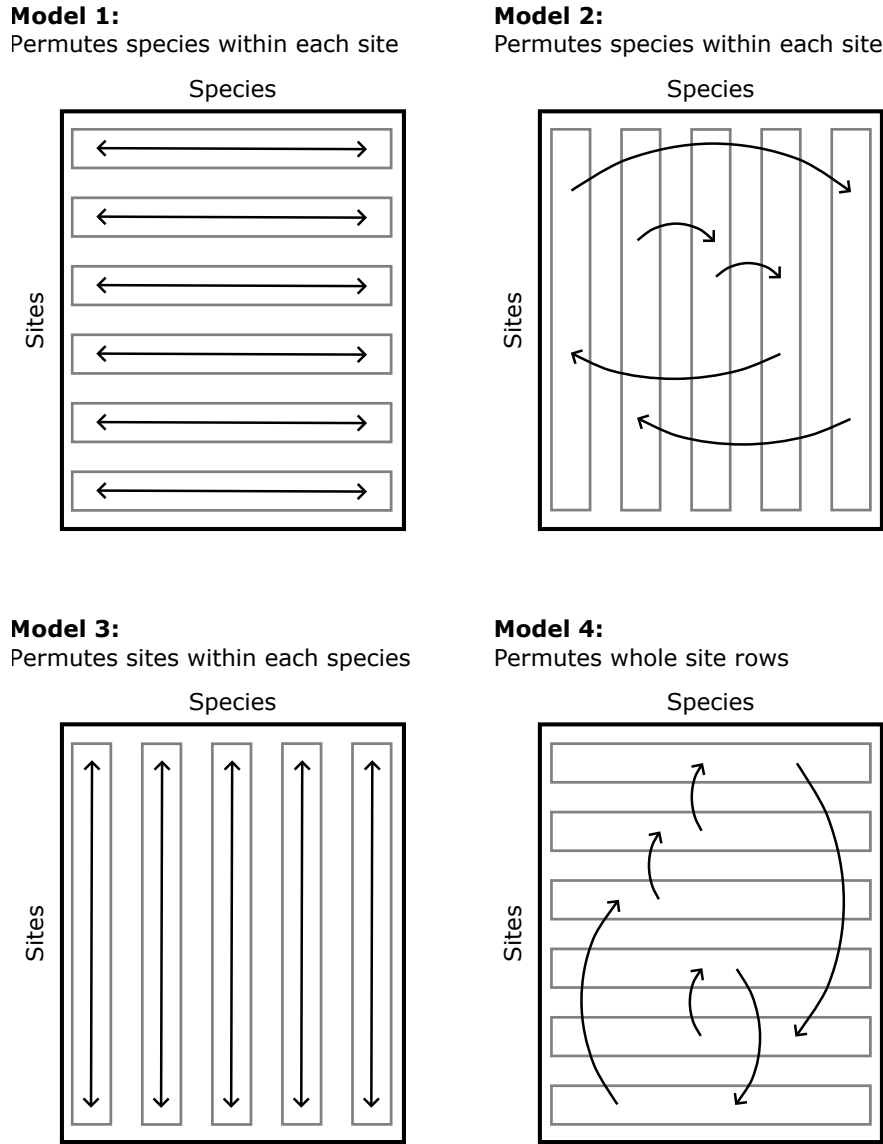


Figure 4.2: Visualisation of the four methods for permutation of the species matrix $\mathbf{L}$. Model 1: The occurrence data for each species is randomly switched along each column (species). Model 2: The whole species assemblage found at each site is randomly switched. Model 3: The occurrence data for each species is randomly switched along each row (site). Model 4: The whole species columns are randomly switched. Adapted from Legendre et al. (1997), who illustrated using species as rows and sites as columns

4.2.2 Combined Fourth-corner RLQ Method

The fourth-corner and RLQ methods are mathematically similar; however, their aims and outputs differ quite significantly (Dray et al., 2014). The most notable of these differences is that the RLQ method produces a graphical ordination, while the fourth-corner analysis produces a series of p-values based on the permutation model used.

While the fourth-corner method had been combined with RLQ for trait analysis in both terrestrial and aquatic environments previously (Lacourse, 2009; Brind'Amour et al., 2011), Dray et al. (2014) were the first to propose a standardised method for combining the two methods. Under the standardised procedure, the data are first analysed by RLQ analysis. The fourth-corner method is then applied to the axis of the RLQ analysis, testing for significant bivariate associations between the RLQ environ-

mental scores and the traits (Dray et al., 2014). The main benefit of this combined approach is that the ecological meaning of the output is readily interpreted. Dray et al. (2014) made use of a single biplot, or two shaded grids to display the results; however, Sutton et al. (2021) presented graphs that were easier to interpret. These graphs consisted of a bi-plot for the environmental factors and separate graphs representing placement of the trait modalities along each of the RLQ axes. This allowed for quick identification of significant trait modalities and of the environmental variables associated with each RLQ axis.

4.2.3 CWM Method

Community weighted means are distinct from the other methods as they rely on ordination of a calculated matrix that represent traits by site. This method was originally applied to plants, using continuous traits (Garnier et al., 2007). The trait by environment matrix is calculated by:

$$t_{agg} = \left(\sum_{i=1}^n p_i \times t_i \right) \quad (4.2)$$

for taxa i , where p_i is abundance of i and t_i is the value of trait t for taxon i , t_{agg} is the aggregated trait value for trait t . Equation 4.2 can be extended to a matrix containing many sites by simply applying it to every trait at every site, resulting in a matrix that represents the average trait values at each site.

This method was originally applied to continuous traits, giving readily understandable outputs, such as average height, at each site. However, the CWM method can be used with fuzzy coded data. When using fuzzy coded data, the data must be converted from the coding scale used to proportional data. This is done by dividing the fuzzy coded value for each trait modality by the sum of the fuzzy coded modalities for that trait. The resulting proportional trait matrix has modalities with values from 0 to 1, and the sum of trait modalities for a single trait is 1. There are two issues with doing this. The first is that missing traits are coded as zeros, thus a trait where all modalities are zero would be treated the same as if those modalities were not exhibited. This can be prevented by replacing each modality of that trait with the mean proportional value of the known traits. The second issue is that, since the proportions are multiplied by the abundances and then summed together, the resulting **LQ** matrix represents a hard-to-interpret value. The output data are technically fuzzy coded, as each value represents the affinity of an area to a trait. Since the data are fuzzy coded, appropriate ordinations, such as fuzzy correspondence analysis (FCA) and fuzzy principal component analysis (FPCA), can be used to analyse **LQ** directly (Beauchard et al., 2017).

When **LQ** is being related to **R**, the data must be transformed first. Sutton et al. (2021) treat the data as though it were fuzzy coded. Thus, they reapply the proportional conversion, producing a matrix that represents the community weighted means as a proportionate value related to how common each modality was at each site. Alternatively, Dong et al. (2021) treat the matrix as if it were community data, applying a transformation to it in this case Hellinger. In both cases, the **LQ** matrix is subjected to redundancy analysis (RDA) to determine the relationship to **R**.

During community weighted means analysis, the **L** matrix can be subjected to transformations prior

to the aggregation of traits. Likewise, **R** was transformed prior to the RDA in both examples referred to (Dong et al., 2021; Sutton et al., 2021). Regardless of transformation, the **LQ** represents traits by site, and the result of the RDA aims to associate those traits to environmental gradients.

4.3 Methods

4.3.1 Datasets

The datasets analysed in chapter 2 were used in this chapter. The definition of a taxonomic observation in this chapter was the same as in chapter 2 for all species; however, in chapter 2, descriptive observations such as “yellow porifera” were considered to be taxonomically different from “white porifera”, since the observations likely represented different species. In terms of traits, “yellow porifera” and “white porifera” were the same. Thus, in this chapter, observations such as these were grouped together as “porifera”. While colour contained no trait information, sizes, sociability, and shapes corresponded to trait codes. In these cases the groups were not merged. For example, in this chapter, “large porifera” and “large white porifera” were both considered to be “large porifera”, and were assigned the same trait codes for all non-size traits as “porifera” (Appendices A and ??). Rather, but were assigned trait values for size to represent that they were towards the larger end of the Porifera size range. No changes were made to the format of the environmental dataset. The results of the correlation tests performed in chapter 2 were used to avoid including correlated (Pearson’s correlation coefficient > 0.75 , $p < 0.05$) environmental variables. As in chapter 2, the named substrata were indicated in colour. Likewise, the bottom type clay and sponge spicules, was not included because of its low representation in the dataset (chapter 2).

4.3.2 Biological Traits

As mentioned in chapter 3, the primary source of trait information for this study was The Arctic Traits Database (Degen and Faulwetter, 2019). All groups were also checked against the BIOTIC (MarLIN, 2006) database, since it included expanded definitions for body form. Only six taxa belonging to the class Polychaetea were observed; additional trait information for the polychaetes was obtained from PolyTraits (Faulwetter et al., 2014). A small number of fish were included in the BIOTIC database, but all additional fish traits were obtained from FishBase (Froese and Pauly, 2021) and, where necessary, confirmed by additional literature. Groups for which traits could not be found in any of the databases mentioned above were subjected to literature review. The traits assigned from literature sources are described in chapter 3. It should be noted that not every entry is complete in the trait databases; in these cases, the missing traits were obtained from literature where possible. Since these taxa were partially covered in the existing databases, and only traits relevant to the analysis performed in this chapter were assigned, these taxa do not appear in chapter 3 (Appendix C).

Since The Arctic Traits Database was the primary source for traits; all traits in chapters 3 and 4 are presented using the same format. This means that the trait data are fuzzy coded (Chevenet et al., 1994). Fuzzy coding was done using a zero to three scale. This scale has been used in previous studies in the North Atlantic (Bolam et al., 2014; Degen and Faulwetter, 2019; Sutton et al., 2021). The exact meaning of each fuzzy code value and the definition of trait modality are presented in chapter 3. Based on this scale, *Sebastes*, which only contains species that swim, was assigned a three for the

trait modality “swimming”. While, *Munida*, which contains species that can both swim and crawl, was assigned a value of two for both trait modalities. When a taxa expressed one modality more commonly than another, the less common modality was assigned a value of one. In a few cases only negative information was available for a species; in those cases medium affinity was assigned to the remaining trait modalities and zero was assigned to the modalities that the taxa were known not to exhibit.

The traits and trait modalities used in this study can be found in table 4.1, which also provides ecological justification for the selection of the trait. The full trait definitions are reported in chapter 3. Traits are grouped as morphological, relating to life history, and behavioural (Degen and Faulwetter, 2019). Sociability and Larval Development are notably absent from the table; these traits were left out for statistical reasons, which will be discussed later in section 4.5. Additionally, while The Arctic Traits Database and many other sources made a distinction between surface and subsurface deposit feeders, under-representation of the latter resulted in these traits being grouped together as FH1. Grazing was added as an additional feeding method, given the presence of many taxa that would be considered “deposit feeders” but grazed on algae, coral or kelp in the system (Degen 2021/09/21, personal communication). Following the logic of the personal communication with Degen (2021/09/21) and the traits covered in BIOTIC, additional modalities were added to body form. These traits were branching, to account for the presence of branching corals and sponges, and pisciform, to account for the presence of fish. Likewise, for reasons that will be covered in section 4.5.1, a distinction was made between active and passive filter feeders. The resulting trait matrix contained eight biological traits across 43 modalities (table 4.1).

Substrate affinity is not commonly used by other benthic trait studies. It was included in this study partly to distinguish between the hard and soft bottom sponges. The ecological benefit of including substrate affinity is that, if it does not strongly associate with the percentage cover of related substrates, it may indicate the presence of other drivers that are more influential than substrate affinity.

Table 4.1: Biological traits, their modality codes, the definitions of each code, and the reason for including the trait, based on Degen and Faulwetter (2019) and Beauchard et al. (2017). Light grey indicates morphological traits (size, form, and skeleton), dark grey indicates life history traits (reproduction), white indicates behavioural traits. The definitions of each trait name can be found in chapter 3.

Trait	Modality	Modality definition	Reason for inclusion
Size	S1	Less than 1cm	Size is indicative of energy flows, secondary and primary production, sensitivity to disturbances, and is a proxy for fecundity.
	S2	1cm to 5cm	
	S3	5cm to 10cm	
	S4	10cm to 30cm	
	S5	30cm to 50cm	
	S6	More than 50cm	
Body form	BF1	Globulose	Provides information on diversity of the system. As a functional trait body form is indicative of energy flows and vulnerability.
	BF2	Vermiform or elongated	
	BF3	Dorso-ventral compressed	
	BF4	Laterally compressed	
	BF5	Upright	
	BF6	Pisciform (Fish-shaped)	
	BF7	Branching	
Skeleton	SK1	Calcareous	Indicator of susceptibility to both physical disturbances and changes in chemical and pH levels.
	SK2	Siliceous	
	SK3	Chitinous	
	SK4	Cuticle or Cartilaginous	
	SK5	None	
Reproduction	R1	Asexual	Reproductive method indicates the ability to recover from damage. It also influences recolonisation potential.
	R2	External fertilisation	
	R3	Internal fertilisation	
	R4	Brooding	
Living Habit	LH1	Free living	Provides information on diversity of the system. Functionally living habit is indicative of energy flows and vulnerability.
	LH2	Crevice dwelling	
	LH3	Tube dwelling	
	LH4	Burrowing	
	LH5	Epi/endo zoic/phytic	
	LH6	Attached	
Movement	MV1	Sessile	Indicative of energy flows and ability to escape physical and chemical changes. Influences recolonisation potential.
	MV2	Burrower	
	MV3	Crawler	
	MV4	Swimmer	
Feeding method	FH1	Deposit feeder	Determines nutrient cycling and energy flows. Additionally indicates production and sensitivity to disturbances.
	FH3a	Active filter feeder	
	FH3p	Passive filter feeder	
	FH4	Opportunist or scavenger	
	FH5	Predator	
	FH6	Parasite	
	FH7	Grazer	
Substrate affinity	SA1	Soft	Not included in many trait studies, it indicates restrictions for recovery. A detailed explanation is given in the text.
	SA2	Hard	
	SA3	Biological	
	SA4	None (Hyperbenthic)	

4.3.3 Combined RLQ and Fourth-Corner Analyses

All statistical analyses were conducted using R (R Core Team, 2022). The observations of taxa (**L**), represented as densities, were fourth-root transformed prior to any analysis. The environmental variables representing longitude and latitude were not included in the combined RLQ and fourth corner analyses, as this method does not allow for this. As required by the method all other environmental

variables were standardised to a mean of zero and a variance of one.

The fuzzy coded trait matrix ($\mathbf{Q}$) was converted to proportional data. In order to correct for missing trait data, this conversion was performed using the ADE4 package (Chessel et al., 2004; Dray and Dufour, 2007; Dray et al., 2007; Bougeard and Dray, 2018; Thioulouse et al., 2018). Missing data are accounted for by assigning the average value of the corresponding known modalities to each modality within the missing trait.

In order to prepare the data for an RLQ analysis, a correspondence analysis was performed on the $\mathbf{L}$ matrix, while the $\mathbf{Q}$ and $\mathbf{R}$ matrices were each subjected to principal coordinate analysis. An RLQ analysis was performed using the results of these ordinations. The significance of the model was tested for models 2 and 4 using Monte-Carlo tests with 4999 permutations.

The results of the RLQ analysis were subjected to a fourth-corner analysis, testing the associations between the traits and the RLQ scores that relate to the environmental gradients. Thus, both trait and environmental associations were linked to the axes of the RLQ analysis and the significance of their bivariate associations was tested by the fourth-corner methods.

Since the fourth-corner method is used to test the association between traits and the RLQ scores, p-adjustments were required to reduce the type I errors. The p-values were adjusted using the false-discovery rate (FDR). The FDR method is less conservative than some of its counterparts, resulting in increased power (Benjamini and Hochberg, 1995).

The plotting method for the results of the combined analysis was adapted from Sutton et al. (2021), as these graphs were the most readily interpretable. Additionally, since Sutton et al.'s (2021) plotting routine utilised ggplot2 (Wickham, 2016), the method was readily adaptable to customised formatting.

4.3.4 CWM-RDA Methods

As in the combined RLQ and fourth-corner analysis, the fuzzy coded trait table ($\mathbf{Q}$) was converted to a proportional 0 to 1 scale, with missing information included as averages. This trait table was combined with the fourth-root transformed species observation table ($\mathbf{L}$), using equation 4.2. The $\mathbf{LQ}$ table representing the community was standardised again, so that for every video sequence, the trait modalities for each trait summed to 1.

An RDA was performed on $\mathbf{LQ}$ and $\mathbf{R}$ in order to investigate the relationship between the environment and the CWM values. The environmental data used were standardised, excluding longitude and latitude. The effect of longitude and latitude were considered as conditions in the RDA. The variance inflation factor (VIF) was used to detect for multicollinearity. This test specifically detects multicollinearity, which can be present even after pairs of correlated variables have been removed. A VIF value of 10 was used as a cut-off for the presence of multicollinearity (O'Brien, 2007). AIC stepping (Venables and Ripley, 2002) was used to remove unnecessary variables; the significance of the remaining variables was analysed by ANOVA.

4.3.5 Functional composition

The functional compositions of each of the nine reefs were calculated. This was done by summing the species observations for each video sequence on each reef, producing an **L** matrix for the reefs. The data were fourth-root transformed, and the community weighted means were calculated.

The resulting **LQ** matrix was visualised via radar plots using the ggradar package (Bion, 2022). Since the **LQ** matrix represents the proportionate representation of each trait modality within each trait on each reef, the graphs, combined with the raw data in the matrix, were analysed to identify patterns.

4.4 Results

4.4.1 Combined RLQ fourth-corner

The fourth-corner test, performed on the data prior to combined analysis, indicated no significant relationships between the trait modalities and environmental variables (FDR adjusted $p < 0.086$, 9999 permutations). It is worth noting that the relationships for which the adjusted p-value was 0.086 were negative associations between gradient and burrowing and dead *Lophelia* and burrowing. This non-significant relationship was better expressed in the combined RLQ and fourth-corner method.

The RLQ analysis was found to be significant for both models 2 and 4 (model descriptions in figure 4.2, $p < 0.001$ and $p < 0.05$, respectively, 4999 permutations), and the relationship between the environmental gradients and biological traits composition was globally significant (FDR adjusted $p = 0.043$, 4999 permutations, inertia = 1.672)(table 4.2). The first two axes accounted for 84.5% of the cross-variance between the traits and the environment; when the third axis was included, 95.7% of the variance was accounted for (table 4.2).

Table 4.2: Summary of the RLQ analysis, showing the total inertia of the RLQ analysis, the eigenvalues of each RLQ axis, and the percentage of the total inertia projected on each axis. The grey text represents axes that are not displayed in the combined RLQ fourth-corner analysis. The eigenvalue decomposition sections indicate the eigenvalue (eig), covariance (covar), standard deviation of R and Q (sdR, sdQ), and the correlation (corr) for the scores projected on RLQ axes 1 and 2. The inertia and coinertia tables indicate the inertia projected onto the RLQ axes (inertia), the maximum inertia of the PCA ordinations for **R** and **Q** (max), and the ratio between these two measures (ratio). The correlation sub-table indicates the correlation that is projected onto the RLQ axes (corr), the maximum correlation of the CA ordination for **L**, and the ratio between these two measures (ratio).

Total inertia:					1.672
Eigenvalues:					
Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	
1.121	0.291	0.187	0.039	0.017	
Projected inertia (%):					
Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	
67.076	17.425	11.199	2.311	1.018	
Eigenvalues decomposition:					
	eig	covar	sdR	sdQ	corr
Axis 1	1.121	1.059	1.607	2.013	0.327
Axis 2	0.291	0.540	1.482	1.513	0.241
Inertia & coinertia R (dudiR):					
	inertia	max	ratio		
Axis 1	2.582	3.164	0.816		
Axes 1 & 2	4.778	5.260	0.908		
Inertia & coinertia Q (dudiQ):					
	inertia	max	ratio		
Axis 1	4.054	8.596	0.472		
Axes 1 & 2	6.343	13.810	0.459		
Correlation L (dudiL):					
	corr	max	ratio		
Axis 1	0.327	0.646	0.507		
Axis 2	0.241	0.573	0.420		

The majority of the variance (67.05%) was accounted for by the first axis (figure 4.3A), which had contributions from **live coral**, gradient, **dead *Lophelia*** (representing the coral skeleton part of the reef), **sandy mud**, and **pebble**. The massively 3-dimensional parts of the coral reef (**living coral** and **dead *Lophelia***), along with gradient, acted antagonistically to the two soft substrata (**sand** and **sandy mud**) and the unconsolidated **pebble** bottom type (figure 4.3A). Ecologically, this implies that **live coral**, gradient, and **dead *Lophelia*** have similar influences on traits, and that these influences are antagonistic to those of **sand** and **sandy mud** and **pebble**.

While **sand** was mentioned in connection with both **sandy mud** and **pebble** when describing figure 4.3A, it must be noted that **sand** and **sandy mud** were mutually exclusive at all but one subsample. Additionally, **sand** did not significantly associate with either of the first two projected axes (adjusted p-values: 0.101 and 0.836).

The fourth-corner analysis indicated that **coral rubble**, mean depth, **cobble**, and **boulder** were sig-

nificantly associated with axis 2 (figure 4.3A). The coral rubble bottom type acted in the negative direction of axis 2, opposite to mean depth, cobble, and boulder. There were no significant trait associations with axis 2 ($p > 0.05$). The low projected inertia on axis 2, coupled with the lack of significant trait associations, hinders a sound ecological implication of the antagonistic relationship between these environmental factors.

Along the first axis, affinity for hard substrate and passive filter feeding were notably more associated with the living and dead parts of the reef. However, these associations were not significant. The only significant association was between the positive direction along axis 1, associated with sandy mud and pebbles, and the living habit of burrowing (LH4) (figure 4.3B). The burrowing living habit is separate from the burrowing movement method (MV2), which was not significantly associated with either of the axes. Thus, living coral, dead *Lophelia*, and gradient tended to have similar influences on biological traits. Traits for passive filter feeding, and a preference for hard substrata (which coral reefs tend to be found on), were associated with these environmental variables. This was contrasted by the traits associated with sandy mud and pebble, with which burrow dwelling taxa are significantly associated.

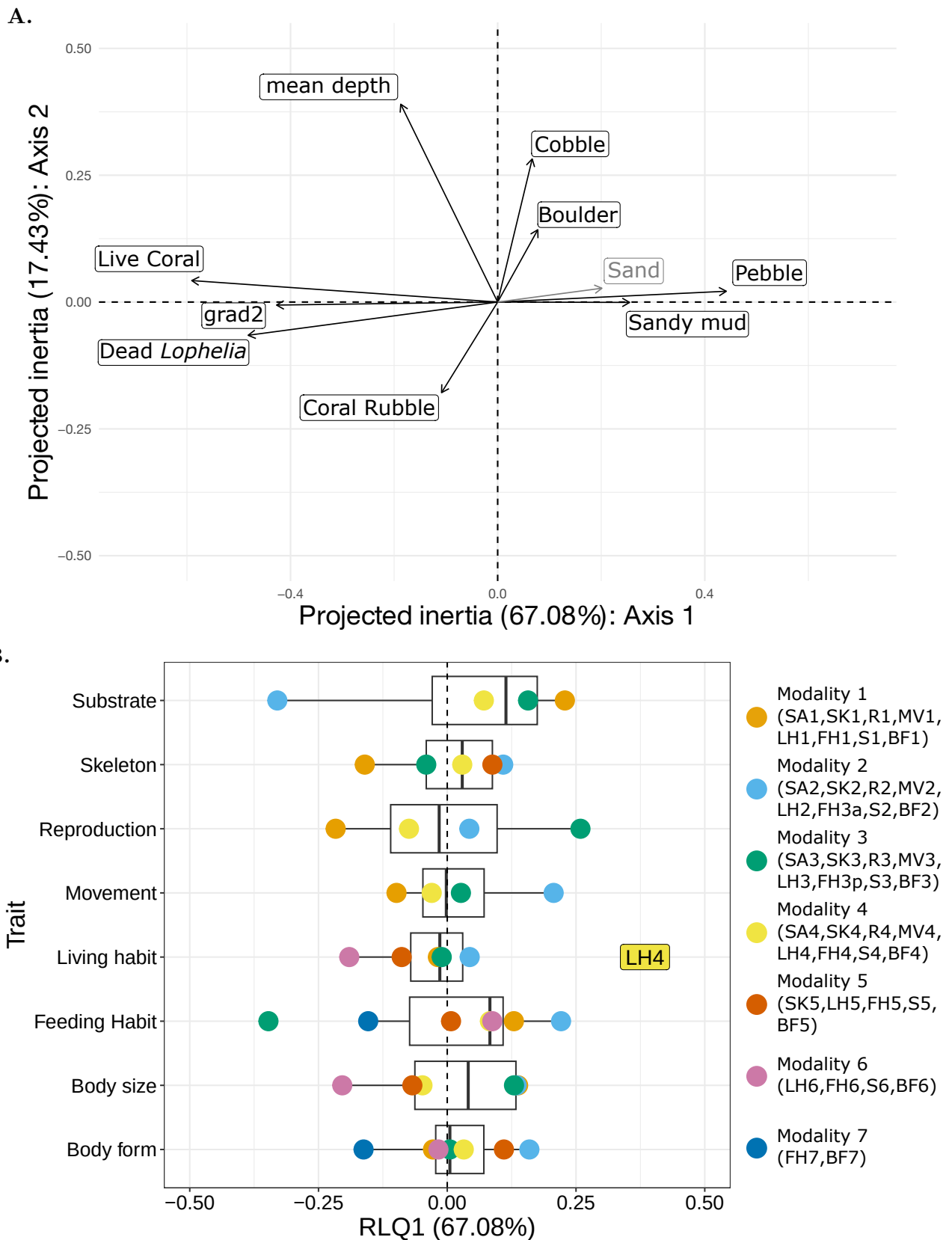


Figure 4.3: Graphical representation of the results of the combined RLQ fourth-corner analysis. A) represents the relationship between the environmental variables and the RLQ axes. Significant variables ($p < 0.05$) are shown in black, while non-significant variables are displayed in grey. B) represents the relationship of the trait modalities with the first axis, which is displayed as the x-axis of this figure. The trait modalities are grouped by trait. Trait modalities that significantly ($p < 0.05$) associate with axis 1 are labelled, while non-significant modalities are indicated by a coloured dot.

4.4.2 CWM-RDA

The variance inflation ratios (VIF) for the full CWM-RDA suggested multicollinearity ($vif > 10$) for many of the environmental variables. The following variables were retained after AIC stepping: mean depth, longitude, latitude, and the percentage cover of the substrata, *live coral*, *coral rubble*, *pebble*, and *dead Lophelia*. The new VIF values indicated no multicollinearity.

The reduced model was significant (ANOVA: $df = 5, 51$, $F = 8.340$, $p \leq 0.001$), with an adjusted R^2 value of 0.330. Longitude and latitude were considered to be conditional variables and accounted for 19.48% of the observed variance. The non-conditional explanatory variables accounted for 36.22% of the variance, leaving 44.30% unexplained.

Table 4.3: Results of the reduced CWM-RDA model. Columns represent names of environmental variables, their values on the first and second axes of the RDA (RDA1 and RDA2 respectively), the F statistic (F), and the associated p-value $Pr(> F)$ (***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$).

Environmental variable	RDA 1	RDA 2	F	$Pr(> F)$	
Live Coral	0.616	-0.340	10.042	0.001	***
Mean depth	0.388	0.765	11.487	0.001	***
Coral Rubble	0.196	-0.302	5.375	0.003	**
Pebble	-0.328	-0.103	3.221	0.022	*
Dead <i>Lophelia</i>	0.633	-0.098	2.586	0.046	*

The positive RDA1 axis was associated with the living and dead parts of the cold-water coral reefs, while the negative RDA1 axis was associated with *pebbles* (table 4.4). Deep video sequences were associated with the positive RDA2 axis. The trait modalities for soft bottom type, burrowing living habit and movement habit (SA1, MV2 and LH4 receptively) were situated opposite the coral substrata (figure 4.3A), implying that this trait composition associated with the absence of these substrata. The active filter feeders (FH3a), a trait modality that in this dataset was dominated by Porifera, was associated with the area between the *pebble* and *coral rubble* environmental factors (figure 4.3A), and the siliceous skeletal modality (SK2) was located nearby. The modalities for attached and sessile (LH6 and MV1) were associated in the direction of the coral substrata, as was the modality for hard substrate preference (SA2). Finally, there was a group of associated trait modalities located in the positive RDA2 direction from the *dead Lophelia* factor; these represented the passive filter feeders with a branching body form and a calcium skeleton (FH3p, BF7, SK1). These traits are typical of corals.

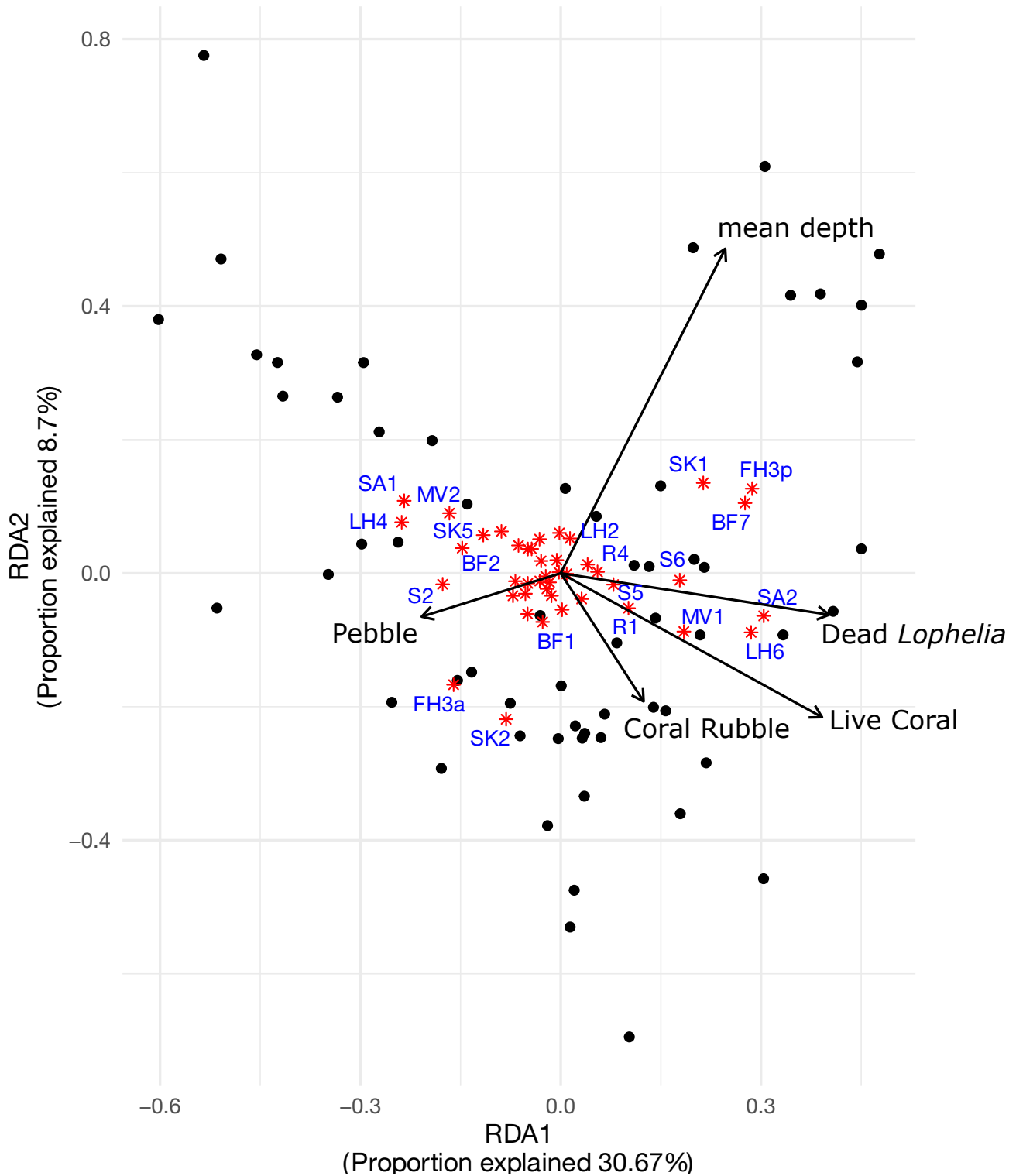


Figure 4.4: The results of the community weighted means redundancy analysis (CWM-RDA). The first two axes are displayed, accounting for 39.46% of the variance. Vectors representing the conditional factors (longitude and latitude) are not plotted. The black dots represent video sequence, while the red stars are the trait modalities (names plotted in blue where graphically possible). The arrows represent the environmental factors, labelled at the arrow head.

4.4.3 CWM profiles

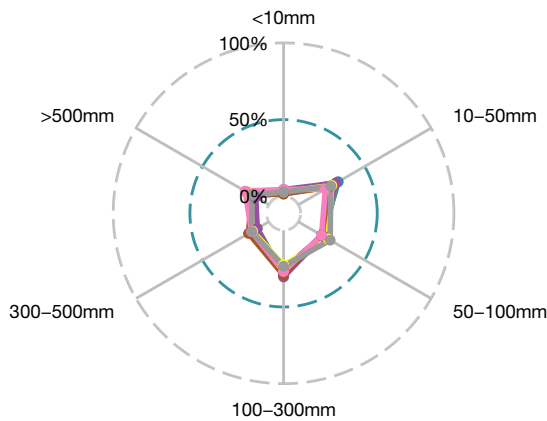
The community weighted representation of size modalities were similar across all nine of the sampled reefs (figure 4.5A). The community weighted trait composition of the reefs analysed in this chapter

showed that calcareous skeletons were more common than siliceous, while chitinous skeletons, cuticles or no skeleton were uncommon on all the reef sites (figure 4.5B). There is variance between the percentage contribution of calcium skeletons and silicon skeletons to the community weighted representation of skeleton modalities for each reef. In particular, the calcium-based skeletons account for more than 50% of the expressed skeleton types on reef R1353.

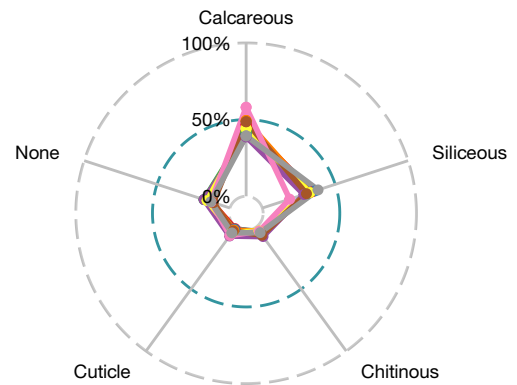
The greatest proportion of the community weighted representation of body form modalities on all reefs was dorso-ventral compressed taxa (figure 4.5C). The second most common body form modality differed between globulose, branching, and upright depending on the reef. The laterally compressed body form was the least common body form modality on all nine reefs. Colonial taxa account for more than 48% of the community weighted representation of the sociability trait on all nine reefs (figure 4.5D).

External fertilisation represented the greatest proportion of the community weighted representation of reproductive methods on all the reefs (figure 4.5E). This was either followed by brooding (reefs R0948 and R1130) or internal fertilisation (all other reefs). In all cases, external fertilisation, internal fertilisation, and brooding accounted for between 20 and 43% of the community weighted representation of reproductive methods for each reef. Internal fertilisation was the least common method on all reefs, accounting for no more than 19% of the community weighted representation of reproductive methods on any given reef. The community weighted representation of larval development modalities were similar between the reefs, with lecithotrophic larval development representing more than 50% of the community weighted representation of this trait on all reefs (figure 4.5F). Benthic and planktotrophic larval development accounted for similar proportions of the community weighted representation of larval development modalities across the different reefs (within 7%), although which of these two modalities was more prevalent differed between the reefs.

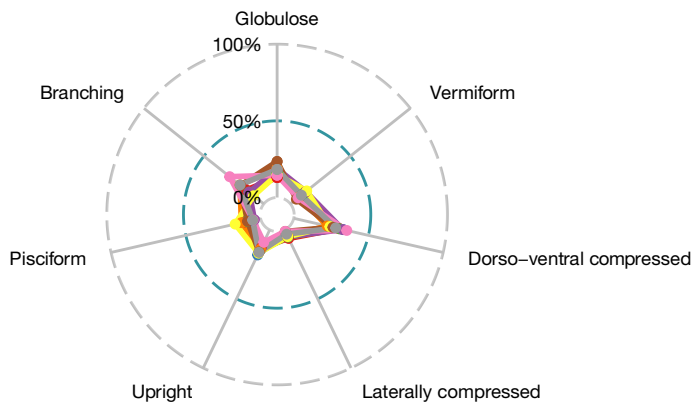
A. Size



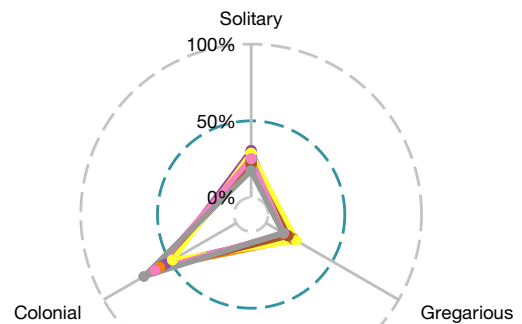
B. Skeleton



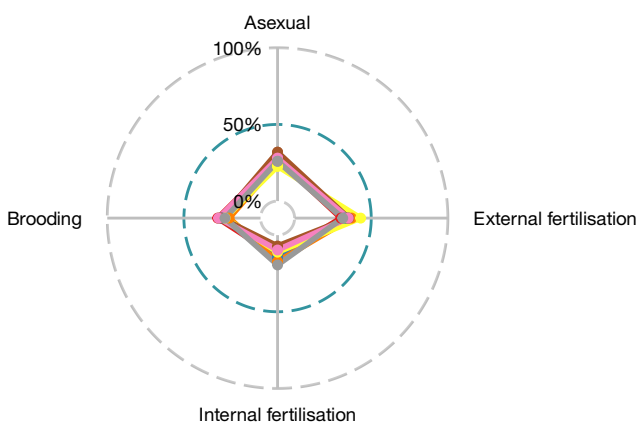
C. Body form



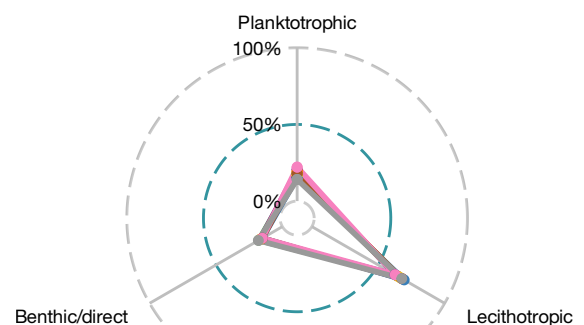
D. Sociability



E. Reproduction



F. Larval development



Reefs

● R0948 ● R0968 ● R1108 ● R1243 ● R1562 ● R0960 ● R0994 ● R1130 ● R1353

Figure 4.5: Radar plots showing the proportionate representation of the community weighted mean values of each trait modality on the nine reefs. Modalities are grouped by their trait, A) Size, B) Skeleton, C) Body form, D) Sociability, E) Reproduction, and F) Larval development. The locations and average environmental variables for each reef can be found in chapter 2. Reefs with similar values are plotted over each other, thus not all reefs may be visible. This method allows for differences to be detected, while similarities are represented by over plotting.

The attached living habit makes up the greatest proportion of the community weighted representation of living habit modalities on all nine reefs (4.6A). The second greatest proportion on all nine reefs are free living taxa, followed by burrowing. Tube and crevice dwelling taxa account for no more than 6 and 7% of the community weighted representation of living habit modalities on the reef sites. The more common of the two differs between reefs. Taxa that live on or in other organisms accounted for

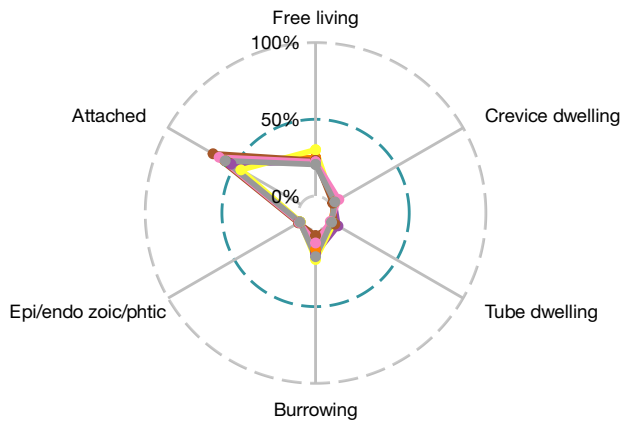
less than 1% of the the community weighted representation of living habit modalities on seven of the nine reefs and less than 1.8% on reefs R1243 and R1353. It should be noted that, while the attached modality was the most common, the actual proportion of the community weighted representation of living habit modalities accounted for by this modality varied between the reef sites.

Sessile taxa dominated the community weighted representation of movement modalities on the nine reefs, in all cases accounting for more than 50% (>60% on all reefs other than R1130) of the community weighted representation of movement modalities (figure 4.6B). The second most common modality on the reef sites was either swimming (R0948, R1108, R1130, R1353) or crawling (R0960, R0968, R0994, R1243, R1562), depending on the reef. The proportion of crawling modality was greater than burrowing on all reefs. However, on R0994 burrowing was more common than crawling.

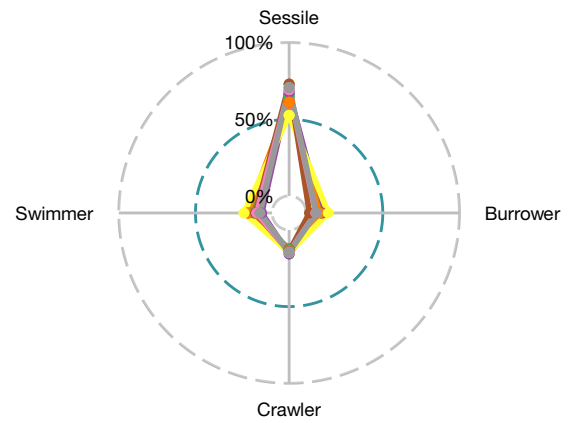
The community weighted representation of feeding modalities on the reefs were the most variable of all the trait modalities investigated. On eight out of the nine reefs, active filter feeding accounted for the largest proportion of the community weighted representation of feeding modalities. On one reef (R1353) passive filter feeding was more common than active filter feeding (figure 4.6C). The community weighted representation of active and passive filter feeders was found to be negatively related ($p=0.001$, adjusted $R^2=0.74$). Predation represented a larger proportion of the community weighted representation of feeding modalities than passive filter feeding on five of the reefs. On all reefs, active filter feeding, passive filter feeding, and predation were the top three feeding methods. There was variability between the reefs as to the fourth most common feeding habit, this either being deposit feeding or scavenging. However, in all cases, deposit feeding was more common than grazing. The least common feeding habit was parasitism, accounting for less than 0.5% of the community weighted representation of feeding habit modalities at each reef site.

Preference for hard substrata accounted for more than 45% of the community weighted representation of substratum affinity modalities at each reef site (figure 4.6D), followed by preference for soft substrata. On all but one of the reefs (R1353) the community weighted representation of substratum affinity modalities showed a greater proportion of preference for biological substrata than a preference for no substratum (hyper-benthic with no preferences).

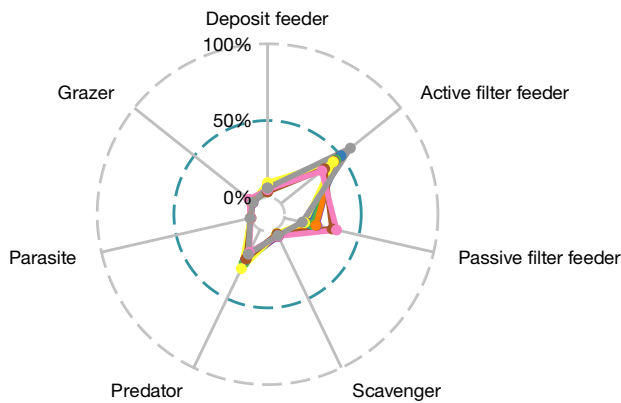
A. Living habit



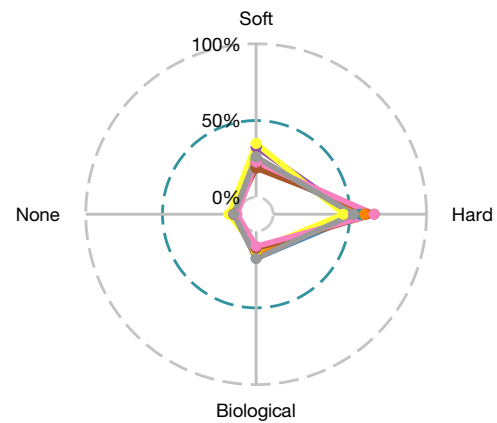
B. Movement



C. Feeding habit



D. Substratum affinity



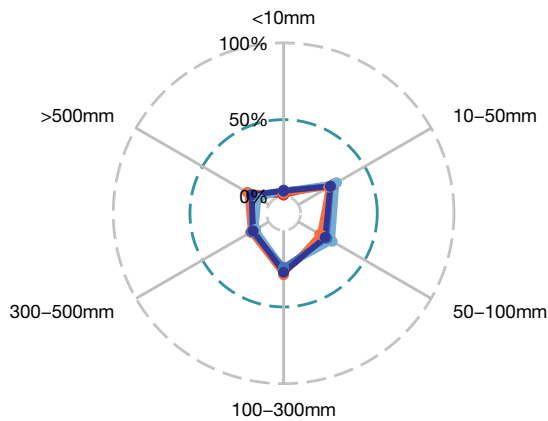
Reefs

● R0948 ● R0968 ● R1108 ● R1243 ● R1562 ● R0960 ● R0994 ● R1130 ● R1353

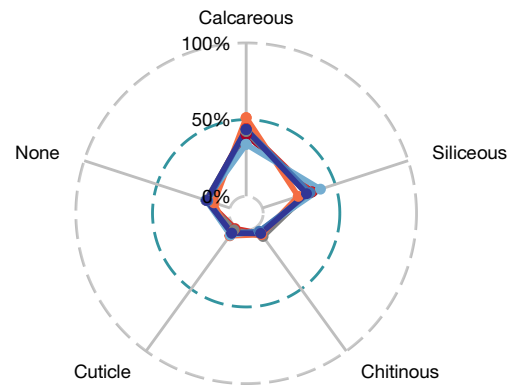
Figure 4.6: Radar plots showing the proportionate representation of the community weighted mean values of each trait modality on the nine reefs. Modalities are grouped by their trait, A) Living habit, B) Movement, C) Feeding habit, D) Substratum affinity. The locations and average environmental variables for each reef can be found in chapter 2. Reefs with similar values are plotted over each other, thus not all reefs may be visible. This method allows for differences to be detected, while similarities are represented by over plotting.

The trends identified in community weighted representation of different modalities based on areas that had different substrata dominance had similar ranges to those for the different reef sites. The functional composition of reef R1353 consisted of a lot of calcium-based skeletons, which is not reflected in the bottom type results. Rather, all substrata had similar levels of calcium-based skeletons, although they were slightly more common on sites where more than 30% of the substratum was *dead Lophelia* (figure 4.7B).

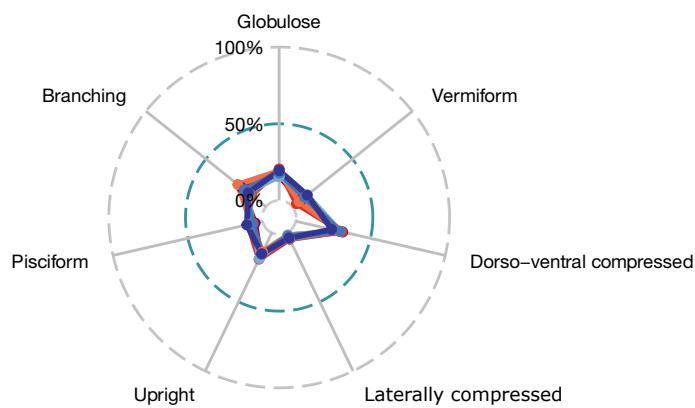
A. Size



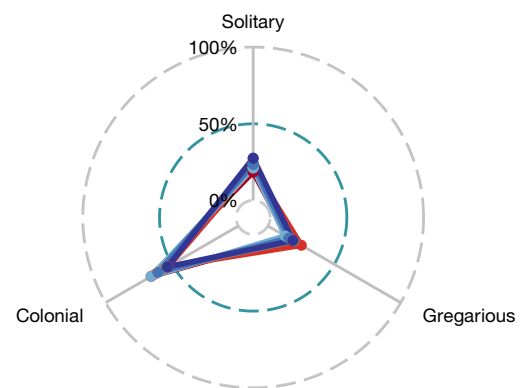
B. Skelton



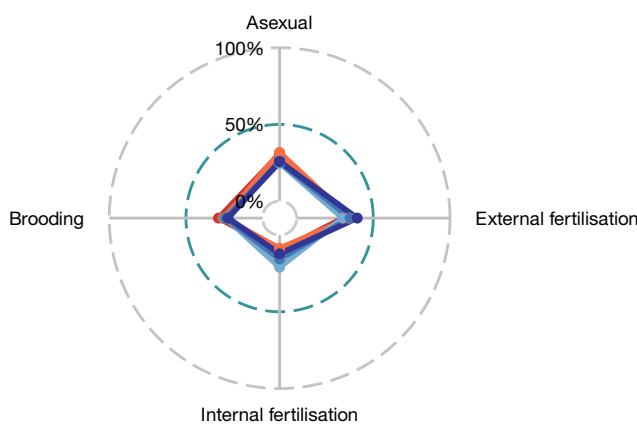
C. Body from



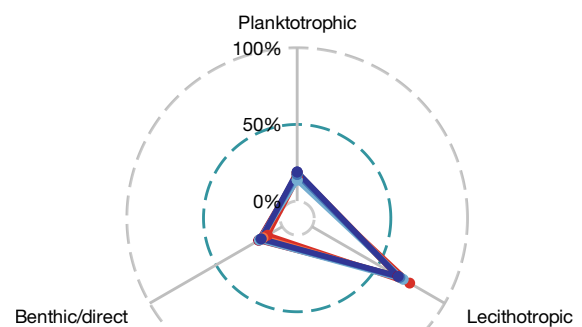
D. Sociability



E. Reproduction



F. Larval development



● Coral Rubble ● Live Coral ● Dead *Lophelia* ● Hetrogenous ● Sand ● Pebble ● Sandy mud

Figure 4.7: Radar plots showing the proportionate representation of the community weighted mean values of each trait modality based on the most common substratum present. Warm colours represent coral-based substrata, while cold colours represent the unconsolidated substrata. Modalities are grouped by their trait, A) Living habit, B) Movement, C) Feeding habit, D) Substratum affinity. The locations and average environmental variables for each reef can be found in chapter 2. Substratum types with similar values are plotted over each other, thus not all substratum types may be visible. This method allows for differences to be detected, while similarities are represented by over plotting.

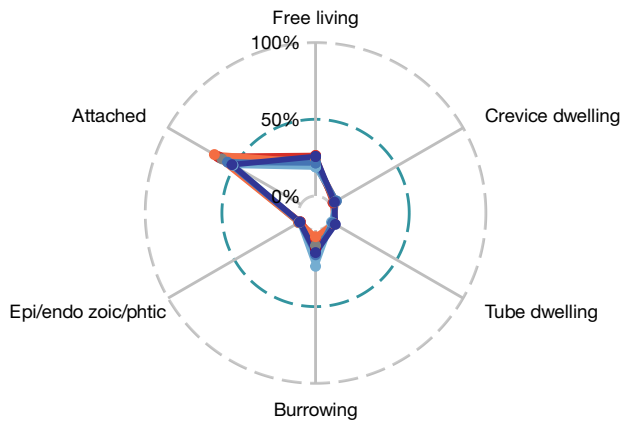
The attached living habit accounted for more of the community weighted representation of living habit modalities on the coral-based substrata than on the sand- and pebble-based substrata. The inverse is true for the burrowing living habit (figure 4.8A). In all cases, though, attached accounted for more of the community weighted representation of living habit modalities than burrowing. This was true when

comparing the different reef sites as well (figure 4.6B). This trend is visible in the burrowing movement type, which accounted for less of the community weighted representation of movement modalities in video sequences, where the most common substratum type was coral-related (figure 4.7B).

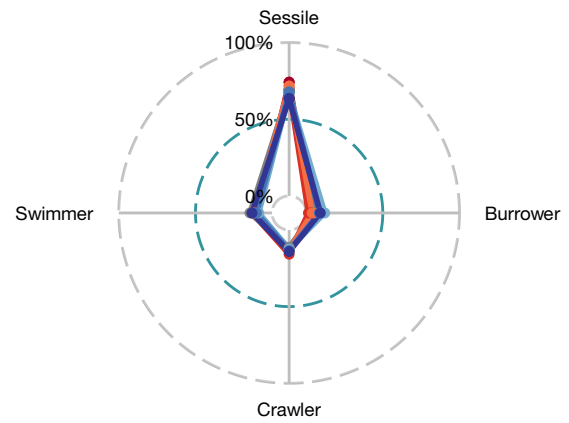
Passive filter feeding accounted for a notably higher proportion of the community weighted representation of feeding habit modalities in video sequences where the most common substratum was *dead Lophelia* (figure 4.8C). The community weighted representation of the passive filter feeding modality in video sequences where the most common substratum was *sand*, was notably low. However, these video sequences had the highest community weighted representation of active filter feeding. This represented a shift between the different forms of filter feeding in video sequences where *sand* is the most common substratum. The trend is further highlighted by noting that the lowest community weighted representation of active filter feeders was found in video sequences where the most common substratum type was *dead Lophelia*.

As was the case when the community weighted representation of substratum affinity modalities were considered for the different reef sites, preference for hard substrata accounted for more than 45% of the community weighted representation of substratum affinity modalities in all video sequences, regardless of the most common substratum type (figures 4.6D and 4.8D). However, all video sequences where coral-related substrata were the most common, had the trait modality for preference for hard substrata. This accounted for more than 58% of the community weighted representation of substratum affinity modalities, which is notably larger than on the non-coral related substrata (4.8D). Preference for soft substrata accounted for more of the community weighted representation of substratum affinity modalities in video sequences where the non-coral related substrata were the most common, compared to video sequence where the coral-related substrata were the most common.

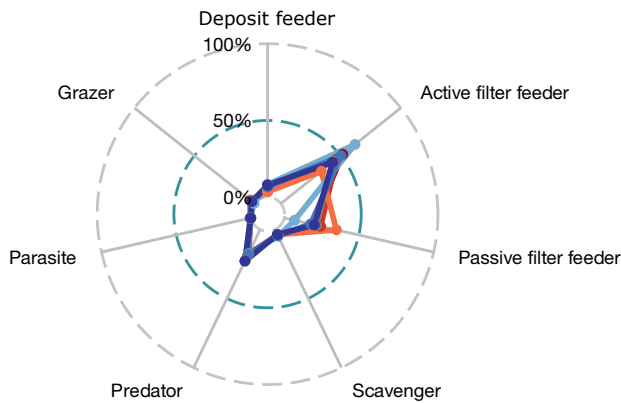
A. Living habit



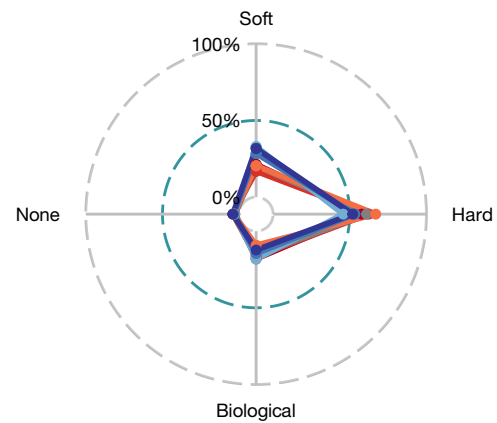
B. Movement



C. Feeding habit



D. Substratum affinity



Most common substratum

● Coral Rubble ● Live Coral ● Dead *Lophelia* ● Heterogenous ● Sand ● Pebble ● Sandy mud

Figure 4.8: Radar plots showing the proportionate representation of the community weighted mean values of each trait modality based on the most common substratum present. Warm colours represent coral-based substrata, while cold colours represent the unconsolidated substrata. Modalities are grouped by their trait, A) Living habit, B) Movement, C) Feeding habit, D) Substratum affinity. The locations and average environmental variables for each reef can be found in chapter 2. Substratum types with similar values are plotted over each other, thus not all substratum types may be visible. This method allows for differences to be detected, while similarities are represented by over plotting.

4.5 Discussion

The biological trait analysis indicated that the traits were similar among the different cold-water coral reef sites. Reef site selection for this chapter was based on addressing the primary hypothesis: That different cold-water coral reefs have similar traits. Every 100m video sequence used in this study was within 400m of a cold-water coral reef section, containing either coral rubble, living coral, or dead coral. The 400m distance was only present in a single video sequence, the majority of the video sequences contained some coral, and those without were typically within 100m of a coral containing video sequence. As such, the results indicate the influence of environmental gradients in close vicinity to cold-water coral reefs.

The biological trait for living in burrows was found to be significantly affected by the environmental variables considered. The burrowing living habit was associated with increased prevalence of the soft or loose substrata. This was expected, as a soft or loose bottom type is required for burrowing (Dorgan,

2015). While the burrowing living habit was significantly associated with these substrata, burrowing as a movement type was not. Ecologically this makes sense, since many organisms that are capable of burrowing are also capable of other movement types. This is evident by the fact that some organisms that live or hide in burrows leave their burrows to feed (e.g. Mantis shrimp (deVries et al., 2012), *Callianassa subterranea*, *Jaxea nocturna*, and *Upogebia stellata* (Nickell and Atkinson, 1995)). While, others utilise burrowing primarily as a means to ambush or hide from predators (e.g. *Lacunicambarus thomai* (Graham et al., 2022)). The organisms capable of burrowing and other movement types were likely not engaging in burrowing behaviour when observed on the reef.

The results of the CWM analysis, which included longitude and latitude as additional explanatory variables, supported the findings of the RLQ fourth-corner method. The burrowing life history was associated with the absence of cold-water coral coverage. Additionally, the CWM analysis indicated an association between the burrowing movement type and reduced reef-related substrata. While the combined RLQ fourth-corner method did not highlight any trait communities, the results of the CWM-RDA suggested that traits associated with sponges (siliceous skeletons, active filter feeders, and upright or globulose body forms) were more common on pebble and coral rubble substrata. The collection of traits that one would associate with corals (namely; passive filter feeder, calcareous skeleton, branching body form) is also grouped together in the CWM-RDA results (figure 4.4).

The cold-water coral reef sites and their near surroundings contained similar traits. Burrow dwelling taxa were less common on the reef sites, which could suggest that bioturbation is reduced on cold-water coral reefs. Both vermiform and dorso-ventral compression body forms are associated with bioturbation (Degen and Faulwetter, 2019). The community weighted representation of body form modalities indicated the dorso-ventral compressed taxa as the prevalent common body form on all the reef sites. Furthermore, vermiform body forms represented a greater proportion of the community weighted representation of body form modalities in video sequences where non-coral related substrata were the most common, compared to those where coral substrata were the most common. Given the presence of nutrient recycling within the reef community (Rix et al., 2016; Maier et al., 2021), the role of bioturbation and resuspension on the reef fringes warrants further ecological investigation.

While mean depth, longitude, and latitude accounted for a more than 19% of the observed variance in trait communities, it seems that no trait community associated with the extreme values of these variables. The presence of depth as an explanatory factor was expected, as depth has been identified as a driver of differences in traits in both marine and riverine systems (Edegbene et al., 2021; Sutton et al., 2021). Furthermore, depth is a known driver of differences in species compositions on cold-water coral reefs (Milligan et al., 2016; Corbera et al., 2019).

It is ecologically interesting that the CWMs of traits are linked to the longitude and latitude of the video sequences. This suggests that the traits associated with the local species pool (local trait pool) still have an influence on the traits found on cold-water coral reefs. It implies that cold-water coral reefs likely act as aggregating sites for the local species, since variances in species and traits are accounted for by longitude and latitude. However, the axis on which the cold-water coral related substrata act in the CWM-RDA accounts for more variance than longitude and latitude. This suggests that the communities associated with cold-water coral reefs have similar traits to each other, as

a result of the presence of the coral-related substrata, with variance in these traits based on the local trait pool. This suggests functional similarities between the cold-water coral reefs.

Comparisons of the community weighted means for each reef, rather than each video sequence, highlight the similarities and differences between the traits expressed on the nine cold-water coral reefs. The prevalence of calcareous and siliceous skeletal traits present on the reef sites are likely linked to the prevalence of sponges and corals. However, calcium and silicon are fairly commonly expressed skeletal traits so little functional information can be drawn from this observation. It should be noted that external calcium based skeletons are sensitive to ocean acidification (Feely et al., 2004; Wood et al., 2008), which might indicate that the species found on cold-water coral reefs are at risk in addition to the corals themselves.

The trait modalities for branching body forms, attached life histories, and sessile movement were found to be associated with the coral-related substrata. These trait modalities are known to be associated with increased sensitivity to physical disturbances of the bottom (Thrush et al., 1998; Thrush and Dayton, 2002; Hewitt et al., 2011). The sessile and attached trait modalities were the most common community weight modalities associated with their respective traits in all video sequences. However, branching body forms were associated more with increased coverage of dead *Lophelia*. This was supported by the community weighted representation of body form traits, which indicated that branching body forms accounted for more of the modalities present in video sequences where dead *Lophelia* was the most common substratum compared to all other substrata. This indicated that the trait community associated with cold-water coral reefs, in addition to the reef itself, are sensitive to physical disturbance.

In addition to indicating sensitivity, branching taxa provide 3-dimensional structure. Thus, cold-water coral reefs, in addition to the presence of *L. pertusa*, appear to support taxa that provide additional structure to the reef. The dead *Lophelia* part of the reef is typically associated with increased diversity (Buhl-Mortensen et al., 1995; Buhl-Mortensen, 2017); both Buhl-Mortensen et al. (1995) and Freiwald (2002) note the presence of other Cnidaria within this zone. The presence of branching body forms on and within the dead *Lophelia* zone was in line with these studies. This was supported by the dominance of sessile and attached trait expression on the reef (figure 4.8), with attached being the dominant living habit on sites where the most common substratum type was related to coral.

The community associated with cold-water coral reefs appeared to be dominated by lecithotrophic larval development. Given the latitudes of the reefs and their depths, this was in line with “Thorson’s rule” (Thorson, 1950; Mileikovsky, 1971). According to this rule, lecithotrophic development and brooding are favoured with increasing depth and latitude. Planktotrophic larval development is uncommon on the cold-water coral reefs in this chapter. Given the depth component of “Thorson’s rule”, it is likely that planktotrophic larval development would be relatively uncommon even on cold-water coral reefs found at lower latitudes.

A negative linear relationship between the community weighted representation of the feeding trait modalities for the active and passive filter feeder modalities was detected. Reefs where active filter feeding was well represented, thus had low representation of the passive filter feeding trait. This trend

was also present when video samples were split based on their most common substratum type. This relationship likely represents differences in the dominance of corals and sponges. Since, almost all, Porifera are active filter feeders (Fish and Fish, 2011), while corals are passive filter feeders (van Oevelen et al., 2018a). The most notable example of this trend is in video sequences when the most common substrata was *dead Lophelia*, where the community weighted representation of the passive filter feeder modality was higher than for any other substratum. The structure of the dead reef zone is known to reduce local current flow and act as a sediment trap (de Haas et al., 2008). The dead coral framework has been described as a “filtration-recycling factory” (Maier et al., 2021). These conditions favour passive filter feeding. Passive filter feeding was not as strongly associated with the living part of the reefs, likely due to competition between *Lophelia* and other passive filter feeders and the presence of living tissue preventing colonisation of the coral matrix (Buhl-Mortensen et al., 1995; Freiwald and Wilson, 1998; Buhl-Mortensen et al., 2017b). The prevalence of active filter feeders on the reef sites should be viewed in the context that the passive filter feeder *L. pertusa* was considered to be a bottom type in this study. The dominance of filter feeders on the reef sites suggested that the reef sites had access to particulate organic matter that could be filtered. Deposit feeders and grazers were likely attracted to the reef to feed on organic matter trapped between the branching structure of the reef corals. Predators might be attracted to the reef to feed on these other organisms, or for shelter from larger predators.

Cold-water corals require a hard substratum for attachment. Thus, it stands to reason that the majority of reef species would share this substratum preference (Roberts et al., 2006). The presence of taxa with a preference for soft substratum indicates one of three possible scenarios: massive dominance of these taxa on the soft bottom near the edges of the coral reef, taxa that have a preference but do not require soft bottoms benefiting more from the reef than from being on a soft bottom, or species that actually prefer hard bottoms, but were only identified at a taxonomic level where bottom preference was split between hard and soft. The latter scenario would explain the fact that, even on sites where the substratum type was coral-related, around 15% to 20% of the functional composition related to a preference for soft substrata.

Future comparison between the composition of reef sites from a wider geographic range, in addition to comparisons between biological and abiotic reefs, will allow for more functional conclusions to be drawn.

4.5.1 Lessons Learned Along the Way

Research produces not only results, but also a chance to reflect on the methods used. This biological trait analysis highlighted two points on which to reflect.

4.5.1.1 Sampling Method Matters

The distinction between what an organism is capable of doing and what an organism is doing can be very important in the context of biological trait analysis. In many botanical biological trait analyses, continuous trait values are used, while in the marine sphere, traits tend to be categorical or fuzzy coded (Törnroos, 2014). When continuous traits are used, the actual value of the trait is sometimes measured (e.g. tree height, Garnier et al., 2007). The bottom dwelling fish, *Brosme brosme*, was found to be generally larger in the waters surrounding cold-water coral reefs (Kutti et al., 2014); this trend

was not possible to analyse using species assigned trait data, since size range is based on population averages rather than observed sizes. When using grabs, size can be measured; however, behavioural traits must be inferred. When working with video footage, expressed behavioural traits in addition to morphological traits can be recorded, allowing the trait analysis to distinguish the actual expression of traits.

The use of video footage is a double-edged sword; the method is non-destructive but come at the cost of certainty in terms of species identification compared to grabs (Flannery and Przeslawski, 2015; Beisiegel et al., 2017). Additionally, video footage tends to capture mainly megafauna (> 1 cm) and the upper end of macrofauna, since larger organisms are easier to spot and identify from a distance. Grabs, while offering more certainty in terms of species identification and better coverage of macrofauna, come at the cost of smaller sampling sites and poor coverage of hyper-benthic organisms (Flannery and Przeslawski, 2015). Biological trait analyses have been conducted on grab and dredge data (e.g. Sutton et al., 2021) and on video or photography data (e.g. Dong et al., 2021). No clear comparison of trait coverage between the methods has been conducted.

The combined RLQ and fourth-corner method appeared to be relatively sensitive to small changes to the trait definitions. In order to quantify trait biases based on sampling methods, a comparison between trait analyses performed on video-based observations and grabs would be advisable. Likewise, such a comparison should investigate the impact of including observed behavioural traits rather than potential traits. Given the nature of the statistical method, this might require careful planning, as it would potentially result in separation of species based on their behaviour. A better approach might be to assign fuzzy coded values to the observed traits, proportionate to their observed rate. The precedent for such studies is well established in terms of community ecology (e.g. Flannery and Przeslawski, 2015).

4.5.1.2 Selection of Traits is Critical

Trait selection plays a crucial role in any biological trait analysis (de Juan et al., 2022). In order for the conclusions to be functional, the traits selected must be functional (Violle et al., 2007). The traits selected for the analysis are often driven by the research question (de Juan et al., 2022). Additionally, there are limitations to trait selection, driven by data availability and statistical methods (de Juan et al., 2022). Not every species has been described (Costello et al., 2013; Moura and Jetz, 2021), and the majority of undescribed species are marine (Mora et al., 2011). A species description does not mean that the biological traits of the species are known. For instance, the reproduction methods of Porifera families and orders are described by Ereskovsky (2018), yet the larval types of ten groups remain unknown. Reproduction and larval development appear to be among the last biological traits described for many species; this is likely related to limitations in observing these traits. Seemingly fundamental traits, such as feeding method and diet (which are related), are less certain for many species than previously thought (e.g. Ericsson and Hansson, 1973; Zintzen et al., 2011; Bouveroux et al., 2014; Martinez et al., 2016; Sampaio et al., 2018).

Trait overlap can render model 4 (figure 4.2) not significant in any system where there are many species with similar traits, if these traits are chosen for biological analysis. This is ecologically valid if there is no difference in the functional traits of these species. Some trait modalities are highly

correlated, and care should always be taken to ensure that this correlation is not linked to all modalities between traits. For example, attached organisms are almost always going to be sessile, but sessile organisms are not always attached, and movement type and living habit are not certain to be correlated across the other modalities.

The results of biological trait analysis in this chapter were influenced by similarities between the Porifera taxa and the coral taxa. As mentioned above, excessive trait overlap can render fourth-corner analyses not significant. The Arctic Traits Database (Degen and Faulwetter, 2019) makes no distinction between active and passive filter feeders. In a system where the majority of observed taxa are filter feeders, this leads to a lot of similarity. In this chapter, the system was dominated by Porifera and corals. The vast majority of Porifera obtain nutrition by filter feeding and reproduce both asexually and sexually, producing a lecithotrophic larva. Additionally, all Porifera are attached, sessile and colonial. Like the Porifera, corals are also attached, sessile, filter feeders. However, Porifera and corals are not functionally similar across all levels.

There are two approaches for dealing with this grouping together of taxa. Within reason, functionally redundant or very common traits that group the species together can be removed from the analysis. Mathematically, if the species are truly functionally similar, and only one or two traits are removed, resulting in the remaining traits still being functional, then model 4 would still be not significant. Another approach is to create finer trait definitions, for example the distinction between surface and subsurface deposit feeding used in The Arctic Traits Database (Degen and Faulwetter, 2019). There is a functional difference between active and passive filter feeders, but this distinction is unnecessary in a system where filter feeding is not the most common feeding method. By acknowledging this distinction, the overall results of the biological traits analysis were improved. Thus, it should be reiterated that biological traits are meant to “group” species with similar functions together, allowing understanding of the links between the environment and ecosystem functioning without having to identify all taxa. When the sampling results in a wide range of different species, it is possible to “over-clump” traits, such as describing branching corals or sponges as upright rather than giving them their own group. Statistically, heavy simplification of traits would reduce the significance of the model, while over splitting the trait groups so that each species is unique would remove the point of the biological trait analysis.

Biological trait analysis is a useful tool in an ecologist’s arsenal. Trait selection and understanding the statistical methods and the system is critical to performing a biological trait analysis. Careful thought must be given to the research question and data collection protocols before a biological trait analysis is carried out. This method is not easy to apply to data that were collected for other purposes, given the need for fine-level taxonomic identifications or measured trait values.

Burrow dwelling organisms were found to be uncommon on cold-water coral reef related substrata. Functionally, this indicates that active bioturbation from digging was likely reduced on the reef itself. This result was expected; as, cold-water coral reefs require a hard substratum for attachment (Roberts et al., 2006). The presence of finer sediments on the cold-water coral reefs is generally uncommon; resulting in conditions that are unsuited for burrowing behaviour. No further functional traits were identified as significantly associating with cold-water coral reef substrata.

4.6 Conclusion

The different cold-water coral reefs and their nearby surrounding area had similar traits, indicating that these cold-water coral reefs are likely functionally similar. The CWM-RDA indicated that the longitude and latitude explained a significant amount of observed variance, indicating that the traits present on cold-water coral reefs are influenced by the traits present in the area. However, the presence of the reef-related substrata accounted for more variance, suggesting that the traits present on the reef are more related to the presence of the reef than its location.

Video data comes with its flaws and merits for biological trait analysis, as do all sampling methods. Bayesian models can include prior assumptions, which in applications where data are limited or the sampling method is biased against certain groups, could prove invaluable. However, since they are based on prior assumptions or observations they require either a strong understanding of a system or large amounts of training data. Bayesian based methodology for analysing biological traits (e.g. Schulz et al., 2021) can provide a solution for sampling bias by leveraging the known biases of different methods against each other to provide data that represent the most probable trait-environmental relationships. This represents a valuable direction for biological trait analyses in the future; however, it requires quantification of biases.

Chapter 5

Synthesis

Abstract

All of the hypotheses set out in chapter 1 were addressed in this thesis. The general findings are that the location of cold-water coral reefs influences the species found on them. While species were related to the local species pool, the traits found on the different reefs were similar. Within the limitations of the study, there were indications that biological traits differ between the different substrata on the reefs. In particular, the living habit of burrowing is negatively associated with the presence of cold-water coral reef related substrata. While the community weighted means of the traits found on the different sites were influenced by the location of the sites, the presence of living coral was a strong driver. The functional composition of the nine different cold-water coral reefs from which the sites were taken supported the conclusion that cold-water coral reefs have similar trait assemblages. The functional composition of areas that share the same most common substrata indicated that, while reefs had similar overall trait assemblages, the distribution of these traits within the reef was influenced by the substratum type. A number of technical recommendations were suggested based on this research. *Eunice norvegica* was not present in the data analysed in this thesis, indicating a likely under-representation of infauna. The known biases should be quantified for different sampling methods, thus allowing Bayesian methods to be used in order to reduce the need for destructive sampling over sensitive habitats. The advantage of video footage in trait analysis is that it can be used to observe trait expression, where other sampling methods result in more certain taxonomic identification but no expression information. In the South African context, cold-water coral reefs are likely to contain species filling the role of the sponge *Mycale (mycale) lingua* and local members of the genus *Sebastes*. Comparison between the traits found on cold-water coral reefs and other abiotic reefs found in cold waters will allow for further identification of functionally important trait patterns. Understanding what traits are present on cold-water coral reefs allows for detailed investigation into the energy pathways present on the reefs.

5.1 Introduction

The dataset used in this thesis was part of MAREANO, which was set up to provide chemical, geological, and biological information on the Norwegian seabed (Buhl-Mortensen et al., 2016). These data were collected using a consistent methodology in order to address a broad range of scientific and management objectives. However, they were not specifically collected to address the hypotheses put forward in this thesis. In biological sciences, especially when dealing with deep benthic systems, field sampling can be both financially and ecologically expensive. Thus, it is not always possible to design data collection routines around each study. At the start of this thesis, it was believed that the

signals present in the system would be sufficient to overcome the limitations of the sampling method. In retrospect however, these signals were weaker than expected. This was particularly true for the trait analysis. The trait signals highlighted trends, but in most cases they were too weak to detect statistically significant differences in these trends.

The first hypothesis was that the geographic position of each reef would account for a significant amount of variance in the species assemblages found on and around cold-water coral reefs. Cold-water coral reefs are known to be areas of increased biodiversity and fish are more abundant in the vicinity of reefs (UK Biodiversity Group, 2000; Freiwald et al., 2004). These species aggregations are related to the species pool in the waters surrounding the reef, with few obligate reef species (Fosså et al., 2002). This hypothesis is supported by the findings of this thesis (chapter 2), as the species found on cold-water coral reefs are related to the substratum type, depth, and location of the reefs. This indicated that the species present on the cold-water coral reefs and the reef edges are represented in the broader local species pool. The results of chapter 2 also indicated that video sequences without coral related substrata still had similar species compositions to those with coral related substrata from the same reef. This supports the statement, that there are very few true obligate reef species.

The second hypothesis was that the biological traits of the species found on the reef would be unrelated to the locations of the reef. Traits are related to species; however, two distinct species assemblages that are functionally similar will have similar traits. If there is a strong benefit for individual traits on the reef, then these traits will be present on the reefs regardless of the location of the reef. The community weighted means of the biological traits indicated these were still influenced by the location of the reefs (chapter 4). However, presence of cold-water coral related substrata was a stronger driver of trait assemblage than longitude and latitude. Thus, while a fully generic set of traits, independent of geographical location, cannot be proposed for cold-water coral reefs, it can be concluded that cold-water coral reefs have similar traits. Coral substrata were associated with trait modalities for large body sizes, attached, sessile, and hard substrata preferences (chapter 4, figure 4.4). This conclusion is also supported by the trait profiles of the reef sites as a whole, which display general trends in the order of dominance of trait modalities (chapter 4, figures 4.5 and 4.6).

The third hypothesis addressed the relationship between the environmental variables and biological traits, stating that a consistent relationship exists across the reef sites. The very foundation of the biological trait concept would imply that, in general, traits must be related to environmental factors. However, the strength or presence of these relationships can differ from region to region (e.g. differences between regions, Sutton et al., 2021). There was only one significant driver of trait differences in this study, namely, burrow dwelling, which was associated with sandy mud and pebble substrata. The community weighted means analysis indicated that variance in the trait composition was, at least in part, accounted for by environmental factors. This indicates that, while environmental factors account for community weighted trait compositions, at similar levels to that of species composition, they do not have significant effects on individual trait modalities within the relatively narrow environmental range covered in this thesis.

The final hypothesis was that the different cold-water coral reefs would have similar traits. Originally, this hypothesis was thought to be related to the third hypothesis, such that a set of traits

would significantly associate with the coral reef substrata. However, it is now understood that a lack of significant relationships between the environmental variables and the biological traits would also support this hypothesis. The results supported the latter understanding of the hypothesis. This is confirmed by the functional compositions of the reefs as a whole. While variability is present within trait modalities, the general trends of traits on the different reefs are similar. Thus, cold-water coral reefs have similar traits to each other and to the benthos within 400m of the reef (chapter 4). The similarities in traits between cold-water coral reefs indicate that the Norwegian reefs have similar functioning. However, there are differences in the functional composition of the different parts of the reefs (chapter 4). This supports the observation that different parts of cold-water coral reefs contain different species (Buhl-Mortensen et al., 1995; Buhl-Mortensen, 2017; Buhl-Mortensen et al., 2017b), and it is now apparent that these areas likely host different trait assemblages. Despite these signals, the results of this thesis imply that the biological function of the reef extends off the reef edges.

A gap in the documentation of biological traits for the observed species became evident during trait assignment. The biological traits of many of the taxa observed at the sites were not present in any of the existing trait databases. In order to address this, a literature-based review of the taxa was performed. The traits and their literature sources are documented in chapter 3, which will act as an additional source of trait information for future biological trait-based studies.

5.2 Technical recommendations

There are multiple methods that can be used to survey benthic species (Flannery and Przeslawski, 2015). Video-based methods allow for both species and substratum observations (Buhl-Mortensen et al., 2012). However, not all video surveying methods yield the same results; there can be significant differences between methods in key observations for variables, ranging from species richness to composition (Sheehan et al., 2016). The data analysed in this thesis were collected using a video surveying platform referred to as CAMPOD (described in chapter 3). This type of platform is considered to be the optimal method used when surveying variable habitats and sensitive bottom types (Sheehan et al., 2016).

Species-level identifications from video data can be relatively challenging (Flannery and Przeslawski, 2015), and tend to produce better taxonomic resolution for larger species. Small and cryptic species are harder to identify from video footage; while, unless a body part is extended out of the sediment infauna are not be visible at all. This results in a bias against infauna in video data. The polychaete *Eunice norvegica* was not observed at any of the reef sites analysed in this thesis, despite being well documented on North Atlantic *Lophelia* reefs (Mueller et al., 2013). Past studies have indicated that *Eunice norvegica* is associated with the living part of the reef (Freiwald et al., 2004). The surveying method alone does not necessarily account for the absence of *Eunice norvegica*, as the species has been observed in video surveys.

The activity levels of some species on cold-water coral reefs have been linked to temporal factors. *Eunice norvegica* is one such species. Buhl-Mortensen et al. (2015c) observed that the polychaetes were active and thus visible between 03:00 and 09:00, and then again between 15:00 and 22:00. Video surveys cannot observe species such as *Eunice norvegica* when they are retracted, unless their tubes

are visible through the coral matrix. The sites selected for this study included areas with high coverage of living and dead coral blocks during times when *E. norvegica* was expected to be active. The lack of observations of this species suggests that the towed camera rig used was poor at detecting species that were contained within the coral matrix. Buhl-Mortensen et al. (2015c) used multiple time-based observations on the same reef to reach their conclusion. However, the data used in this thesis covered multiple reef sites, each sampled at a different time of day. Since the reef sites that were observed between 22:00 and 06:00 in this study had significantly less coral-related substrata, the impact of time of day on species and trait assemblages could not be analysed.

Lophelia reefs are known to provide a complex 3-dimensional habitat for species. The reef provides living surfaces on the living corals, on the dead coral skeleton, between the corals, and within the coral skeleton itself for boring species (UK Biodiversity Group, 2000). The ability to capture this level of taxonomic resolution would require destructive sampling techniques. Since the reefs grow at a rate of millimetres per year (Gass and Roberts, 2006; Järnegen and Kutti, 2008), destructive surveying methods are ecologically costly. Understanding the biases in trait observations between different surveying methods can be leveraged to improve the results of non-destructive sampling methods.

Bayesian statistical methods allow for an approach that uses a prior understanding of a sampling method's biases, as one of the fundamental principles of Bayesian statistics is the informative prior (O'Hagan, 2004). The usefulness of the informative prior is that it generates cumulative knowledge, by leveraging prior observations or findings (Schulz et al., 2021). Such findings can relate to the certainty of an observation representing the true absence of a species or trait, rather than simply the failure to observe it. By basing prior distributions for trait observations on data obtained from a range of different observation methods, method-specific undersampling can be accounted for.

A trait-based Bayesian model was proposed by Sarker et al. (2021) that takes into account both trait-trait and trait-environment relationships. This model allows for links between traits to be modelled. Sarker et al.'s (2021) approach does not represent the only possible Bayesian framework for trait analysis. A wide range of different Bayesian approaches can be taken, some as simple as building a model based on the logic described above. Bayesian search models are well established; they address the idea that not observing the target in a search location provides additional information to the likelihood that the target is in that location (Stone, 1975; Stone et al., 2011). How this additional information is treated is based on a prior assumption about the probability of the search target being located in that location. The probabilities of trait observations, based on the traits observed and prior assumptions, can then be analysed further to identify trait links.

The Bayesian model requires priors, and the nature of the model briefly discussed here is to leverage data from small-scale destructive sampling. Thus, further investigation is required into the biases between static camera, moving camera, and grab methods on cold-water coral reefs, especially with relation to trait coverage. This would allow the collective knowledge obtained from multiple past sampling methods to be utilised when using data collected by tow cameras or ROVs.

In chapter 4, the distinction between what an organism can do and what it is currently doing is discussed. Observing the current behaviour of an organism is only possible using video methods.

This advantage, combined with the smaller ecological impact of video footage over physical sampling, supports the use of video methods for trait analysis. Using Bayesian models to account for bias thus becomes increasingly useful and should allow for conclusions about expressed behavioural traits. These conclusions would allow for complex ecological interactions to be identified.

5.3 The South African context

The state of knowledge regarding cold-water corals in South Africa is discussed in chapter 1. While cold-water corals are likely present in South African waters, little is known about these ecosystems locally (Department of Environmental Affairs, 2014; Sink, 2016). The reef-forming *Solenosmilia variabilis* is known to be present in South African waters (Filander et al., 2021). As discussed in chapter 1, habitat modelling supports the possibility of *Lophelia* occurrences in South African waters (Davies et al., 2008; Davies and Guinotte, 2011). This further supported by the presence of both *S. variabilis* and *Lophelia* in the Southern Atlantic, along the East Coast of South America (Raddatz et al., 2019). Norwegian data were used in this thesis, with the objective of identifying traits that are associated with cold-water coral reefs. These traits would then allow inferences to be made about the ecological functioning on cold-water coral reefs, which could be extended to other cold-water coral reef sites. The reefs analysed in this thesis are situated at higher latitudes than any possible South African reef. However, despite these differences, there were genera and cosmopolitan species observed in the data set that are also documented in South African waters. The results of the combined RLQ fourth-corner analysis indicated that burrow dwelling organisms are likely uncommon on South African cold-water coral reefs (chapter 4). While this was the only significant trait association with the coral substrata, South African reefs and their immediately surrounding waters could be expected to have similar functional diversity to those described in chapter 4. Thus, one would expect to find the functional composition skewed towards sessile and attached taxa, colonial taxa, taxa that produce lecithotrophic larvae, and filter feeding taxa.

Mycale (mycale) lingua was found to associate with living coral blocks (chapter 2). This association has been observed before (van Soest et al., 2007; Buhl-Mortensen, 2017). Since the traits typical of sponges in general, or specifically those of *M. lingua*, are not associated with the increased live coral coverage, the driver of this species association remains unclear. *Mycale lingua* is known to be associated with Norwegian cold-water coral reefs (Järnegen and Kutti, 2008; Kutti et al., 2013). Additionally, *Mycale* species have been observed on five different North-East Atlantic reefs (van Soest and de Voogd, 2013). The ecological role of sponges in nutrient recycling on cold-water coral reefs is well established (Rix et al., 2016; Maier et al., 2021; Montseny et al., 2021). It is therefore hypothesised that equivalent species would exist on cold-water coral reefs in South Africa. The term, species is used in this hypothesis, since the ecological role related to nutrient recycling that is filled by *M. lingua* may be unrelated to it being a sponge.

The most common fish genus observed across the nine reef sites is *Sebastes*, commonly known as redfish or rockfish. It was found to be associated with the dead *Lophelia* reef zone (chapter 2). The presence of *Sebastes* species on cold-water coral reefs is well-documented (Buhl-Mortensen et al., 1995; Fosså et al., 2002; Kutti et al., 2015; Milligan et al., 2016); these species are likely using the reef as protection from predation and strong currents (Buhl-Mortensen et al., 2017b). However, its asso-

ciation with dead *Lophelia* sites contrasted Buhl-Mortensen et al. (1995), who found *Sebastes* to be associated with the living part of the reef. The genus *Sebastes* is cosmopolitan, with the South Atlantic *Sebastes capensis* being found in South African waters. It is hypothesised that this species would be common in the waters surrounding cold-water coral reefs in South Africa. The presence of fish belong to the genera *Sebastes* and *Trisopterus* on cold-water coral reefs is linked to both season and time of day (Buhl-Mortensen et al., 2015c; Kutti et al., 2015). As mentioned before, time of day could not be included as a factor in this thesis; likewise, season could not be included, since most of the sites sampled in summer were significantly deeper than those sampled in autumn.

In addition to *Sebastes*, other fish such as *Molva molva* and *Brosme brosme* were present in the dataset; these have also been associated with cold-water coral reefs (Husebø et al., 2002). However, these fish species did not associate with specific parts of the reef (chapter 2). Fish are known to be present at high densities in the waters surrounding cold-water coral reefs (Husebø et al., 2002; Costello et al., 2005; Kutti et al., 2015). However, none of the trait based analyses performed in chapter 4 indicated this trend. This is likely the result of the on reef fish densities extending into the waters immediately surrounding the reef, since all samples were within 400m of a coral reef. It is thus very likely that a significant difference would exist between the sites analysed here and sites further from the reef. This hypothesis is discussed further in the concluding statements.

5.4 Conclusions

The trait analysis indicated that cold-water coral reefs had similar traits to the surrounding areas, thus, the primary hypothesis could not be directly addressed. Possible statistical and technical limitations relating to these findings have been discussed (chapter 4 and section 5.2). Significant relationships between relative trait abundances and cold-water coral related substrata would have provided the basis for an ecological model, focusing on identifying the processes driving these trait differences. However, the absence of such relationships still informs the discussion about benthic-pelagic coupling, and energy flow in general, on cold-water coral reefs. This discussion has led to new hypotheses regarding the energy flow on cold-water coral reefs and how they drive aggregation. These hypotheses are discussed below.

As discussed in chapter 1, cold-water coral reefs support greater species diversity than the surrounding soft bottoms (UK Biodiversity Group, 2000; Husebø et al., 2002). Additionally, fish are known to be more abundant on cold-water coral reefs compared to the surrounding waters (Husebø et al., 2002; Costello et al., 2005; Mortensen et al., 2005; D’Onghia et al., 2012; Kutti et al., 2015). Neither the RLQ fourth-corner analysis, CWM-RDA or functional composition plots indicated an increase in the abundance of pisciform body forms on coral substrata. These results suggest an alternative hypothesis; the “effect” of the reef extends further than 400m from the reef.

The data used in this thesis are discussed in detail in chapter 2. Of importance in this discussion is that each transect was around 700m long, split into 100m sites. Since every 700m transect was selected to contain at least some cold-water coral reef associated substratum, it would be impossible for a site to be more than 700m from a cold-water coral reef. In practice, all sites were within 300m of a site that contained coral rubble, live coral, or dead coral. Thus the maximum distance between

a reef and a site was 400m. The sizes of these reefs were not taken into consideration, and, for the majority of sites, this distance was closer to 100m. It is possible that the sites that were dominated by non-reef substrata were close enough to the reef for the species observations to be impacted by them. This would provide a logical explanation for the contradiction between past studies, finding that fish were more abundant on cold-water coral reefs and the results of chapter 4.

Purposeful experimental design and statistical considerations are required to investigate whether time of day, season, and distance from the reef influence the presence of traits off the reef. Notably, since location is a significant explanatory variable for both taxa and traits found at the sites, the “non-reef” sites would still have to be in the general geographical location of the “reef sites”. Thus, a number of paired sites, a good distance apart, would be required.

This thesis did not identify a truly distinctive reef community, both in terms of species and traits. However, the functional composition of the reefs indicates that filter-feeding is the most prominent feeding method on cold-water coral reefs, even when the main reef-building species are not taken into account. Filter feeding requires the presence of particulate (POM) and dissolved organic matter (DOM). This implies that all of these reefs, likely as a result of the physical presence of the reef and the local bathymetry, have a ready supply of POM. While there was no significant association between passive filter feeders and the presence of coral, they were most associated with the living and dead coral substrata in the RLQ based trait analysis. The lack of significance was likely due to there being no true non cold-water coral reef sites. This likely indicates that current flow near the reefs favoured passive filter feeding, suggesting vertical and lateral import of carbon into the reef systems.

Even though the area sampled was near to the reef, stronger signals were expected, given that differences have been observed between the species found in the different reef zones. A reasonable hypothesis for this observation is that the benefit of the reef is general rather than specific. The “appeal” of a cold-water coral reef thus appears to be beneficial to all sampled traits. It is clear that the benefits of the reef are limited to species that can physically live on the reef. Hence, the fact that reefs are on hard substrata prohibits permanent burrowing species from utilising them. Beyond the negative association of burrowing species, the lack of a distinctive trait community implies that the reef does not support traits or species that drive species aggregation on the reef. Given the lack of support of trait-environment relationships accounting for the aggregation on the reef, the only remaining possibility is the physical structure of the reef.

Cold-water coral reefs require water between 4°C and 14°C, salinity between 33 and 37, and a source of nutrients (chapter 1). Rocky reefs can form almost anywhere on the seafloor. The temperature and salinity range required for cold-water coral reefs do not imply any significant difference from areas where rocky reefs might form. Given that the driver of the ecosystem enhancements appears to be the physical presence of the reef, the question arises. Does the reef need to be living? Previous research indicates that there are differences in species between the living and dead parts of the cold-water coral reefs (Buhl-Mortensen et al., 1995; Buhl-Mortensen et al., 2017b). This would imply that there is a difference between living and dead reefs. However, Grabowski et al. (2012) indicated significantly higher densities of *Sebastes* species on boulder or laval field substrata relative to the surrounding sandy substrata. It should be noted, that in the case of rocky reefs the transitional zone between

the reefs supported high fish densities as well (Grabowski et al., 2012). This supports the hypothesis suggested earlier that cold-water coral reefs have an area of effect or a transition zone around them. The shape of a cold-water coral reef differs from rocky reefs. Branching corals produce a very different 3-dimensional matrix to stacked rocks. It is thus not immediately clear if non-living and particularly rocky reefs, or dead but physically intact cold-water coral reefs, would provide the same benefit as living cold-water coral reefs.

Comparative studies between rocky and coral reefs have been performed in the tropics (Benfield et al., 2008). Differences in community assemblages between cold-water coral reefs formed *Oculina varicosa* and *Lophelia* have been observed, despite similarities in the geomorphological structures of these reefs (Reed, 2002). The predominant difference between the two reefs types was that large porifera and gorgonians are common on *Lophelia* reefs and uncommon on *O. varicosa* reefs (Reed, 2002). Several taxa that were previously only observed on boulder or cobble substrata, were noted as appearing on coral rubble substrata during reef recovery (Beazley et al., 2021). This suggests that there are similarities between these substrata, although these taxa exhibit a preference to the boulder related substrata. Beazley et al. further notes that the nature of coral rubble, may prevent larger sessile taxa from colonising it. Understanding the difference between living and non-living reefs would help highlight the ecological interaction between cold-water coral reefs and the organisms found on them.

Comparing the differences between living and non-living reef sites highlights the role that the living part of the reef has in influencing the energy pathways present on the reef. Further investigation into the flow of energy on cold-water coral reefs should be conducted. There is a general assertion that benthic-pelagic coupling takes place over cold-water coral reefs, which is supported by previous research (Cathalot et al., 2015). Known and suspected pathways between the cold-water coral reefs and the pelagic zone are described in chapter 1. A better understanding of the energy pathways on cold-water coral reefs will allow for the role they play in the greater ecosystem to be more explicitly defined.

Appendix A: Table of Taxa

Table A.1: Table listing all the taxa observed in the video sequences used, taxa grouping for the BTA are marked in blue (darker shades used when groups board each other). List is alphabetical by taxonomic names, colours and sizes are grouped together.

Taxa in chapter 2	Taxa in BTA	Taxa in chapter 2	Taxa in BTA
<i>Acesta excavata</i>	<i>Acesta excavata</i>	<i>Geodia atlantica</i>	<i>Geodia atlantica</i>
Actiniaria		<i>Geodia barretti</i>	<i>Geodia barretti</i>
Actiniaria buried redish		<i>Geodia macandrewii</i>	<i>Geodia macandrewii</i>
Actiniaria dark		Gorgonocephalus	Gorgonocephalus
Actiniaria orange	Actiniaria	<i>Gracilechinus acutus</i>	<i>Gracilechinus acutus</i>
Actiniaria pink		Henricia orange	
Actiniaria white		Henricia white	Henricia
Actiniaria yellow		Henricia yellow	
<i>Actinostola callosa</i>	<i>Actinostola callosa</i>	<i>Hippasteria phrygiana</i>	<i>Hippasteria phrygiana</i>
Alcyonacea	Alcyonacea	Hippolytidae	Hippolytidae
Antedonoidea	Antedonoidea	Hydrozoa	
<i>Antho dichotoma</i>	<i>Antho dichotoma</i>	Hydrozoa bush	Hydrozoa
Anthomastus	Anthomastus	Hydrozoa tree	
<i>Anthothela grandiflora</i>	<i>Anthothela grandiflora</i>	<i>Hymedesmia paupertas</i>	<i>Hymedesmia paupertas</i>
Aphroditidae	Aphroditidae	<i>Kophobelemnnon stelliferum</i>	<i>Kophobelemnnon stelliferum</i>
<i>Aplysilla sulfurea</i>	<i>Aplysilla sulfurea</i>	Latrunculia	Latrunculia
Argentina	Argentina	<i>Lithodes maja</i>	<i>Lithodes maja</i>
<i>Asbestopluma pennatula</i>	<i>Asbestopluma pennatula</i>	Lithodidae	Lithodidae
Ascidia	Ascidia	<i>Lophelia pertusa</i>	<i>Lophelia pertusa</i>
<i>Asconema setubalense</i>	<i>Asconema setubalense</i>	<i>Madrepora oculata</i>	<i>Madrepora oculata</i>
Asteroidea	Asteroidea	<i>Mellonympha mortenseni</i>	<i>Mellonympha mortenseni</i>
Asteroidea orange		<i>Molva molva</i>	<i>Molva molva</i>
<i>Azinella infundibuliformis</i>	<i>Azinella infundibuliformis</i>	Munida	Munida
Balticina	Balticina	Muriceides	Muriceides
<i>Bolocera tuediae</i>	<i>Bolocera tuediae</i>	<i>Muriceides kükenthali</i>	<i>Muriceides kükenthali</i>
Bonelliidae	Bonelliidae	<i>Mycale lingua</i>	<i>Mycale lingua</i>
Brachiopoda	Brachiopoda	Nemertea	Nemertea
<i>Brosme brosme</i>	<i>Brosme brosme</i>	Nemertea pink	
Bryozoa calcareous branched	Bryozoa calcareous branched	Neohela	Neohela
Burrow big	Burrow big	Nephtheidae	Nephtheidae
Burrow cave big		Oceanapia	Oceanapia
Burrows in group small		Ophiuroidea	Ophiuroidea
Burrows small	Burrows small	Paguridae	Paguridae
<i>Cancer pagurus</i>	<i>Cancer pagurus</i>	Pandalidae	Pandalidae
Caridea	Caridea	<i>Paragorgia arborea</i>	
Cephalopoda	Cephalopoda	Paragorgia pink	<i>Paragorgia arborea</i>
<i>Ceramaster granularis</i>	<i>Ceramaster granularis</i>	Paragorgia red	
Cerianthidae		Paragorgia white	
Cerianthidae dark	Cerianthidae	<i>Paramuricea placomus</i>	<i>Paramuricea placomus</i>
Cerianthidae violet		<i>Parastichopus tremulus</i>	<i>Parastichopus tremulus</i>
Chelonaplysilla	Chelonaplysilla	Phakellia	Phakellia
<i>Chimaera monstrosa</i>	<i>Chimaera monstrosa</i>	<i>Phycis blennoides</i>	<i>Phycis blennoides</i>
<i>Cidaris cidaris</i>	<i>Cidaris cidaris</i>	Plakortis	Plakortis
<i>Clavularia borealis</i>	<i>Clavularia borealis</i>	Pleuronectiformes	Pleuronectiformes
<i>Craniella zetlandica</i>	<i>Craniella zetlandica</i>	<i>Pollachius virens</i>	<i>Pollachius virens</i>
Didemnidae	Didemnidae	Polychaeta	Polychaeta
<i>Drifa glomerata</i>	<i>Drifa glomerata</i>	Polymastiidae	Polymastiidae
<i>Dysidea fragilis</i>	<i>Dysidea fragilis</i>	<i>Pontaster tenuispinus</i>	<i>Pontaster tenuispinus</i>
Echinoidea regular	Echinoidea regular	Porania	Porania
Echinus	Echinus	Porania white	
<i>Echinus esculentus</i>	<i>Echinus esculentus</i>	Poraniidae	Poraniidae
Echiuroidea	Echiuroidea	Porifera	
<i>Gadidulus argenteus</i>	<i>Gadidulus argenteus</i>	Porifera dirty yellow	
Gadidae	Gadidae	Porifera grey	Porifera
Gastropoda	Gastropoda	Porifera yellow	
Geodia	Geodia	Porifera fragment	

Table A.1: (Continued): Table listing all the taxa observed in the video sequences used, taxa grouping for the BTA are marked in blue (darker shades used when groups board each other). List is alphabetical by taxonomic names, colours and sizes are grouped together.

Taxa in chapter 2	Taxa in BTA
Porifera encrusting	Porifera encrusting
Porifera encrusting bluegrey	
Porifera encrusting brown	
Porifera encrusting green	
Porifera encrusting grey	
Porifera encrusting orange	
Porifera encrusting white	
Porifera encrusting whiteyellow	
Porifera encrusting yellow	
Porifera various encrusting	
Porifera fan	Porifera fan
Porifera fan white	
Porifera coral	
Porifera bat yellow	Porifera globulose
Porifera egg	
Porifera parabol	
Porifera round white small	Porifera globulose small
Porifera small	Porifera small
Porifera green small	
Porifera yellow small	
Porifera white small	
Porifera various small	
Porifera brown small	
Porifera irregular yellow small	
Porifera irregular white small	
Porifera medium	Porifera medium
Porifera white medium	
Porifera yellow medium	
Porifera irregular white medium	
Porifera irregular yellow medium	
Porifera white big	Porifera big
Porifera yellow big	
<i>Primnoa resedaeformis</i>	<i>Primnoa resedaeformis</i>
<i>Prothanthea simplex</i>	<i>Prothanthea simplex</i>
Quasillina	Quasillina
Reteporella	Reteporella
<i>Reteporella beaniana</i>	<i>Reteporella beaniana</i>
Sabellidae	Sabellidae
Sebastes	Sebastes
Serpulidae	Serpulidae
Sertulariidae	Sertulariidae
Stelletta	Stelletta
<i>Stichastrella rosea</i>	<i>Stichastrella rosea</i>
<i>Stryphnus ponderosus</i>	<i>Stryphnus ponderosus</i>
<i>Stylocordyla borealis</i>	<i>Stylocordyla borealis</i>
Teleostei	Teleostei
<i>Tethya citrina</i>	<i>Tethya citrina</i>
Thenea	Thenea
<i>Thenea abyssorum</i>	<i>Thenea abyssorum</i>
<i>Tubularia indivisa</i>	<i>Tubularia indivisa</i>
Tunicata colonial green	Tunicata colonial green
Tunicata solitary blue	Tunicata solitary
Tunicata transparent solitary	
Tunicata transparent solitary green	
<i>Virgularia mirabilis</i>	<i>Virgularia mirabilis</i>

Appendix B: Summary of reefs and video sequences

Table B.1: Summary of the reef each video sequence and each reef site. The latitude (Lat), longitude (Long), minimum, mean and maximum depth (min, mean and max), the mean gradient (Grad) are presented for each video sequence on each reef. Percentage cover of each of the bottom types boulder (B), clay with sponge spicules (Css), pebble (P), sandy mud sM, dead *Lophelia* (DL), Live coral (LC), and Coral rubble (CR) are also displayed for each video sequences. The average across the whole reef of all variables are presented, these are separated from the rest of the sites by a dotted line.

Reef ID	No. Video sequences	Sequence	Lat	Long	min	depth mean	max	Grad	B	Css	C	P	S	sM	DL	LC	CR
R0948	6	1	65.16	9.46	273.12	280.07	282.69	0.21	1.12	0.0	2.18	7.38	69.43	0.0	11.29	3.66	4.94
		2	65.16	9.46	256.98	269.1	277.64	0.61	0.0	0.0	0.0	0.0	19.3	0.0	42.87	28.64	9.19
		3	65.15	9.46	255.54	263.3	270.87	0.56	0.0	0.0	0.0	0.0	14.0	0.0	47.07	27.08	11.84
		4	65.15	9.46	259.99	269.06	277.45	0.21	0.0	0.0	0.0	0.0	37.48	0.0	34.55	7.02	20.96
		5	65.15	9.46	274.13	277.65	278.47	0.12	0.78	0.0	4.4	9.49	60.99	0.0	0.0	0.0	24.34
		6	65.15	9.46	268.83	274.3	278.04	0.17	0.0	0.0	0.53	2.25	44.85	0.0	11.51	3.15	37.71
		Average	65.15	9.46	264.76	272.25	277.53	0.31	0.32	0.0	1.19	3.19	41.01	0.0	24.55	11.59	18.16
R0960	7	1	64.14	8.19	313.44	314.17	315.08	0.07	9.5	0.0	0.0	7.6	82.9	0.0	0.0	0.0	0.0
		2	64.14	8.19	312.78	313.4	314.43	0.08	14.34	0.0	0.0	9.37	76.29	0.0	0.0	0.0	0.0
		3	64.14	8.2	298.1	305.92	313.27	0.25	0.0	0.0	0.0	4.05	34.04	0.0	19.23	3.12	39.56
		4	64.14	8.2	300.83	305.97	311.98	0.15	0.0	0.0	1.33	4.4	58.97	0.0	9.21	3.11	22.98
		5	64.14	8.2	293.06	300.92	311.26	0.23	0.45	0.0	0.0	0.85	30.37	0.0	27.13	19.09	22.11
		6	64.14	8.2	292.06	294.47	296.61	0.26	0.0	0.0	0.0	0.0	28.19	0.0	49.42	17.74	4.64
		7	64.14	8.2	293.46	296.3	298.85	0.22	0.0	0.0	0.0	0.0	35.22	0.0	35.74	22.1	6.93
Average	64.14	8.2	298.38	302.83	307.73	0.2	2.47	0.0	0.22	3.11	43.85	0.0	23.45	10.86	16.04		
R0968	6	1	63.93	7.89	273.48	281.83	291.52	0.45	0.0	0.0	0.0	3.45	22.62	0.0	23.38	25.64	24.9
		2	63.93	7.89	270.62	278.17	286.21	0.44	1.0	0.0	1.77	3.02	23.7	0.0	26.74	13.64	30.13
		3	63.93	7.89	273.54	279.87	286.38	0.27	1.18	0.0	1.1	3.86	27.0	0.0	16.53	9.55	40.78
		4	63.93	7.89	282.05	284.75	286.08	0.1	3.63	0.0	8.07	30.89	50.25	0.0	0.0	0.14	7.03
		5	63.93	7.89	263.42	274.81	287.99	0.47	0.0	0.0	0.08	5.82	24.67	0.0	18.68	6.05	44.7
		6	63.93	7.89	287.6	289.51	291.16	0.05	0.12	0.0	4.7	50.16	45.03	0.0	0.0	0.0	0.0
		Average	63.93	7.89	275.12	281.49	288.22	0.3	0.99	0.0	2.62	16.2	32.21	0.0	14.22	9.17	24.59
R0994	6	1	62.53	5.3	267.22	272.79	274.28	0.06	0.0	0.0	0.09	0.14	0.0	85.02	7.88	0.0	6.87
		2	62.53	5.3	254.09	261.23	269.01	0.38	0.0	0.0	0.0	0.0	0.0	54.39	10.48	2.21	32.93
		3	62.53	5.3	257.36	269.94	275.03	0.29	0.0	0.0	0.0	0.0	0.0	64.27	17.7	9.53	8.49
		4	62.53	5.3	255.49	263.52	272.61	0.13	0.15	0.0	0.0	0.0	0.0	51.67	11.88	0.7	35.6
		5	62.53	5.3	272.62	273.95	274.92	0.04	0.32	0.0	0.1	0.0	0.0	99.58	0.0	0.0	0.0
		6	62.53	5.3	271.46	272.86	274.24	0.05	0.0	0.0	0.04	0.0	0.0	98.33	0.0	0.0	1.63
		Average	62.53	5.3	263.04	269.05	273.35	0.16	0.08	0.0	0.04	0.02	0.0	75.54	7.99	2.07	14.25
R1108	6	1	65.67	5.93	324.92	335.15	343.09	0.17	0.15	0.0	9.79	14.15	0.0	59.35	0.15	2.44	13.96
		2	65.67	5.93	338.98	345.38	351.26	0.18	0.37	0.0	2.85	10.66	0.0	46.0	11.76	11.28	17.08
		3	65.67	5.93	338.09	340.86	343.23	0.15	1.69	0.0	9.81	29.1	0.0	58.83	0.0	0.0	0.56
		4	65.67	5.93	334.66	339.43	346.46	0.32	3.08	0.0	10.15	15.09	0.0	45.86	10.37	2.11	13.33
		5	65.67	5.92	334.94	338.6	341.27	0.12	0.0	0.0	6.46	17.57	0.0	47.56	11.49	2.22	14.71
		6	65.67	5.92	338.68	345.18	350.48	0.42	0.33	0.0	5.36	10.31	0.0	47.24	15.79	9.12	11.85
		Average	65.67	5.93	335.05	340.77	345.96	0.23	0.94	0.0	7.4	16.15	0.0	50.81	8.26	4.53	11.92
R1130	7	1	65.23	6.29	345.26	347.07	349.76	0.08	1.0	0.0	7.74	7.64	0.0	83.61	0.0	0.0	0.0
		2	65.23	6.29	348.56	350.02	351.87	0.22	0.65	0.0	5.41	7.72	0.0	86.22	0.0	0.0	0.0
		3	65.23	6.28	348.77	350.01	352.42	0.1	1.78	0.0	6.96	15.42	0.0	75.83	0.0	0.0	0.0
		4	65.23	6.28	350.26	351.49	353.01	0.12	0.92	0.0	5.68	15.02	19.53	51.11	0.79	0.0	6.94
		5	65.23	6.28	351.26	352.14	353.05	0.1	0.34	0.0	12.26	17.54	68.04	0.0	0.25	0.12	1.45
		6	65.23	6.28	352.15	353.85	359.33	0.16	0.12	0.0	4.82	10.36	74.14	0.0	2.38	0.0	8.19
		7	65.23	6.28	354.59	356.83	359.16	0.21	0.54	0.0	6.18	9.37	57.29	0.0	10.32	0.42	15.88
Average	65.23	6.28	350.93	352.39	354.81	0.15	0.72	0.0	6.88	12.57	36.5	35.53	2.29	0.09	5.41		
R1243	7	1	62.6	3.56	282.16	294.76	305.2	0.25	0.0	0.0	0.41	0.0	1.54	0.0	16.05	47.02	34.98
		2	62.6	3.56	282.43	289.27	292.89	0.17	0.0	0.0	0.0	0.0	1.6	0.0	19.97	78.43	0.0
		3	62.59	3.56	284.62	288.3	297.29	0.17	0.0	0.0	0.0	0.0	6.0	0.0	9.7	72.34	11.96
		4	62.59	3.55	276.05	289.38	297.86	0.36	0.0	0.0	0.0	0.0	13.1	0.0	0.25	54.63	32.02
		5	62.59	3.55	268.14	271.83	275.5	1.0	0.0	0.0	0.0	0.0	19.57	0.0	4.94	75.27	0.22
		6	62.59	3.55	270.11	275.1	280.23	0.23	1.35	0.0	0.0	0.0	14.2	0.0	22.23	62.22	0.0
		7	62.59	3.55	264.27	268.33	274.07	0.33	0.0	0.0	0.0	0.0	17.84	0.0	28.95	32.25	20.96
Average	62.59	3.55	274.27	280.37	286.31	0.38	0.23	0.0	0.0	0.0	12.05	0.0	14.34	62.52	10.86		
R1353	7	1	63.72	5.6	450.2	456.43	463.66	0.24	1.51	0.0	9.8	1.91	21.59	0.0	14.42	50.76	0.0
		2	63.72	5.6	451.48	460.15	467.39	0.27	1.74	0.0	8.77	6.14	42.08	0.0	19.21	21.02	1.03
		3	63.72	5.6	454.73	459.34	462.59	0.27	6.0	0.0	9.3	7.77	48.53	0.0	16.26	12.14	0.0
		4	63.72	5.6	446.57	452.22	457.36	0.12	7.01	0.0	7.57	2.89	35.0	0.0	26.19	20.73	0.6
		5	63.72	5.6	446.42	451.1	454.9	0.22	3.18	0.71	22.39	2.71	42.33	3.19	7.67	14.63	3.19
		6	63.72	5.6	438.93	444.45	450.01	1.14	0.0	0.01	0.71	0.76	28.86	0.03	23.69	45.24	0.71
		7	63.72	5.6	444.59	451.63	462.64	0.33	1.79	0.0	1.47	1.07	24.35	0.0	24.39	46.25	0.67
Average	63.72	5.6	447.12	453.15	459.15	0.39	3.29	0.12	8.37	3.56	36.86	0.54	19.57	26.67	1.03		
R1562	7	1	66.67	7.74	337.56	341.77	348.39	0.17	4.51	0.0	6.25	45.83	43.41	0.0	0.0	0.0	0.0
		2	66.67	7.73	336.23	340.38	343.23	0.19	2.39	0.0	1.97	8.77	34.06	0.0	2.19	4.35	46.27
		3	66.66	7.73	341.68	344.03	348.73	0.15	0.0	0.0	3.22	17.67	45.32	0.0	4.53	0.0	29.26
		4	66.66	7.73	339.28	342.09	346.36	0.18	1.52	0.0	7.93	35.59	54.96	0.0	0.0	0.0	0.0
		5	66.66	7.73	338.98	339.64	340.39	0.05	0.06	0.0	7.57	31.28	58.38	0.0	0.0	0.0	2.7
		6	66.66	7.73	338.75	342.57	345.98	0.11	0.0	0.0	7.89	31.97	43.96	0.0	0.0	0.0	16.19
		7	66.66	7.73	338.11	339.59	340.61	0.06	2.38	0.0	4.86	43.06	49.7	0.0	0.0	0.0	0.0
Average	66.66	7.73	338.84	341.38	344.22	0.12	1.06	0.0	5.57	28.06	47.73	0.0	1.12	0.72	15.74		

Appendix C: New and modified trait information

C.1 Methods used for assigning information to missing traits

The trait databases used are not complete for every taxon. Where trait information was missing from the databases, expert opinion and literature were used to assign values. This was not possible for every missing trait. Where literature could be found, values were assigned based on the literature; however, in cases where literature could not be found for the taxa in question expert opinion was used. This expert opinion consisted primarily of judgments about, inheritance of traits from parent groups, inferences based on children groups, and visual reference guides (used for size and body form). Where group size and information allowed for it, bottom up inferences (child groups inferring traits) were used over inferences from the parent group. Likewise, in some cases the species in a genus present in the region were known, in these cases inference was based on the local species pool.

Substratum preferences defined in the ATD implied that anything with no known preference would be assigned equal values for hard and soft, since “none” refers to hyperbenthic species with no preference. As a result expert opinion placed many taxa in this list as SA1:2 and SA2:2. These opinions were often based on the life history of the taxa, since non-hypobenthic taxa could not express SA4. Negative information like this was used as seldom as possible, and is based on the logic that encoding one trait as 0 and the remaining traits as 1 or 2 would provide more information than leaving the trait unassigned.

Citations in the table are to the best source that could be found, in some cases they link to papers that described the species in an off-hand manner (i.e. “and the burrowing amphipod *Neohela lamia*” (Soltwedel, 2021)) is used to support the burrowing behaviour of *Neohela*. This was done in connection with expert opinion, these citations should be considered to represent the best published record of the trait modality that could be found.

Data are presented for missing traits (table C.1) and for where traits were reassigned (table C.2).

C.2 Reassigned modalities

New trait definitions were used in this trait analysis, traits for body form and feeding method needed to be reassigned for some groups.

The deposit feeding groups from the ATD (surface and subsurface) were combined. This was done due to challenges in assigning surface and subsurface from the literature. In all cases the higher of the two values were assigned to the the new combined group (i.e. 2 and 1 because 2); however, if this change resulted in the new group representing the only feeding method then a value of 3 was assigned. This is in accordance with the definitions of the fuzzy coded values.

Filter/suspension feeding was split into two groups, active and passive. Reassignment of taxa between

these two modalities was possible at relatively high taxonomic levels, in all cases the value associated with the new combined group was assigned to the relevant new group.

Size:

The ATD used five trait modalities for size with an open upper definition of > 300mm, to better represent the larger taxa observed in this study a S5 was defined as 300mm to 500mm and a new S6 modality was added > 500mm.

Body Form:

Based on definitions from the BIOTIC database two new body forms were added Pisciform (BF6) and Branching (BF7), species that were better described by these modalities had to have body form reassigned.

Feeding method:

Three changes were made to the trait modalities used for feeding. Firstly, grazing (FH7) was added as a trait modality. Secondly, filter/suspension feeding (FH3) was split into passive and active (FH3a and FH3p, note in the tables these are the 2nd and 3rd modalities of feeding method). Finally, deposit feeding was presented as two modalities the ATD and BIOTIC databases (surface and subsurface) these were merged into a single deposit feeding group FH1.6

Table C.1: Trait values for missing trait descriptions in the databases used. Modality columns (1-8) represent the modalities of each trait. For example the first line shows a taxa where R3 was assigned a value of 3. In the case of Feeding habit modality 2 and 3 refer to FH3a and FH3p, rather than FH2 and FH3. The modality code F2 was not used in this dataset, as it was combined with FH1.

Taxa	Trait	Modalities							Source
		1	2	3	4	5	6	7	
Antedonoidea	Reproduction	0	3	0	0	0			From order (Brusca et al., 2016)
	Living Habit	2	0	0	0	0	1		From order (Brusca et al., 2016; Kasumyan et al., 2020)
	Movement	0	0	2	2				Inferred from descriptions (Brusca et al., 2016; Kasumyan et al., 2020)
	Substrate affinity	0	3	0	0				Expert opinion
Aphroditidae	Size	0	2	2	1	1	0		Range inherited from order (ATD and Polytraits)
	Feeding method	0	0	0	2	1	0	0	From order (ATD)
	Substrate affinity	2	2	0	0				Expert opinion(Inferred from living habit and trait definitions).
Ascidia	Body Form	1	1	0	0	2	0	0	Species descriptions and photographs
	Living Habit	0	1	0	0	0	0	2	From Class (Fish and Fish, 2011; Brusca et al., 2016)
	Movement	3	0	0	0				From Class (Brusca et al., 2016)
	Substrate affinity	0	3	0	0				Expert opinion (Based on living habits described in Fish and Fish (2011))
Bonelliidae	Size	1	2	2	0	0	0		Jumars et al. (2015)
	Reproduction	0	3	0	0				From Order (Barnes, 1982)
	Living Habit	0	1	0	2	0	0		Jumars et al. (2015)
	Movement	0	2	1	0				Jumars et al. (2015)
	Feeding method	3	0	0	0	0	0	0	Jumars et al. (2015)
	Substrate affinity	2	2	0	0				Expert opinion
<i>Cancer pagurus</i>	Body Form	0	0	3	0	0	0	0	From images
	Skeleton	2	0	1	0	0			From Phylum
Cephalopoda	Substrate affinity	2	2	0	2				Expert opinion (Inferred from living habit and trait definitions)
Cerianthidae	Body Form	0	2	0	0	0	0	0	Species descriptions (e.g. Fish and Fish, 2011; Molodtsova et al., 2011)
	Substrate affinity	3	0	0	0				Expert opinion (Based on living habit descriptions in (Hayward and Ryland, 2017))
Didemnidae	Body Form	0	0	2	0	1	0	0	From Class (Hayward and Ryland, 2017)
	Living Habit	0	0	0	0	0	3		Inferred from mobility
	Movement	3	0	0	0				Inferred from mobility
	Substrate affinity	0	2	1	0				Expert opinion
Echiuroidea	Size	1	2	1	0	0	0		From species descriptions (e.g. Richards, 2009) (Large species <i>Ikeda taenioides</i> not pre
	Reproduction	0	3	0	0				Brusca et al. (2016)
	Living Habit	0	1	0	2	0	0		Brusca et al. (2016)
	Movement	1	2	0	0				Brusca et al. (2016)
	Feeding method	2	2	0	0	0	0	0	Brusca et al. (2016)
	Substrate affinity	2	1	0	0				Expert opinion (Based on (Fish and Fish, 2011))

Table C.1: (Continued): Trait values for missing trait descriptions in the databases used. Modality columns (1-8) represent the modalities of each trait. For example the first line shows a taxa where R3 was assigned a value of 3. In the case of Feeding habit modality 2 and 3 refer to FH3a and FH3p, rather than FH2 and FH3. The modality code F2 was not used in this dataset, as it was combined with FH1.

Taxa	Trait	Modalities							Source
		1	2	3	4	5	6	7	
<i>Dysidea fragilis</i>	Skeleton	0	0	3	0	0			Rowley (2020)
<i>Echinus esculentus</i>	Skeleton	3	0	0	0	0			Campbell (1972)
<i>Hippasteria phrygiana</i>	Reproduction	0	3	0	0				Ruppert et al. (2004)
	Living Habit	3	0	0	0	0	0		From Order (ATD)
	Movement	0	0	3	0				From Order (ATD)
<i>Lithodes maja</i>	Body Form	0	0	3	0	0	0	0	Inferred from species photographs, family (Hall and Thatje, 2009)
	Skeleton	2	0	2	0	0			Inherited from phylum (Brusca et al., 2016), and family (Hayward and Ryland, 2017).
	Reproduction	0	0	0	3				From Order (Brusca et al., 2016)
	Living Habit	3	0	0	0	0	0		From Family (e.g. Collins et al., 2002)
	Movement	0	0	3	0				From Family (Collins et al., 2002)
	Feeding method	0	0	0	2	1	0	0	Stevens and Lovrich (2014) and Dvoretzky and Dvoretzky (2021)
	Substrate affinity	2	2	0	0				Observed on both rocks and sand (Collins et al., 2002)
Neohela	Size	0	3	0	0	0	0		Inferred from species
	Body Form	0	2	0	1	0	0	0	Brusca et al. (2016)
	Living Habit	1	0	0	2	0	0		Inferred from local species (Buhl-Mortensen et al., 2015b; Soltwedel, 2021)
	Movement	0	2	0	1				Inferred from local species (Buhl-Mortensen et al., 2015b; Soltwedel, 2021)
	Feeding method	3	0	0	0	0	0	0	Inferred from local species (Buhl-Mortensen et al., 2015b)
	Substrate affinity	3	0	0	0				Inferred from local species (Buhl-Mortensen et al., 2015b; Soltwedel, 2021)
Pandalidae	Size	0	2	2	2	0	0		Inherited from Infraorder (ATD)
	Living Habit	3	0	0	0	0	0		Brusca et al. (2016)
	Movement	0	0	1	2				Hessler (1981) and Brusca et al. (2016)
	Feeding method	2	0	1	0	2	0	0	Rice et al. (1980) and Fanelli and Cartes (2004)
	Substrate affinity	2	2	2	0				Expert opinion
Poraniidae	Size	0	0	2	2	0	0		Jensen (2014)
	Reproduction	0	2	0	1				Lambert (2000)
	Feeding method	2	0	1	2	1	0	0	Inferred from local species
	Substrate affinity	2	2	2	0				Expert opinion
<i>Protanthea simplex</i>	Body Form	1	0	0	0	2	0	0	Photographs (Jackson, 2008)
	Skeleton	0	0	0	3				Jackson (2008)
Serpulidae	Substrate affinity	0	3	0	0				Expert opinion
<i>Virgularia mirabilis</i>	Skeleton	0	0	0	0	3			Hill and Wilson (2000)

Table C.2: Trait values that were changed from those presented in the databases used. Modality columns (1-8) represent the modalities of each trait. Changed modalities are presented in bold. For example the first line shows a taxa where LH1 was modified to have have fuzzy code 1, which differs from the reported value in the database. In the case of Feeding habit modality 2 and 3 refer to FH3a and FH3p, rather than FH2 and FH3. The modality code F2 was not used in this dataset, as it was combined with FH1.

Taxa	Trait	Modalities							Source
		1	2	3	4	5	6	7	
Actiniaria	Living habit	1	1	0	1	1	2		Evidence of crevice dwelling and epiphhytic members of Actinia
	Feeding Habit	0	0	1	0	2	0		Smaller members now better described as passive suspension feeders.
<i>Actinostola callosa</i>	Reproduction	2	0	0	2				Larson (2017) lists as brooding, ATD definitions make R2 or R3 impossible at a species level if R4 is expressed.
	Feeding Habit	0	0	2	0	2	0	0	Filter feeding method is passive
Alcyonacea	Body form	0	0	1	0	2	0	2	Body forms better described by branch then upright
	Feeding Habit	0	0	3	0	0	0	0	From Octocoralia (Ribes et al., 2003; McDonald, 2014)
Antedonoidea	Feeding Habit	0	0	3	0	0	0	0	Filter feeding is passive
Aphroditidae	Movement	0	2	2	0				Appears in both ATD and Polytraits, swimming removed and crawling as per Polytraits. Burrowing was retained.
Ascidia	Reproduction	2	2	0	0				From Family (Kürn et al., 2011)
	Feeding Habit	0	3	0	0	0	0	0	Brusca et al. (2016)
Asteroidea	Size	0	2	2	2	2	2	1	(Hayward and Ryland, 2017)
	Feeding Habit	1	0	1	2	2	1	1	Suspension feeding, grazing (Lambert, 2000; Brusca et al., 2016). Predation dropped
<i>Axinella infundibuliformis</i>	Body Form	1	0	0	0	2	0	0	Upright and globulose better describes the shape.
	Feeding Habit	0	3	0	0	0	0	0	From Porifera (Fish and Fish, 2011)
<i>Bolocera tuediae</i>	Reproduction	2	2	0	0				Asexual reproduction by fragmentation (Schnytzer et al., 2017)
	Feeding Habit	0	0	1	0	2	0	0	Appears in both ATD and BIOTIC, used BIOTIC Feeding Habit.
	Substrate affinity	0	2	2	0				Appears in both ATD and BIOTIC, used BIOTIC substrate affinity.
Brachiopoda	Feeding Habit	0	3	0	0	0	0	0	Brusca et al. (2016)
Cancer pagurus	Living Habit	2	1	0	1	0	0		Burrows during feeding and breeding, hides under rocks (Lawton, 1989; Hall et al., 1991)
	Feeding Habit	0	0	0	1	2	0	0	Known as an active predator, will engage in scavenging (e.g. Kaiser et al., 1996; Depireux et al., 2016)
Cephalopoda	Size	2	2	2	2	2	2	2	(Wood, 2000)
	Living Habit	2	1	0	0	0	0	0	Some Cephalopoda (e.g. Octopuses) live/hide in crevices (e.g. Aronson, 1986)
Cerianthidae	Living Habit	0	0	2	1	0	0		More tube dwelling then burrowing (Brusca et al., 2016)
	Feeding Habit	0	0	2	0	2	0	0	Passive suspension feeder (Feder et al., 1991).
Didemnidae	Reproduction	2	0	0	2				Ritzmann et al. (2009)
	Feeding Habit	0	3	0	0	0	0	0	From Tunicata (Brusca et al., 2016)

Table C.2: (Continued): Trait values that were changed from those presented in the databases used. Modality columns (1-8) represent the modalities of each trait. Changed modalities are presented in bold. For example the first line shows a taxa where LH1 was modified to have have fuzzy code 1, which differs from the reported value in the database. In the case of Feeding habit modality 2 and 3 refer to FH3a and FH3p, rather than FH2 and FH3. The modality code F2 was not used in this dataset, as it was combined with FH1.

Taxa	Trait	Modalities							Source
		1	2	3	4	5	6	7	
<i>Drifa glomerata</i>	Body Form	0	0	0	0	0	0	3	Moen and Svensen (2004)
	Feeding Habit	0	0	3	0	0	0	0	Feder et al. (1991)
<i>Dysidea fragilis</i>	Living Habit	0	1	0	0	0	2		Crevice dwelling added to represent growing under boulders (Picton et al., 2011)
Echinoidea	Living Habit	2	1	0	2	0	0		Some Echinoidea hide under rocks (e.g. Young and Bellwood, 2011)
	Feeding Habit	2	0	1	0	2	0	2	Suspension feeding (Brusca et al., 2016), grazes by definition.
<i>Echinus esculentus</i>	Feeding Habit	1	0	0	1	0	0	2	Surface deposit feeder implied from grazer traits in BIOTIC. Carrion feeding has been observed (Kaiser et al., 1996).
Gastropoda	Feeding Habit	2	2	2	2	2	2	2	Moen and Svensen (2004)
	Movement	2	2	2	1				Some Gastropoda swim (Brusca et al., 2016) (ATD didn't observe any swimming Gastropod).
Geodia	Size	0	0	2	2	2	2		van Soest et al. (2000)
	Feeding Habit	0	3	0	0	0	0	0	From Porifera (Fish and Fish, 2011)
Gorgonocephalus	Feeding Habit	0	0	2	2	2			Emson et al. (1991), Feder et al. (2006) and Deja et al. (2016)
Henricia	Feeding Habit	0	0	1	0	2	0	0	Lambert (2000)
Hippasteria phrygiana	Size	0	0	0	2	1	0		Citations on ATD suggest S4 is more common than S5
Hydrozoa	Size	2	2	2	2	2	2	2	ATD states, size range as mm to m
	Feeding Habit	0	0	2	0	2	0	0	Gili et al. (1998)
<i>Mycale lingua</i>	Feeding Habit	0	3	0	0	0	0	0	From Porifera (Fish and Fish, 2011)
Nemertea	Size	2	2	2	2	2	2	2	Hayward and Ryland (2017)
Neohela	Reproduction	0	0	0	3				Was given a 2 for R4 by ATD, no evidence of any method other than brooding hence R4 was reassigned to 3.
Nephtheidae	Body Form	0	0	0	0	0	0	3	From species (van Ofwegen et al., 2005; van Ofwegen, 2016; Neves et al., 2020)
	Feeding Habit	0	0	3	0	0	0	0	Feder et al. (1991)
Ophiuroidea	Size	1	2	2	2	1	1		ATD focused on smaller Arctic species, range is disc size 3mm - 150mm (most under 50mm), commonly 2-3 times disc but up to 20 (Stöhr et al., 2012).
	Feeding Habit	1	0	1	2	2	0	1	(Lambert and Austin, 2007)
Paguridae	Feeding Habit	2	0	2	2	2	0	2	Macdonald et al. (2010)
Phakellia	Body Form	0	0	0	0	2	0	1	Some species are fan shaped (Taboada et al., 2022)
	Feeding Habit	0	3	0	0	0	0	0	From Porifera (Fish and Fish, 2011)

Table C.2: (Continued): Trait values that were changed from those presented in the databases used. Modality columns (1-8) represent the modalities of each trait. Changed modalities are presented in bold. For example the first line shows a taxa where LH1 was modified to have have fuzzy code 1, which differs from the reported value in the database. In the case of Feeding habit modality 2 and 3 refer to FH3a and FH3p, rather than FH2 and FH3. The modality code F2 was not used in this dataset, as it was combined with FH1.

Taxa	Trait	Modalities							Source
		1	2	3	4	5	6	7	
Polychaeta	Size	2	2	2	2	2	1		For ATC species up to 500mm (Degen and Faulwetter, 2019), species larger than 500mm are known.
	Feeding method	2	2	1	2	2	1	1	Wide range of feeding methods (Fish and Fish, 2011).
Polymastiidae	Body Form	2	0	2	0	0	0	1	Some species judged to have some branching characteristics (Plotkin et al., 2017).
	Feeding Habit	0	3	0	0	0	0	0	From Porifera (Fish and Fish, 2011)
Porifera	Size	0	2	2	2	2	2		Hayward and Ryland (2017)
	Body Form	2	0	2	0	2	0	1	Hayward and Ryland (2017), breaching taxa are present in the study region.
	Feeding Habit	0	2	0	0	1	0	0	Fish and Fish (2011)
	Substrate Affinity	1	2	2	0				Soft bottom aggregations known in the region (Buhl-Mortensen et al., 2019)
<i>Protanthea simplex</i>	Feeding method	0	3	0	0	0	0	0	From Porifera (Fish and Fish, 2011)
<i>Reteporella</i>	Body Form	0	0	0	0	2	0	1	Inferred from photographs
	Feeding method	0	3	0	0	0	0	0	From Porifera (Fish and Fish, 2011)
Sabellidae	Feeding method	1	0	2	0	0	0	0	Jumars et al. (2015)
Serpulidae	Feeding method	0	0	3	0	0	0	0	Jumars et al. (2015)
Sertulariidae	Body Form	0	0	0	0	1	0	2	Photographs, additionally from descriptions in Medel and Vervoort (1998)
	Feeding method	0	0	2	0	0	0	0	Macdonald et al. (2010)
Thenaea	Feeding Habit	0	0	3	0	0	0	0	From Porifera (Fish and Fish, 2011)
<i>Thenaea abyssorum</i>	Feeding Habit	0	0	3	0	0	0	0	From Porifera (Fish and Fish, 2011)
<i>Tubularia indivisa</i>	Body Form	0	1	0	0	2	0	0	Stalk better described as vermiform
	Reproduction	2	0	0	2				Regenerative potential, Hydroids use asexual reproduction to regenerate (Stamp and Tyler-Walters, 2018).

Appendix D: Full Trait Matrix

Table D.1: Full trait matrix for Chapter 4, taxa sorted alphabetically. Blank cells represent missing data. Column names are the modality codes and consistent with the definitions in table 4.1. Only traits used in the BTA (chapter 4) are displayed.

Taxon	S1	S2	S3	S4	S5	S6	BF1	BF2	BF3	BF4	BF5	BF6	BF7	SK1	SK2	SK3	SK4	SK5	R1	R2	R3	R4	LH1	LH2	LH3	LH4	LH5	LH6	MV1	MV2	MV3	MV4	FH1	FH3a	FH3p	FH4	FH5	FH6	FH7	SA1	SA2	SA3	SA4		
Acesta excavata	0	0	2	1	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	0	2	2	0	0	0	0	2	2	0	1	0	0	3	0	0	0	0	0	0	0	3	0	0
Actiniaria	0	2	2	2	0	0	2	0	0	0	2	0	0	0	0	0	2	2	2	2	2	0	2	1	1	0	1	2	2	1	1	1	0	0	1	0	2	0	0	2	2	0	0		
Actinostola callosa	0	0	0	3	0	0	1	0	0	0	2	0	0	0	0	0	2	2	2	2	0	0	2	0	0	0	0	3	3	0	0	0	0	0	2	0	2	0	0	2	2	0	0		
Alcyonacea	0	0	2	2	0	0	0	0	1	0	2	0	2	2	0	0	0	2	2	2	0	0	0	0	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	3	0	0		
Antedonoidea	0	0	0	0	0	0	0	0	0	0	3	0	0	3	0	0	0	0	0	3	0	0	2	0	0	0	0	1	0	0	2	2	0	0	3	0	0	0	0	0	3	0	0		
Antho dichotoma	0	0	0	3	0	0	0	0	0	0	1	0	2	0	3	0	0	0	0	2	0	2	0	0	0	0	0	3	3	0	0	0	0	3	0	0	0	0	0	0	3	0	0		
Anthomastus	0	3	0	0	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0		
Anthothela grandiflora	0	0	0	3	0	0	0	0	0	0	1	0	2	3	0	0	0	0	0	2	0	0	0	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0		
Aphroditidae	0	2	2	1	1	0	0	3	0	0	0	0	0	0	0	0	0	3	0	3	0	0	2	0	0	2	0	0	2	0	2	0	0	0	2	1	0	0	0	2	2	0	0		
Aplysia sulfurea	0	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0	0	3	2	0	2	0	0	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0		
Argentina	0	0	0	1	2	2	0	0	0	0	0	0	3	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	0	3		
Asbestopluma pennatula	0	2	2	0	0	0	0	2	0	0	2	0	0	0	3	0	0	0	2	2	0	2	0	0	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	2	2	0	0		
Ascidia	0	0	2	2	0	0	1	1	0	0	2	0	0	0	0	0	3	0	2	2	0	0	0	1	0	0	2	3	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0		
Asconema setubalense	0	0	0	1	2	0	1	0	0	0	2	0	0	0	3	0	0	0	0	0	3	0	0	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0		
Asteroidea	0	2	2	2	1	0	0	3	0	0	0	0	0	3	0	0	0	0	0	2	0	1	2	0	0	1	0	0	1	2	0	0	1	0	1	2	2	1	1	2	2	0	0		
Axinella infundibuliformis	0	0	2	2	0	0	1	0	0	0	2	0	0	0	3	0	0	0	2	0	2	0	0	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0		
Balticina	0	0	0	0	3	0	0	1	0	0	2	0	1	2	0	0	0	1	2	2	0	0	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0		
Bolocera tuediae	0	0	0	3	0	0	2	0	0	0	2	0	0	0	0	0	2	2	2	0	0	0	2	0	0	0	2	3	0	0	0	0	0	0	1	0	2	0	0	0	2	2	0		
Bonellidae	1	2	2	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3	0	3	0	0	0	1	0	2	0	0	2	1	0	0	3	0	0	0	0	0	0	2	2	0	0		
Brachiopoda	2	2	2	0	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	2	0	2	2	0	0	2	2	3	0	0	0	0	0	3	0	0	0	0	0	0	2	2	0		
Brosme brosmie	0	0	0	0	0	3	0	0	0	0	0	0	3	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	3	0	0		
Bryozoa calcareous branched	2	2	2	2	0	0	0	0	0	0	0	0	3	3	0	0	0	0	2	0	0	2	1	0	0	0	2	3	0	0	0	0	0	3	0	0	0	0	0	1	2	2	0		
Burrows big	0	2	1	0	0	0	1	2	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0		
Burrows small	1	2	0	0	0	0	1	2	0	2	0	1	0	0	0	0	0	0	0	0	0	2	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0		
Cancer pagurus	0	0	0	1	2	0	0	0	3	0	0	0	0	2	0	1	0	0	2	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	2	0	0	0	0	2	2	0	0		
Caridea	0	2	2	2	2	0	0	2	0	2	0	0	0	0	0	3	0	0	0	2	0	2	2	1	0	0	0	0	1	1	2	0	0	0	0	3	0	0	0	2	2	0	2		
Cephalopoda	2	2	2	2	2	2	0	2	2	0	0	0	0	2	0	0	0	2	0	0	0	3	2	1	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	2	0	0			
Ceramaster granularis	0	2	2	0	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	2	0	1	3	0	0	0	0	0	0	3	0	0	0	0	2	2	0	0	0	0	3	0	0		
Cerianthidae	0	3	0	0	0	0	0	2	0	0	2	0	0	0	0	0	0	3	2	2	0	0	0	2	1	0	0	2	2	0	0	0	0	2	0	0	0	0	0	3	0	0	0		
Chelonaplysilla	0	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	3	2	0	2	0	0	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	3	0	0			
Chimaera monstrosa	0	0	0	0	0	3	0	0	0	0	0	3	0	0	0	0	3	0	0	3	0	3	0	0	0	0	0	0	0	0	0	3	0	0	3	0	0	0	1	0	0	2			
Cidaris cidaris	0	0	3	0	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	1	0	0	0	0	2	2	2	0	0			
Clavularia borealis	0	3	0	0	0	0	0	0	0	0	1	0	2	3	0	0	0	0	2	2	0	0	0	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0		
Craniella zetlandica	0	2	2	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	2	2	0	0	0	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	0	2	1	0		
Didemnidae	0	0	0	0	0	0	0	2	0	0	1	0	0	1	0	0	2	0	2	0	0	2	0	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	0	2	1	0		
Drifa glomerata	0	0	0	3	0	0	0	0	0	0	0	0	3	2	0	0	0	2	2	0	0	2	0	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	2	2	0	0		
Dysidea fragilis	0	0	0	3	0	0	2	0	2	0	0	0	0	0	0	0	3	0	2	0	2	0	0	1	0	0	2	3	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0		
Echinoidea	0	2	2	2	0	0	2	0	1	0	0	0	0	3	0	0	0	0	0	2	2	2	2	1	0	2	0	0	2	2	0	0	2	0	1	0	2	0	2	2	0	0	0		
Echinus	0	0	2	2	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	1	0	0	1	0	0	2	0	3	0	0	
Echinus esculentus	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	1	0	0	1	0	0	2	0	3	0	0	
Echiuroidea	1	2	1	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3	0	3	0	0	0	1	0	2	0	0	1	2	0	0	2	2	0	0	0	0	0	2	1	0	0		
Gadiculus argenteus	0	0	2	1	0	0	0	0	0	0	0	3	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	2	2	0	0		
Gadidae	0	0	0	1	2	2	0	0	0	0	0	3	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	2	0	0	1	
Gastropoda	2	2	2	2	1	0	2	2	2	0	0	0	0	2	0	0	0	2	0	2	2	2	2	2	0	2	1	1	2	2	2	1	2	2											

Table D.1: (Continued): Full trait matrix for Chapter 4, taxa sorted alphabetically. Blank cells represent missing data. Column names are the modality codes and consistent with the definitions in table 4.1. Only traits used in the BTA (chapter 4) are displayed.

Taxon	S1	S2	S3	S4	S5	S6	BF1	BF2	BF3	BF4	BF5	BF6	BF7	SK1	SK2	SK3	SK4	SK5	R1	R2	R3	R4	LH1	LH2	LH3	LH4	LH5	LH6	MV1	MV2	MV3	MV4	FH1	FH3a	FH3p	FH4	FH5	FH6	FH7	SA1	SA2	SA3	SA4		
Munida	0	2	2	0	0	0	0	0	3	0	0	0	0	2	0	2	0	0	0	0	0	0	3	2	1	0	2	0	0	0	1	2	2	2	0	0	2	2	0	0	2	2	2	2	
Muriceides	0	0	1	2	2	1	0	0	0	0	1	0	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	
Muriceides kükenethali	0	0	1	2	2	1	0	0	0	0	1	0	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	
Mycale (Mycale) lingua	0	0	0	3	0	0	2	0	2	0	2	0	0	0	0	3	0	0	0	2	0	2	0	0	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	2	2	0	0	
Nemertea	2	2	2	2	2	2	0	3	0	0	0	0	0	0	0	0	0	0	3	1	2	1	0	2	2	0	2	2	0	0	2	2	2	0	0	0	2	2	1	0	2	2	2	0	
Neohela	0	3	0	0	0	0	0	2	0	1	0	0	0	0	0	3	0	0	0	0	0	0	3	1	0	0	2	0	0	0	2	0	1	3	0	0	0	0	0	0	3	0	0	0	
Nephtheidae	0	2	2	2	0	0	0	0	0	0	0	0	3	2	0	0	0	2	0	2	0	0	2	2	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	2	2	0	0	
Oceanapia robusta	0	0	2	2	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	2	2	0	0	0	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0	
Ophiuroidea	1	2	2	2	1	1	0	0	3	0	0	0	0	3	0	0	0	0	0	0	2	0	2	2	2	0	2	0	0	2	2	1	1	0	1	2	2	0	1	2	2	0	0		
Paguridae	2	2	1	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0	0	0	2	0	2	3	0	0	0	0	0	0	3	0	0	2	0	2	2	2	0	2	2	0	0		
Pandalidae	0	2	2	2	0	0	0	2	0	2	0	0	0	0	0	3	0	0	0	0	2	0	2	3	0	0	0	0	0	0	1	2	2	0	1	0	2	0	0	0	2	2	0	0	
Paragorgia arborea	0	0	0	0	2	1	0	0	0	0	0	0	3	3	0	0	0	0	0	2	0	0	2	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	
Paramuricea placomus	0	1	2	2	2	1	0	0	0	0	0	0	3	3	0	0	0	0	0	2	1	0	1	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	
Parastichopus tremulus	0	0	0	2	1	0	0	3	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	2	1	1	0	
Phakellia	0	0	0	2	2	0	0	0	0	0	2	0	1	0	3	0	0	0	0	2	0	2	0	0	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	3	0	0		
Physic blennoides	0	0	0	0	1	2	0	0	0	0	0	3	0	3	0	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	0	3	0	0	0	
Plakortis simplex	0	2	1	0	0	0	0	0	3	0	0	0	0	0	3	0	0	0	0	2	0	0	2	0	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0	
Pleurometiformes	0	0	0	0	1	2	0	0	2	0	0	2	0	3	0	0	0	0	0	0	3	0	0	2	0	0	1	0	0	0	1	0	2	0	0	0	0	3	0	0	0	1	0	0	
Pollachius virens	0	0	0	0	2	1	0	0	0	0	0	3	0	3	0	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	0	3	
Polychaeta	2	2	2	2	2	1	0	3	0	0	0	0	0	0	0	0	0	3	1	2	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2	1	1	2	2	2	0	
Polymastiidae	0	2	2	2	0	0	2	0	2	0	0	0	1	0	3	0	0	0	0	2	2	0	0	0	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0	
Pontaster tenuispinus	0	0	0	3	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	
Porania	0	0	0	3	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	1	0	0	1	2	0	0	2	2	0		
Poraniidae	0	0	2	2	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	2	0	1	3	0	0	0	0	0	0	0	3	0	0	2	0	1	2	1	0	0	2	2	0		
Porifera	0	2	2	2	2	2	2	0	2	0	2	0	1	2	2	0	0	1	2	2	2	2	0	0	0	1	0	2	3	0	0	0	0	0	2	0	0	1	0	0	1	2	2	0	
Porifera big	0	0	0	1	2	2	2	0	1	0	2	0	1	1	2	0	0	1	2	2	2	2	0	0	0	1	0	2	3	0	0	0	0	0	2	0	0	1	0	0	1	2	2	0	
Porifera encrusting	0	2	2	2	1	0	0	0	3	0	0	0	0	2	2	0	0	1	2	2	2	2	0	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	0	0	2	2	0
Porifera fan	0	2	2	2	2	2	0	0	0	0	1	0	2	2	2	0	0	1	2	2	2	2	0	0	0	1	0	2	3	0	0	0	0	0	0	3	0	0	0	0	0	0	2	2	0
Porifera globulose	0	2	2	2	2	2	3	0	0	0	0	0	0	2	2	0	0	1	2	2	2	2	0	0	0	1	0	2	3	0	0	0	0	0	0	3	0	0	0	0	0	1	2	2	0
Porifera globulose small	0	2	1	0	0	0	3	0	0	0	0	0	0	2	2	0	0	1	2	2	2	2	0	0	0	1	0	2	3	0	0	0	0	0	0	3	0	0	0	0	0	1	2	2	0
Porifera medium	0	1	2	1	0	0	2	0	2	0	2	0	1	2	2	0	0	1	2	2	2	2	0	0	0	1	0	2	3	0	0	0	0	0	2	0	0	1	0	0	1	2	2	0	
Porifera small	0	2	1	0	0	0	2	0	2	0	2	0	1	2	2	0	0	1	2	2	2	2	0	0	0	1	0	2	3	0	0	0	0	0	3	0	0	0	0	0	1	2	2	0	
Primnoa resedaeformis	0	0	0	0	0	3	0	0	0	0	0	0	3	3	0	0	0	0	0	2	2	0	0	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	
Prothemia simplex	0	3	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	3	2	2	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	0	2	2	0	
Quasillina	0	3	0	0	0	0	2	0	0	0	1	0	0	0	3	0	0	0	2	2	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	
Reteporella	0	2	2	0	0	0	0	0	0	0	2	0	1	3	0	0	0	0	2	0	0	2	0	0	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	0	2	2	0	
Reteporella beaniana	0	3	0	0	0	0	0	0	0	0	2	0	1	3	0	0	0	0	2	0	0	2	0	0	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0	
Sabellidae	2	2	2	2	2	0	0	3	0	0	0	0	0	0	0	0	0	3	1	2	0	2	0	0	3	0	0	0	3	0	0	0	0	1	0	2	0	0	0	0	2	2	1	0	
Sebastes	0	0	0	0	1	2	0	0	0	0	0	3	0	3	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	1	2	2	0	
Serpulidae	2	2	2	0	0	0	0	3	0	0	0	0	0	2	0	0	0	2	0	2	0	2	0	0	3	0	0	0	3	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0	
Sertulariidae	0	2	2	2	0	0	0	0	0	0	1	0	2	0	0	3	0	0	2	0	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	2	0	2	0	0	0	2	2	0	
Stelletta	0	1	2	2	0	0	2	0	2	0	2	0	0	0	3	0	0	0	0	2	0	0	0	0	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0	
Stichastrella rosea	0	0	0	3	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	1								

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