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Ocean and Earth Science

SPATIAL PATTERNS IN BENTHIC SEAMOUNT HABITATS: SCALES, DRIVERS AND EFFECTS ON BIODIVERSITY

by

Lissette Victorero Gonzalez

Thesis for the degree of Doctor of Philosophy

August 2018

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

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The deep sea is the largest ecosystem on our planet, but its sheer size and remoteness causes it to be one of the least explored frontiers. One of the most common deep-sea habitat types are seamounts, which are mountains that can elevate thousands of meters above the seabed. For deep-sea fauna, seamounts provide a distinctive setting amongst the surrounding abyssal plains, with their hard substrate, steep slopes and dynamic hydrographies. Only a small fraction of seamounts have been sampled, but many ecological hypotheses have been generated, which suggest that these habitats have an important ecological function in the deep-sea. Here, I investigate a series of seamounts within the Equatorial Atlantic using ROV video footage, CTD and ship-based multibeam data collected during the Tracing Ocean Processes Using Corals and Sediments (TROPICS) research expedition. This thesis presents new data on megabenthic communities and describes ecological and biodiversity patterns in a region in which seamount research has been extremely limited.

The aim of this thesis is to characterise the benthic communities and their diversity patterns on seamounts across the poorly sampled Equatorial Atlantic. More specifically, this work aims to 1) improve the understanding of the beta diversity pattern of seamount megabenthos, 2) understand the basin-wide spatial distribution and biodiversity patterns of cold-water coral taxa on Equatorial Atlantic seamounts and 3) provide a high-resolution biological data set and an ecological insight into a transverse ridge –habitat, which is currently being proposed as an area of conservation in relation to deep-sea mining. The findings suggest that seamounts have high beta diversity, which is dominated by species replacing each other in response to changing environmental conditions, an ecological process, which is likely to enhance the overall biodiversity on seamounts. The new coral data produced in this thesis show that the Equatorial Atlantic seamounts harbour a high number of cold-water coral species, with species richness decreasing east-to west, potentially as a result of a decreasing productivity regime. The data from the transverse ridge reveal a set of complex geomorphologies, which host vulnerable marine ecosystems. The results and data sets from this thesis provide new observations of species from many previously uncharacterised seamounts, which contribute towards the wider biogeography of deep-sea fauna. The findings also provide a platform and basis for future deep-sea exploration and biogeographical studies within the region of the Equatorial Atlantic.

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Academic Thesis: Declaration Of Authorship

I, Lissette Victorero Gonzalez, declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

Spatial Patterns in Benthic Seamount Habitats: Scales, Drivers and Effects on Biodiversity

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
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3. Where I have consulted the published work of others, this is always clearly attributed;
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   Victorero, L., Robert, K., Robinson, L.F., Taylor, M.L. and Huvenne, V.A., 2018. Species replacement dominates megabenthos beta diversity in a remote seamount setting. *Scientific reports*, *8*(1), p.4152.

   Victorero, L., Watling, L., Deng Palomares, M.L. and Nouvian, C., 2018. Out of sight, but within reach: A Global History of Bottom-Trawled Deep-Sea Fisheries from> 400 m depth. *Frontiers in Marine Science*, *5*, p.98.

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Acknowledgements

I would like to acknowledge my supervisors Dr. Veerle Huvenne, Professor Laura Robinson and Dr. Michelle Taylor and thank them for their guidance and expertise throughout my PhD. I would also like to thank Katleen Robert and Leigh Marsh for “showing me the ropes” during my PhD. I appreciate the funding I have received from the NERC SPITFIRE DTP enabling me to partake in conferences, statistical courses and a secondment at the University of Hawai’i at Manoa. I would like to thank Professor Les Watling for hosting me and for his infectious enthusiasm about deep-sea science. Mahalo to Natalie and Kate for taking me under their wings and showing me the beauty of island life. Thank you to all my office mates through time, but in particular to Matt, Rhi and Lavinia, for creating a fun and friendly work environment.

I am extremely grateful for the PhD community we have at NOC, where I have made many friendships through the years. In particular I would like to thank my sister from another PhD, Lucie, whose optimism, joy and support are unparalleled and a great source of motivation in life (and at the gym). Thank you also to Izzy, Sarah, Steph, Katie, Neela, Jonny, Gavin and many others for all the fun times and stimulating conversations at the pub. I would also like to thank my two best friends Milla and Karo, although they live in the faraway land of Finland, are always just a Whatsapp away and made sure that I always have their support, love and the jokes that no one else understands. And last, but not least, I would like to thank my boyfriend Richard for the loving support and patience during the last two years of my PhD and for being one of my biggest fans.

Finally, this journey would have not been possible without the encouragement, support and love of my parents, Meljayi and Alberto, who are integral in everything I do and always believe in me.

Chapter 1 Introduction

Chapter 1

1.1 The importance of biodiversity

Biodiversity is the broad umbrella term given to the biological variety of life encountered on our planet, ranging from the scale of single genes, over species and communities through to whole ecosystems such as rainforests and coral reefs (DeLong, 1996). It is now relatively well established that biodiversity is essential for the provisioning of ecosystem services (Danovaro et al., 2008). That is, biodiversity enhances ecological processes, such as the provision of food and water, climate and disease regulation, support of nutrient cycles and oxygen production and cultural services such as spiritual and recreational benefits (Lefcheck et al., 2015; Worm et al., 2006). Accordingly, ecosystem services are considered essential for humanity's well-being (Agarwala et al., 2014; Costanza et al., 1998, 2017) and therefore changes in biodiversity can be considered of high global importance (Sala et al., 2000).

Currently, global biodiversity is in decline (Butchart et al., 2011; Pereira et al., 2010; Sala et al., 2000) with many scientists suspecting the planet is in the initial stages of the sixth mass extinction (Barnosky et al., 2011; Ceballos et al., 2017; McCallum, 2015; Pievani, 2014; Sala, 2000). While the previous five mass extinctions have occurred across geological timescales and have been prompted by events such as the impact of meteorites, ice ages and large-scale volcanic eruptions, the sixth mass extinction is likely caused by anthropogenic activities (Barnosky et al., 2011; Ceballos et al., 2010, 2017; McCallum, 2015; Pievani, 2014; Sala, 2000). In order to counteract biodiversity loss and optimise conservation efforts, it has been deemed crucial to understand the distribution and environmental drivers of biodiversity so strategic decisions can be made for the prioritisation of conservation areas and the allocation of resources (Brooks et al., 2006; Possingham and Wilson, 2005).

The oceans cover two thirds of our planet's surface area and therefore contribute ~ 60 % to the monetary value of global ecosystem services (Costanza, 1999; Costanza et al., 1998). There is a particular lack of consensus on the spatial and temporal patterns of biodiversity and how to best conserve these in the most cost-effective ways (Devillers et al., 2015; Gray, 1997; Redpath et al., 2013). Simultaneously, the marine environment is experiencing an increase in anthropogenic impacts in the form of climate change leading to ocean acidification, increased temperatures and expansion of deoxygenated zones, pollution from agricultural run-off, overexploitation of fisheries, habitat destruction, and oil and gas extraction (Worm and Lenihan, 2014).

The lack of knowledge on the organisation of biodiversity is most pronounced in the deep sea, i.e. below water depths of 200 m. The deep sea is the largest habitat on our planet with an area of 434 million km^2 and a water volume of 1.34 billion km^3 encompassing a total of 50% of the Earth's surface (Costello, 2009). Since most of the deep sea remains unexplored, here biodiversity studies are very much still in an exploratory phase, with new discoveries rapidly emerging and confounding scientists by shifting old classical paradigms (Danovaro et al., 2014). Despite this lack of knowledge, it is clear that the deep sea hosts important ecosystem services. Those identified thus far include regulatory services (temperature, atmospheric greenhouse gases, absorption of waste and pollutants) and provision of food, hydrocarbons and novel biological compounds (Armstrong et al., 2010, 2012; Thurber et al., 2013). Here, changes in biodiversity and hence ecosystem services are threatened primarily by deep-sea trawling, waste disposal, rising CO_2 levels and the potential of near-future deep-sea mining (Ramirez-Llodra et al., 2011; Thurber et al., 2013). Therefore, in order to conserve the deep sea, which is still considered to be a relatively pristine ecosystem, the knowledge gaps on biodiversity and how this ecosystem functions must be filled (Ramirez-Llodra et al., 2011). This information will contribute towards understanding the resilience and vulnerability of the deep sea in the face of growing pressure from anthropogenic impacts (Armstrong et al., 2010).

1.2 Patterns of biodiversity in the deep sea

The deep sea was originally thought to be void of life (Forbes, 1844). The azoic theory, which stems from the early 19th century, considered temperature, light and food availability to be too low and the pressure too high to support any type of life forms. These hypotheses, showing that life could not exist below 550 m were supported by the results of dredging activities in the oligotrophic regions within the Mediterranean Sea (Anderson and Rice, 2006). The scientific community held on to these beliefs, despite a more modern dredging apparatus hauling corals and other invertebrates from the depths of 730 m in 1818 (Anderson and Rice, 2006). Finally, in 1868, following a series of expeditions set out to disprove the azoic theory using modern dredges, which yielded hundreds of species around the British Isles alone, one of the most drastic misconceptions in ecology was overturned (Anderson and Rice, 2006 and references therein).

As time passed, deep-sea exploration and sampling was enabled by technological advances, leading to a radical re-evaluation of what we think about deep-sea life. For example, species richness in the deep sea was considered to be significantly lower than in the shallow waters (Ekman, 1953), but in 1960 epibenthic sledge sampling introduced the idea of comparable species numbers and abundances between the two (Hessler and Sanders, 1967). The development of manned and unmanned submarine vehicles was another key breakthrough, enabling experimentation and visual sampling of the fauna, in addition to prolonged in situ observations, including those from extreme environments such as hydrothermal vents (Lonsdale, 1977).

Despite the remarkable advances facilitating access to remote depths, deep-sea exploration and hence biodiversity studies within this ecosystem are still in their infancy with a mere 0.0001 % of total deep-sea habitat having been sampled (Costello, 2009). The sheer size and remoteness of the deep sea means that sampling this ecosystem is both time consuming and expensive. The lack of information has led to an array of speculation of how many species exist within the deep sea. Initial estimates ranged from millions of species to over ten million species (Grassle and Maciolek, 1992). The latter was considered an overestimate and a new estimate of 0.5 million species was provided (Poore and Wilson, 1993). However, these calculations are most likely plagued by a historical bias (Higgs and Attrill, 2015). The bias is introduced by wide-ranging species, which are discovered first in the deep sea, and as such estimates of how many species are left to be discovered are unreliable resulting in that deep-sea species richness cannot be estimated with confidence (Higgs and Attrill, 2015).

How this richness is organised through time and space is less clear, with the latter being of particular importance to the research presented here. With time, two main concepts regarding the spatial organisation of deep-sea biodiversity have become established within the literature (Rex and Etter, 2010). These theories overall address the relationship between biodiversity and 1) latitudinal gradients and/or 2) depth and depth-related gradients.

1.2.1 The effect of latitude on deep-sea biodiversity

The distribution of biodiversity in relation to latitude is a well-established trend within the terrestrial realm, where there is reduced diversity within the polar regions and higher diversity within the equatorial regions (Willig et al., 2003). The reasons behind such patterns are more debatable. One popular explanation is that the polar regions are characterised by extreme temperatures, which vary seasonally permitting such regions to be inhabited only by species with wide climatic tolerances (Brown et al., 2014). In high latitude regions, such species have an advantage over their narrow-range counterparts in terms of natural selection, which does not exist in tropical regions (Stevens, 2016). Apart from extreme temperatures, polar regions have also experienced higher variability in climatic conditions through geological time scales leading to periodic extinctions (Mannion et al., 2014). Conversely, tropical species are well-adapted to stable climatic conditions with the high temperatures generating and maintaining higher ecological and evolutionary rates and hence diversity (Brown et al., 2014). The high kinetic energy in the tropics, which is an area that has remained stable over geological time-scales, is expected to lead to higher diversification rates through a higher occurrence of mutations and reduced generation time (Allen et al., 2006).

In the deep sea, similar latitudinal biodiversity patterns have also been observed with similar explanations prevailing within the literature (Rex et al., 2000). Here, depressed diversity in higher latitude bathyal habitats has been assigned to high and seasonally varying nutrient loading supporting highly dominant and opportunistic species (Rex et al., 2000). However, this latitudinal gradient is less apparent towards the southern pole, as the deep-sea biodiversity of the Southern Ocean is considered to be particularly high, potentially because fauna has survived and evolved throughout glacial cycles (Brandt et al., 2014). Recent modelling approaches predict that maximum deep-sea species richness occurs at higher latitudes and in proximity to continental slopes, because of high carbon flux (Woolley et al., 2016). Alternatively, it has been proposed that the equatorial shallow water biodiversity hotspots of the Indo-west and east Pacific are evolution epicentres from which dispersal into deeper waters and higher latitudes creates an impression of latitudinal biodiversity pattern (Gage et al., 2004). There is also a hypothesis relating specifically to the Atlantic Ocean, where reduction in deep-sea area with increasing latitude is thought to be a driver of latitudinal patterns, since species richness has a positive relationship with seabed area (Lambshead et al., 2000).

1.2.2 The effect of depth and depth-related variables on deep-sea biodiversity

The relationship of biodiversity with depth has been relatively well studied (Rex and Etter J., 2010), but because depth is intrinsically linked to an array of different chemical and physical parameters, mainly temperature, nutrient availability, pressure, salinity and oxygen, it is difficult to disentangle the effect of each environmental driver. Many studies in the deep-sea have found that biodiversity patterns are often unimodal in certain regions (Fig. 1.1), peaking at the middle of the depth gradient, with apparent reduction in species richness towards abyssal depths (Rex and Etter J., 2010). However, there is variability between different studies depending on the taxa and region that has been sampled. For example, in the NE Atlantic polychaete peak diversity occurs at 1800 m (Paterson and Lambshead, 1995), while in the tropical Atlantic the highest diversity is at 2000 m (Cosson-Sarradin et al., 1998). Meanwhile, gastropod diversity gradients show high variability between different ocean regions within the Atlantic ocean (Stuart and Rex, 2009).

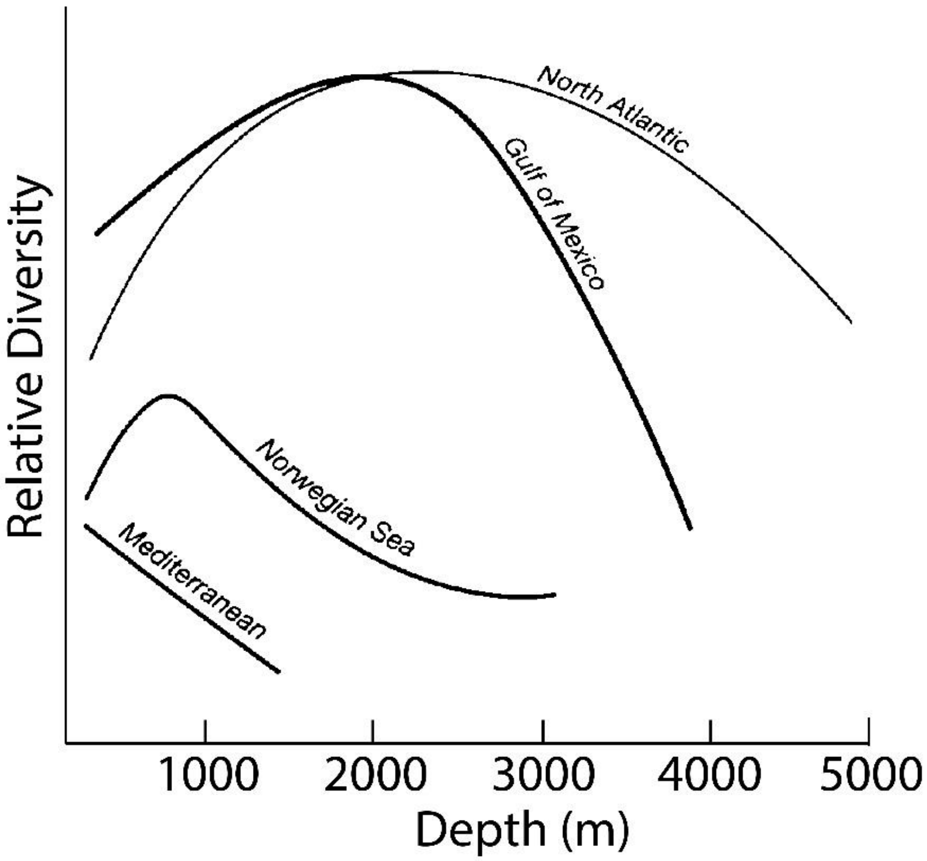


Figure 1.1 An example of megafaunal diversity plotted against depth for different regions. Source: Rex and Etter J. (2010).

There are numerous theories attempting to explain deep-sea biodiversity patterns by considering both ecological and evolutionary processes. The ecological ones revolve around food supply and hence energy availability in a similar fashion to latitudinal gradients. For example, it has been proposed that continental slope depths harbour the greatest diversity, because they are stable environments which have high enough food supply leading to peak diversity at mid-slope depths (2300 -2800 m) (Rex, 1981). Similarly, it has been argued that intermediate food supply at continental slope depths allows greater co-existence of species as it reduces competitive interactions between species (Cosson-Sarradin et al., 1998). Furthermore, high food availability is thought to decrease diversity by reducing habitat heterogeneity thus providing opportunistic species the chance to dominate biological assemblages (Levin et al., 2001; Mengerink et al., 2014). The effect of temperature has also been tested, with contrasting results between different studies and regions. In the Atlantic, some studies have shown that temperature does not have a high impact on diversity and POC flux was the main factor (McClain et al., 2012; Tittensor et al., 2011), while in the Pacific cooler temperatures were associated with higher species richness (O'Hara and Tittensor, 2010). On the other hand, a global study by Yasuhara and Danovaro (2016) found that the unimodal pattern of species diversity in the deep sea could be explained primarily by high and low temperatures, which can constrain the physiological tolerance ranges of species (Yasuhara and

Danovaro, 2016). Other explanations for patterns of deep-sea diversity refer to a variety of physical parameters, which could increase diversity at continental slope depths. These include the presence of complex topographic features, heterogeneous sediments, varied food supply and the occurrence of catastrophic disturbances, such as turbidity flows causing intermediate levels of disturbance (Etter and Grassle, 1992; Hattori et al., 2009; Levin et al., 2001). Additionally, water-mass interfaces, where benthic assemblages include species typical to each water-mass, are considered to increase diversity (Henry et al., 2014). Despite this array of research, attempts to piece together biodiversity patterns in the deep sea are still considered mostly incomplete, since the patterns are rarely applicable across different taxa, across different regions and across different sampling equipment (Snelgrove and Smith, 2002). Future studies, along with applying more advanced analytical techniques, are needed to address the geographical biases and the faunal gaps in order to achieve a holistic understanding of the deep sea ecosystem.

1.3 Patterns of biodiversity on seamounts and seamount-like topographies

Seamounts are submarine mountains which, historically, were defined as features elevated 1000 m above the seafloor (Menard, 1964), but the more contemporary definition includes features rising a minimum of 100 m from the seabed (Staudigel et al., 2010). The term seamount encompasses a variety of isolated topographic heights occurring below 200 m water depths (Rogers, 2018). Seamounts can occur in a wide range of morphologies, such as conical, flat-topped (“guyot”) or in other complex shapes (Staudigel and Clague, 2010). Thus the seamount term can include hills (< 500m elevation), knolls (>500m seafloor) and fracture zones formed at transform faults, since these are suspected to be functionally similar in terms of their biology and ecology (Yesson et al., 2011). For the purposes of the present study, which has an ecological focus, the umbrella term of seamounts will be applied to our four study sites, comprising two guyots, a ridge-shaped elongated seamount and a transverse ridge within a fracture zone.

Seamount features have a global distribution (Fig. 1.2.), but are most abundant around the boundaries of the tectonic plates. Their high occurrence means that overall they amount to a landform the size of Europe and this ubiquitous nature makes seamounts important deep-sea ecosystems (Costello, 2009). Despite being relatively common geological seafloor features within the deep sea, their ecological characteristics remain poorly understood, with only a small minority having been scientifically investigated (Fig. 1.2) (Clark et al., 2010b; Rowden et al., 2010a). The seamounts that have been sampled, however, have led scientists to speculate that they might be important in the context of deep-sea biological communities (Rowden et al., 2010a and references therein). Expeditions have shown the seamount terrain comprises a varied landscape of hard substrates and geomorphologies, often in regions surrounded by abyssal plains, with the communities living on them typically comprising of slow-growing and long-living species (Auster, 2005). The importance of seamounts has also been considered from the perspective that seamounts could offer future "refugia" to deep-sea species against rising ocean temperatures as their slopes are bathed in deep cool waters (Rowden et al., 2010a). Similarly, their summit waters are projected to maintain high aragonite saturation under future ocean acidification scenarios, thus still providing suitable habitat for scleractinian corals (Tittensor et al., 2010).

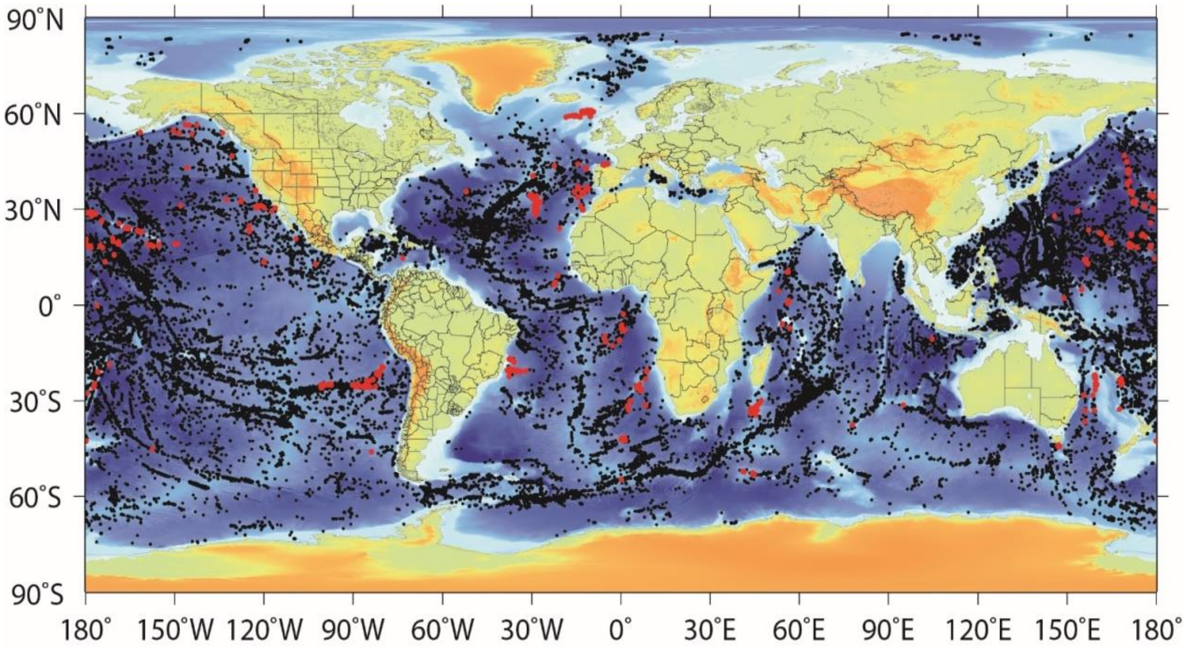


Figure 1.2 The global distribution of seamounts (black dots) based on 30 arc seconds bathymetry data overlaid with sampled seamounts data (red dots). The seamount distribution data is based on Yesson et al. (2011) and the sampled seamount data is from SeamountsOnline (Stocks, 2010). Note that the number of sampled seamounts is likely to be slightly higher, since the sampled data set only runs till 2009.

Seamounts host abundant communities of diverse fish and benthic species (Samadi et al., 2006). In fact, globally seamounts support at least 77 commercially important fish species (Rogers, 1994) while in total it is estimated that 794 fish species occur on seamounts (Morato and Clark, 2007). This makes them ideal targets for deep-sea trawling, which is extremely damaging for the benthos with no apparent recovery observed over decadal time scales (Williams et al., 2010). Trawling physically removes vast amounts of demersal fish species and hence biomass from the deep sea, in addition to removing large quantities of non-target (benthic) species, such as sponges and corals along with other invertebrates. Another potential future anthropogenic threat to seamount communities is deep-sea mining. Seamounts are often covered with ferromanganese crusts, which can be a source of cobalt, tellurium and other valuable metals that are currently under global demand (Hein et al., 2003). Similar to deep-sea trawling, mining would also cause the removal of the benthos with long-lasting or even permanent impacts to the biological assemblages on seamounts (Levin et al., 2016). The vulnerability of seamount communities has been identified by the United Nations General Assembly (Clark et al., 2011) and calls have been made to manage seamounts as single Vulnerable Marine Ecosystem units (Watling and Auster, 2017).

The fact that seamounts are poorly understood biologically has delayed conservation activities "until more is known" (Clark et al., 2011, p. 20). The lack of knowledge combined with interests to continue to exploit the resources on them, makes it pivotal to urgently understand their biogeographical patterns (changes in biodiversity in geographical space and through geological time), which in turn would provide an opportunity for sustainable ecosystem based management of fisheries and benthic habitats (Clark et al., 2011). However, as previously discussed, establishing patterns of biodiversity within the deep sea remains difficult as most of the deep sea is unexplored, with lack of cohesiveness between different studies (Snelgrove and Smith, 2002) and it is suspected that seamounts are likely to add another layer of complexity to larger biogeographical patterns within this ecosystem. The variability within seamounts caused by their different shapes, summit depths, sizes, locations and evolutionary histories leads to such features altering their local environment in distinct ways (Rowden et al., 2005). This variation in the local setting is reflected in differences in the biological communities on seamounts from the same bathyal or abyssal province (Watling et al., 2013) and from the same region (Clark and Bowden, 2015). However, systematic regional and basin-wide comparisons are rare, and often incorporate data acquired through different methodologies introducing a certain degree of uncertainty.

Consequently, the variability found between seamounts and the array of focus points in different studies have produced a wide array of theories relating to their ecological role and function within the context of deep-sea biogeography (Clark et al., 2010b). In the next sections, I review historical paradigms relating to seamount biodiversity and ecology, with two main concepts focusing on 1) their wider ecological role within the deep sea as either submarine islands leading to high endemicity or as dispersal "stepping stones" and 2) contemporary observations of seamounts as biodiversity and biomass "hotspots".

1.3.1 The ecological role of seamounts and seamount-like habitats in the deep sea

One of the most persistent and longest lasting theories in marine ecology involves endemism on seamounts (Clark et al., 2010b; McClain et al., 2009; Rowden et al., 2010a). Historically, the uniqueness of seamounts was thought to lie in the idea that they were spatially isolated submarine "islands" surrounded by oceanographic regimes creating barriers for dispersal leading to the occurrence of endemic species (de Forges et al., 2000). The specific mechanisms thought to promote endemism include juvenile recruitment back to the seamount due to the occurrence of favourable habitats, hydrodynamic barriers entrapping larvae around the seamount and specific larval behaviour (Rogers, 1994). The island biogeography and seamount endemism theories gained momentum, from the description and observations of new deep-sea fauna due to limited sampling effort (McClain, 2007), with studies such as those conducted in the Tasman Sea and SW Coral Sea seamounts reporting that up to 34% of the species sampled could be considered to be endemics (de Forges et al., 2000).

Modern studies, however, have provided contradictory evidence showing that seamount species are drawn from a regional species pool (O'Hara et al., 2008) and occur under a similar environmental regime as found in other deep-sea habitats such as the continental slope (McClain et al., 2009). A comprehensive study on the Davidson Seamount using over 60 000 megafaunal records found only 7% of species to be potentially endemic with the vast majority of species having a cosmopolitan distribution while also occurring on the adjacent continental margins (McClain et al., 2009). However, further studies are needed in different regions under a variety of oceanographic conditions to understand the distribution of different seamount fauna and their biogeographical patterns. Despite the low endemism on seamounts, some species are likely to have a more localised distribution in certain regions, thus increasing their vulnerability to the exploitation of seamount resources.

Different seamounts sharing communal taxa, however, does not necessary imply modern connectivity, which can only be revealed through genetic studies and a comprehensive understanding of connectivity within the deep sea (Clark et al., 2010a, Clark et al., 2010b). This point is illustrated by the mixed results presented in a connectivity study based on genetics of seamount fish populations. Here, some species have homogenous populations within ocean basins while others show regional differentiation (Clark et al., 2010b). In the near-future the prevalence of molecular techniques combined with increased sampling could also reveal the presence of cryptic species, which theoretically represent an unexplored opportunity for high endemism within seamounts and thus clarify patterns of modern connectivity (Rowden et al., 2010a).

An alternative hypothesis to seamounts acting as isolated islands is the suggestion that they might in fact behave as "stepping stones", facilitating long-distance dispersal across ocean basins. In the case of the cold-water coral *Desmophyllum dianthus* from the Tasmanian Seamount Region, there is evidence for gene flow occurring across hundreds of kilometres with intermediate seamounts contributing towards the species' widespread distribution (Miller and Gunasekera, 2017). Conversely, the same study found that the gene flow patterns of *Solenosmilia variabilis* are opposite, with high genetic differentiation among populations from different seamounts over small spatial scales supporting the isolated island hypothesis. Furthermore, it has been hypothesized that all tectonic islands and submerged banks act as stepping stones between the continents affecting both biogeographical and paleogeographical patterns of marine fauna (Palmiotto et al., 2017). Thus targeted biological sampling on strategic features, such as the Vema transverse ridge, which used to be above sea level and since subsiding encounters a dynamic circulation pattern, could significantly contribute towards enhancing our understanding on the stepping stone theory. However, so far there is no overall established pattern for faunal migration between seamounts (Rowden et al., 2010a).

1.3.2 Seamounts and seamount-like habitats as biodiversity hotspots

Contemporary seamount research interests have shifted more towards understanding and comparing biodiversity patterns in relation to neighbouring habitats, such as the continental slope, in order to resolve if seamounts really have special ecological attributes. Seamounts are often termed biodiversity "hotspots" as they have been affiliated with elevated species richness, biomass and abundance of organisms (de Forges et al., 2000). The reasons behind this oasis hypothesis are complex, but are often related to enhanced productivity and habitat heterogeneity, with the specific mechanisms discussed in detail in the next section. This heterogeneity in terms of food and habitat provision has led to speculations if seamounts could be biodiversity hotspots, either because of greater species co-existence or because frequent species turnover between habitats (McClain et al., 2010). Studies examining beta diversity on the scale of an individual seamount are rare (Henry et al., 2014; Lundsten et al., 2009; McClain et al., 2009; McClain and Lundsten, 2015), but are likely to be key in understanding the biodiversity hotspot hypothesis and also how seamounts contribute to the regional deep-sea diversity (McClain et al., 2010).

Seamounts have also been suggested to be abundance and biomass "hotspots", which such claims dating back to observations and exploitation of pelagic and benthopelagic fish species and precious corals (Rowden et al., 2010a). There is some support for the idea that seamounts indeed have higher biomass in comparison to the adjacent continental slope, with New Zealand seamounts having up to four times the biomass, mainly because of the occurrence of stony corals (Rowden et al., 2010b). Similarly, Sautya et al. (2011) found that seamounts had a higher abundance of coral and sponges in comparison to surrounding areas. The higher benthic biomass in the form of habitat forming species attracts deep-sea fish, for example for spawning activities, thus further enhancing the biomass of seamounts (Koslow, 1996). The thriving communities found on seamounts have also been proposed to act as a source for larvae for non-seamount habitats in geographical proximity (McClain et al., 2009).

Currently, there is a lack of evidence to suggest that seamounts have more diverse or species rich communities than comparable habitats in the deep sea. For example, comparative samples of ophiuroids from seamounts and the continental slope showed similar species richness (O'Hara, 2007). Species richness of fish has been found to be ~ 26 % higher on the continental slopes in comparison to seamount habitats around New Zealand (Tracey et al., 2004). On the contrary, a larger scale analysis using fisheries data from the Pacific found seamounts to have higher pelagic megafauna species richness than coastal or oceanic areas (Morato et al., 2010). The species, namely tunas, sharks and pelagic fish are attracted to seamounts, where they aggregate and it is likely that seamounts might serve as a migratory pathway (Morato et al., 2010). On the South-Pacific seamounts, squat lobster species richness was elevated in comparison to the New Caledonian slope (Samadi et al., 2006).

Another debatable argument is whether seamount assemblage structures differ from neighbouring habitats. Coral assemblages on NE Atlantic seamounts differ from those on the continental slope (Hall-Spencer and Rogers, 2007) and relative abundance of taxa between Davidson Seamount and adjacent slope is markedly different (McClain et al., 2009). Furthermore, equivalent samples of ophiuroids in terms of depth and area, showed different community compositions between seamounts and nearby continental slope areas due to certain ophiuroid species on seamounts being repeatedly associated with *Solenosmilia variabilis* (O'Hara et al., 2008). Similarly, Howell et al. (2010b) found that when comparing fauna sampled from similar settings from a conical-shaped seamount, a guyot-shaped seamount, and a bank, there are no distinct differences between the megafaunal communities. These contradictory results might indicate that seamounts harbour distinct fauna or act as biodiversity hotspots for certain fauna only in specific areas, where they are surrounded by markedly different marine systems or when they are highly isolated from the continental slope.

1.3.3 Environmental drivers and gradients of seamount biodiversity

Like other deep-sea ecosystems, seamount fauna appears to be influenced by the same environmental parameters that affect faunal biogeography at a large scale. These include latitudinal turnover (O'Hara, 2007), primary productivity, oxygen concentration (Wishner et al., 1990) and aragonite saturation, which impacts the distribution of stony corals (Tittensor et al., 2009). In this section, I evaluate a set of oceanographic and topographic characteristics, which influence the diversity and composition of seamount fauna ranging from a local-scale (>10's of km) to a fine-scale (< 10's of m).

The oceanographic setting of seamounts has been hotly contested since they were first discovered (Rogers, 2018; Rowden et al., 2010a).Their abrupt topography is thought to influence flow patterns, leading to enhanced productivity above and in the vicinity of seamounts with the energy cascading across different trophic levels resulting in biodiversity "hotspots" (Rowden et al., 2010a). One of the flow patterns often mentioned is the presence of Taylor columns above seamounts, which remains as one of the most prevalent paradigms present in the literature (Clark et al., 2010b). These columns, which are isolated water cells with an anticyclonic circulation above the seamount, were thought to act as an isolating mechanism entrapping larvae and plankton, but there is a lack of evidence supporting this theory (Mullineaux and Mills, 1997; Rowden et al., 2010a). Other seamount productivity enhancing mechanisms include upwelling, bringing nutrient-rich water from the bottom, which would remain trapped by the Taylor columns thus enhancing productivity above seamounts (Roden, 1987). However, there is limited data showing the existence of such hydrographies, with some arguing that the effect of Taylor columns would be too brief (two days to six weeks) to support energy transfer across trophic levels (McClain, 2007; White et al., 2007). Furthermore, a study across six seamounts, specifically trying to capture this phenomena, found no evidence for Taylor columns and suspected that the strong currents associated with mesoscale eddies prevents their formation (Read and Pollard, 2017).

Recent research, however, has found tidally generated internal waves interacting with seamounts (Turnewitsch et al., 2016; Vlasenko et al., 2018). This hydrography is considered an important mechanism for the export of particulate organic carbon (POC) (Turnewitsch et al., 2016). On Senghor seamount (near Cape Verde), POC export can be two to four times higher than in neighbouring areas with the highest export rates found on the downstream side of the seamount (Turnewitsch et al., 2016). The advection is considered to increase upward transport of nutrients to the euphotic zone, causing pulses of productivity with subsequent export of aggregated particles forming bigger and faster sinking particles (Turnewitsch et al., 2016). Isotopic studies also show fresh, high quality suspended particulate organic matter around seamounts, which is hypothesized to be delivered either by advection, downwelling or passive sinking of locally produced phytoplankton (Kiriakoulakis et al., 2009). Since tidally generated internal waves have also been consistently observed at seamounts (Read and Pollard, 2017; Vlasenko et al.), they are likely to be an important aspect of seamount hydrography and hence a key element for transferring food particles to the benthos. Other important local water-column properties include depth and correlated parameters, such as temperature, oxygen, pressure and food availability, all of which are acknowledged to be key in shaping faunal patterns on seamounts (Clark et al., 2010), because they affect biological and physiological aspects of organisms, such as settlement, survival and growth.

Seamount biodiversity is also governed by habitat heterogeneity, which is generated by the geological processes resulting in a mosaic of substrates ranging from hard exposed rock, often of volcanic origin and forming complex surfaces, to sediment flats, occurring across a depth gradient. The habitat mosaic creates differences in the hydrodynamic flow affecting benthic species leading to high patchiness (Genin et al., 1986b; Levin and Thomas, 1989). This habitat patchiness increases beta diversity (species turnover) through the provision of different substrata, which are colonized by a variety of taxa (Zeppilli et al., 2016). The availability of hard substrate is explicitly important for habitat-forming species, such as cold-water corals and sponges which can affect faunal composition at the scale of ~10s m – 10s km (Buhl-Mortensen et al., 2010). These taxa can form biogenic structures providing further habitats (down to microhabitat scale <1 m), with elevated species richness often associated with cold-water corals (Henry and Roberts, 2007). Cold-water corals can also affect assemblage patterns through the commensals living on them (O'Hara et al., 2008). In addition biogenic structures can influence local fine-scale environmental conditions, such as hydrodynamic flow and topography (Rowden et al., 2010a). In particular, species such as *Lophelia pertusa* have been coined as "ecosystem engineers", meaning it significantly impacts species richness and the heterogeneity of the benthoscape, making it particularly important in terms of ecosystem services (Jones et al., 1994). In summary, seamounts, through the provision of hard substrate at shallower depths than their surroundings, are particularly important in off-shore environments which are dominated by sedimented abyssal plains, and can have a wide implication on biogeographic patterns and hence the functionality of the deep sea (Clark, 2009a).

Advances in multibeam echosounder mapping allow the fine-scale (< 10's of m) variability of seafloor features to be characterised at various scales and linked to species richness, abundance and species turnover (beta diversity). The characteristics of interest to ecologists and to marine resource managers include quantitative variables such as slope, aspect, rugosity and elevation or suppression of the seabed surface, which have been shown to influence community composition depending on the species' traits and adaptations (Wilson et al., 2007). Changes in invertebrate faunal beta diversity and density on seamounts have been linked to slope at an individual seamount scale (McClain and Lundsten, 2015). The results show that faunal density is highest at flattest and steepest slope values indicating functional specialisation from a broad range of invertebrate species. On Alaskan seamounts highest megafaunal diversity was associated with topographical variation and microrelief (Raymore, 1982). Similarly Serrano et al., (2017) found that slope and aspect govern the distribution of gorgonians and anthipatharians, as the steep rocky surfaces on seamounts experience enhanced current activity providing an ideal elevated habitat with augmented food flux for filter and suspension feeders (Genin et al., 1986b). Furthermore, low seabed relief has been linked with a faunal composition of mobile deposit feeders, such as holothurians and echinoids (Lundsten et al., 2009). However, one of the most persistent problems when gathering environmental data for studying biodiversity is determining the appropriate scale in which the taxa are influenced by environmental covariates. The appropriate scale is poorly constrained in the deep sea, because scientific endeavours are still in exploratory phases (Higgs and Attrill, 2015). Furthermore, it appears that the effect differs between taxa and size groups (meio, macro- and megafauna) (Sellanes et al., 2010) . Currently, the most robust method to overcome this uncertainty is by collecting and comparing data over multiple spatial scales. However, it must be noted that this is not always possible or cost-effective. Nevertheless, certain terrain variables, such as topographic position index, lend themselves to multiscale analysis since the analysis scale can be manipulated by the user in respect to the resolution of the multibeam (Wilson et al., 2007). As such these habitat mapping techniques hold great promise in the field of understanding seamount biodiversity patterns, particularly because seamounts might be merely patchworks of different (deep-sea) habitats, with intrinsically complex response scales (Clark et al., 2010b).

1.4 Scientific objectives and research questions

A very small minority of seamounts have been sampled (0.004-0.4%) globally (Kvile et al., 2014) with relatively large gaps in the Equatorial Region (Fig. 1.3) (Rogers et al., 2007; Secretariat of the Convention on Biological Diversity, 2008). The aim of this thesis is to fill part of this knowledge gap by characterising the benthic communities and their diversity patterns on a series of seamounts across the Equatorial Atlantic. These patterns will then be evaluated against the known and debated theories on seamount ecology as discussed in the previous sections.

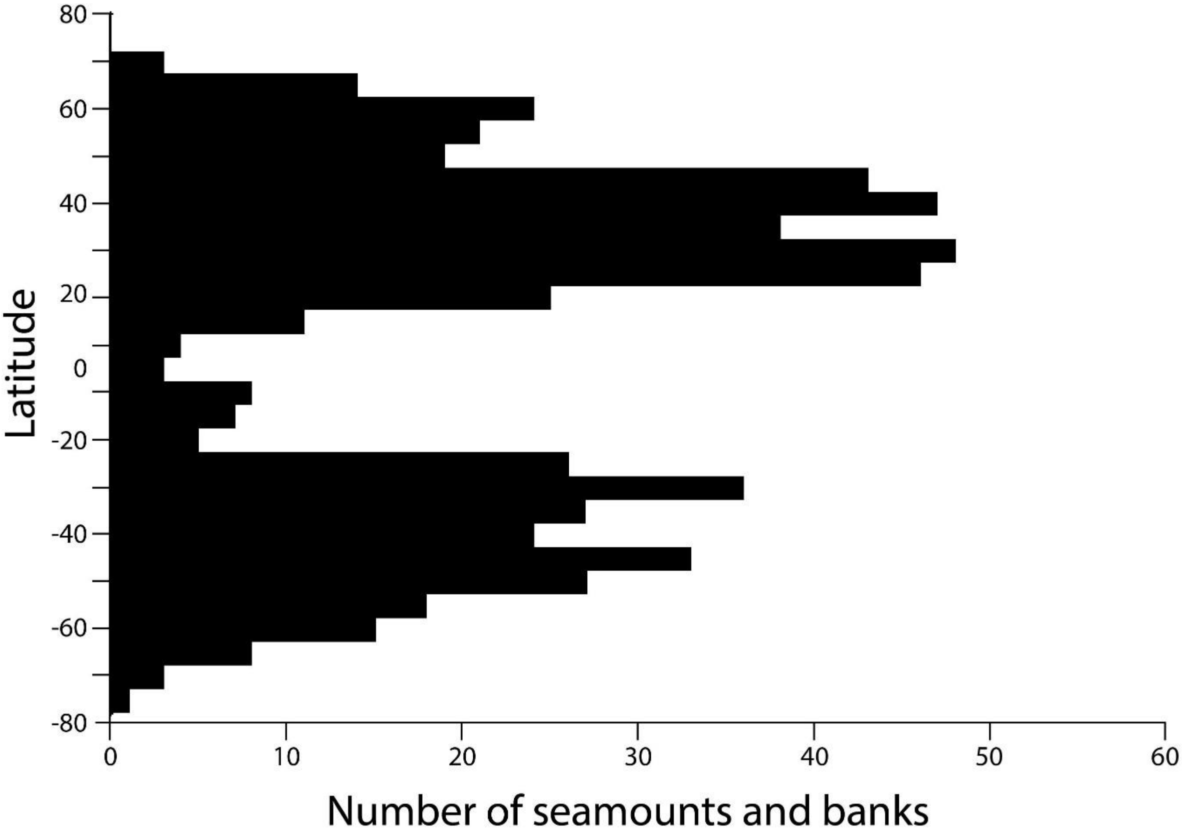


Figure 1.3 The number of seamounts sampled per latitude. Figure adapted from Rogers et al., 2007.

The data for this thesis were collected during the Tracing ocean processes using corals and sediments (TROPICS) research expedition, which had the primary aim of collecting coral fossils for reconstructing past ocean chemistry of the Equatorial Atlantic and as such has supplied opportunistic video and mapping data for different sites. The data were collected using the ROV *ISIS*, a CTD and an EM120 ship-based multibeam system. A detailed methodology about the processing steps related to video annotations, acquisition of terrain variables and the joining of all data sets is described in Appendix A. This thesis produces the first biological characterisation of the study sites, within the poorly studied deep-sea area of the Equatorial Atlantic, with image catalogues of the fauna and data to be submitted to open access data repositories following publications. The data within this project aims to contribute further knowledge towards seamount research and addresses the following research questions.

Chapter 2. Beta diversity structure on an Equatorial Atlantic seamount

1) Which communities and species increase beta diversity in a remote seamount setting?

I will test the generality of such findings by using novel methods developed specifically for addressing which communities significantly increase beta diversity. I will then also discuss the type of fauna that shows the highest variance across the study site and as such is most likely to affect changes in spatial beta diversity.

2) Is beta diversity on seamounts driven by species replacement or changes in the number of species along environmental gradients?

The second part of this chapter evaluates seamount beta diversity from a different perspective, by quantifying beta diversity and decomposing it into two ecological processes; species replacement and species richness difference. This breakdown allows to assess whether biodiversity patterns on seamounts are governed by beta diversity or high species co-existence in a heterogeneous landscape.

3) How do ecological processes control beta diversity?

The third part of this chapter allows for testing the effect of environmental variables on each of the beta diversity components, thus depicting ecological processes spatially shaping the community patterns. I evaluate how bathymetric and oceanographic variables affect each component and discuss how this information can be used to enhance our understanding of deep-sea biodiversity patterns and for monitoring deep-sea communities under anthropogenic impact.

Chapter 3. The biodiversity and spatial distribution of cold-water corals on Equatorial Atlantic Seamounts

1) Do Equatorial Atlantic seamounts harbour high cold-water coral diversity?

Here, I present values for the biodiversity of the cold-water coral fauna of Equatorial Atlantic seamounts across three sites. I will compare my results to an existing global database showing the number of cold-water coral species on different seamounts.

2) How does seamount cold-water coral diversity change on a basin-wide scale?

In this section, I will discuss the biodiversity patterns of cold-water corals from three distant seamounts. I will unveil any potential trends and the possible environmental conditions that may cause them.

Chapter 1

3) Are the cold-water coral community assemblages different across distant seamounts within the Equatorial Atlantic in comparable depths and habitats? If so, why?

The final analysis of this chapter will focus on comparing the assemblages from the three sites across a similar depth band with the data collected within one cruise ensuring a consistent methodology. I discuss similarities and differences between communities and discuss variations in environmental variables, which could be responsible for causing differences in the species composition between the three seamounts.

Chapter 4. Ecological communities and drivers of biodiversity within the transverse ridge of the Vema Fracture Zone

1) What are the biological communities and environmental drivers of biodiversity on a transverse ridge?

This section examines the megabenthos of the ridge, showing vulnerable marine ecosystems and a functionally similar benthic community to the other study sites examined in this project. I also model biodiversity metrics in relation to bathymetric and oceanographic variables in order to enhance our understanding of environmental drivers in this type of deep-sea habitat.

2) How does the transverse ridge fauna within this region compare to non-vent Mid-Atlantic Ridge fauna?

I draw qualitative comparisons between the species encountered here and the records obtained during ECOMAR and MAR-ECO research projects.

3) Does Vema Fracture Zone warrant a conservation status to off-set the impacts of deep-sea mining on the Mid-Atlantic Ridge?

Recently, the Mid-Atlantic Ridge ecosystems have received a great deal of attention, since the administration of exploration licences for deep-sea mining within this area. Scientists have recommended that Vema Fracture Zone should be incorporated into an environmental management plan in order to maximise conservation efforts from deep-sea mining. I evaluate the appropriateness of such plans, based on the high resolution biological data set acquired during this study.

Chapter 5. Synthesis

In the final chapter, the results of this thesis will be brought together and discussed in the light of scientific contribution towards the field of seamount research. In particular, I will discuss:

- Evidence gathered in this thesis with regard to the interpretation of seamounts as biodiversity hotspots and islands or stepping stones
- Technical contributions towards studying beta diversity in the deep sea
- Contributions towards conservation of biodiversity in seamounts

Finally, I will summarise the outcomes of this thesis, evaluate its strengths and limitations, and make suggestions towards future research.

Chapter 2 Species replacement dominates megabenthos beta diversity in a remote seamount setting

Author contributions. This chapter has been published in the peer-reviewed journal *Scientific Reports*. L.V collected the data from ROV imagery, conducted the statistical analysis and wrote the manuscript. L.F.R was the principal investigator on the RSS James Cook 094 voyage, and along with M.A.T. and V.A.I.H acquired the data and supervise the PhD project of which this manuscript is a part of. K.R contributed towards the spatial analysis. All authors reviewed the manuscript.

2.1 Abstract

Seamounts are proposed to be hotspots of deep-sea biodiversity, a pattern potentially arising from increased productivity in a heterogeneous landscape leading to either high species co-existence or species turnover (beta diversity). However, studies on individual seamounts remain rare, hindering our understanding of the underlying causes of local changes in beta diversity. Here, we investigated processes behind beta diversity using ROV video, coupled with oceanographic and quantitative terrain parameters, over a depth gradient in Annan Seamount, Equatorial Atlantic. By applying recently developed beta diversity analyses, we identified ecologically unique sites and distinguished between two beta diversity processes: species replacement and changes in species richness. The total beta diversity was high with an index of 0.92 out of 1 and was dominated by species replacement (68%). Species replacement was affected by depth-related variables, including temperature and water mass in addition to the aspect and local elevation of the seabed. In contrast, changes in species richness component were affected only by the water mass. Water mass, along with substrate also affected differences in species abundance. This study identified, for the first time on seamount megabenthos, the different beta diversity components and drivers, which can contribute towards understanding and protecting regional deep-sea biodiversity.

2.2 Introduction

Seamounts are prominent, globally distributed, isolated features, rising a minimum of 100 m from the surrounding seafloor (Staudigel et al., 2010). Estimates suggest that there are ~33 000 (Yesson et al., 2011) to ~ 100 000 such features worldwide (Wessel et al., 2010), but < 4 % of seamounts have been sampled for scientific purposes (Kvile et al., 2014). Seamounts are an important deep-sea habitat type (Costello, 2009) since they host diverse benthic communities (Samadi et al., 2006) and can host abundant fish stocks (O'Driscoll and Clark, 2005). The latter factor makes seamounts prominent targets for deep-sea bottom trawling (Clark et al., 2007). Moreover, at present some seamounts covered with ferromanganese crusts are being considered as a potential source of cobalt, tellurium, and other valuable metals for mining (Hein et al., 2009). Both these activities involve immense physical disruption through removal of bottom habitat and habitat-forming species in an ecosystem defined by slow-growing, long-lived organisms (Clark and Bowden, 2015; Levin et al., 2016). The impacts on the benthos are likely to be long-lasting or even permanent, as observed in the wake of bottom trawling fisheries on seamounts off New Zealand, where there has been no recovery over decadal time scales (Williams et al., 2010). Such continuing interest to exploit deep-sea ecosystems provides a challenge for sustainable management (Watling and Auster, 2017), which should be underpinned by knowledge on the spatial distribution of seamount biodiversity and its environmental drivers.

Seamounts, however, are not one single entity, as they have varied morphologies, depths and locations with consequently different local environments (Rowden et al., 2005), which results in different faunal compositions across seamounts (Clark et al., 2010b). At a broad regional scale, seamount benthic communities appear to be influenced by latitudinal turnover (O'Hara, 2007), oxygen concentration (Wishner et al., 1990), aragonite saturation for stony corals (Tittensor et al., 2009) and primary productivity. Seamount morphology might also play a role in controlling local particulate organic carbon (POC) export, as it has been shown that a tall seamount increased the POC export due to its interaction with tidal dynamics (Turnewitsch et al., 2016). Furthermore, seamount seabed morphology leads to complex habitat mosaics at different depths that modify the hydrodynamic flow (Genin et al., 1986; Levin and Thomas, 1989). This diverse geomorphology coupled with the occurrence of habitat-forming species, causes high habitat heterogeneity, increases local (alpha) diversity (Henry and Roberts, 2007) and affects assemblage patterns through provision of a physical habitat for other invertebrates (O'Hara et al., 2008). To date, seamount research has had a strong focus on comparing different sites, so there are only a handful of studies focusing on changes in megafaunal beta diversity (spatial differentiation of diversity) on single seamounts (Henry et al., 2014; Lundsten et al., 2009; McClain et al., 2009; McClain and Lundsten, 2015), hindering our understanding of how species are partitioned amongst habitats. This knowledge is crucial for linking alpha and gamma (regional) diversity, leading to improved understanding of large-scale biogeographical gradients on seamounts, and more generally, within the deep-sea.

Deep-sea research has shown that depth differences result in greater beta diversity than horizontal distances (McClain and Rex, 2015; Rex and Etter J., 2010). Accordingly, previous research on the megafauna of Davidson Seamount found that depth influences changes in assemblage structure (McClain et al., 2010; Schlacher et al., 2014), but does not affect alpha diversity or species density (McClain et al., 2010). Conversely, in the off-shore Taney Seamount Chain, slope affected both beta diversity and density while depth affected alpha- and beta diversity (McClain and Lundsten, 2015). The disparities in diversity patterns at different seamounts have been proposed to be driven by variations in surface productivity and depth gradients (McClain and Lundsten, 2015). To build a complete understanding of spatial patterns on seamounts, however, it is beneficial to split beta diversity into components. This approach involves understanding which sites and species contribute to beta diversity, followed by the untangling of beta diversity into distinct processes, such as replacement (species replace each other along ecological gradients) and richness difference (different communities have a different number of species) (Legendre and De Cáceres, 2013; Lennon et al., 2001). This detailed information will allow for the understanding of the ecological processes behind each component and, subsequently, how these are spatially shaping the community assemblages.

Here we apply recently developed beta diversity analyses to benthic megafaunal communities in order to increase our comprehension of beta diversity patterns on seamounts. This study uses a multidisciplinary data set of Remotely Operated Vehicle (ROV) transects, bathymetry derived environmental variables, and oceanographic information to illustrate how beta diversity changes across a depth gradient and how different areas and species affect beta diversity. Furthermore, we show for the first time in a seamount benthos, the influence of an array of environmental variables on two distinct beta diversity processes: species replacement and species richness difference.

2.3 Methodology

2.3.1 Study site

Annan Seamount, in the Equatorial-Atlantic, is part of the Grimaldi Bathymetrists Seamount Chain (Jones et al., 2002), where it lies at depths of 200 – 4500 m (Fig. 2.1). Previous publications from the same research expedition have also referred to this feature as Carter Seamount. It is a conical guyot occurring at the northern termination of the large volcanic edifice, formed by the Sierra Leone Rise, with the rest of the topography consisting of long-offset fracture zones (Jones et al., 2002; Kumar and Embley, 1977). Annan Seamount has been hypothesised to have formed

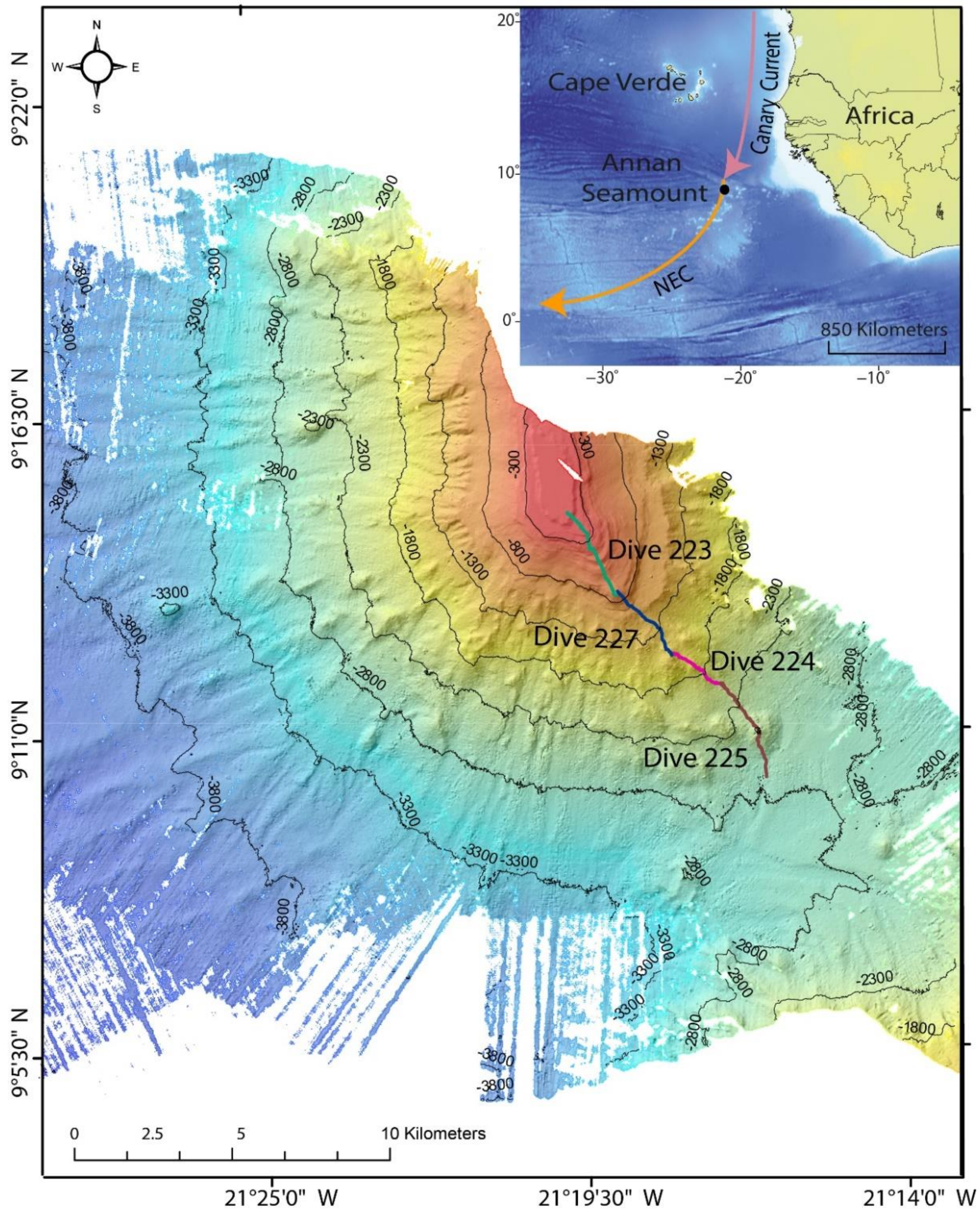


Figure 2.1 Map of the south of Annan Seamount showing the location of the ROV tracks with bathymetry of 25 m pixel resolution. NEC = North-Equatorial Current. The site map was created in ESRI ArcMap (version 10.2.2). The insert map is ETOPO1 relief data created using Generic Mapping Tools (Amante and Eakins, 2009).

during the Palaeocene ~54.4 ± 1.1 Ma (Jones et al., 2002). The seamount is bathed by three water masses, North-Atlantic Deep Water (NADW) at the base and slope up to ~ 2500 m depth, Antarctic Intermediate Water (AAIW) covering the flank up to ~1500 m, and South–Atlantic Central Water (SACW) to the summit (Sarafanov et al., 2007). Annan Seamount is affected by two current systems as it lies within the transition zone between the colder Canary Current flowing southwest and the warmer North Equatorial Current flowing east to west (Bischof et al., 2004; Gyory et al.2017) (Fig. 2.1.). To date, little is known about the benthic communities of Annan seamount with this study presenting its first biological characterisation.

2.3.2 Data collection and processing

The data for this study were collected on board the RRS *James Cook* in 2013 as part of the ERC funded Tracing Oceanic Processes using Corals and Sediments programme (TROPICS) (Robinson, 2013). The ROV *Isis* was used to collect video footage at Annan Seamount over four dives from depths of 200 –2730m, covering 11 km in distance and generating a total of 87 h of video material (Table 2.1). The video material was used to identify and count benthic fauna. It was also used to annotate and classify substrates into six categories; 1) volcanic, 2) volcanic and biogenic, 3) sediment, 4) sediment and biogenic, 5) volcanic and sediment, 6) volcanic, sediment and biogenic (Fig.2.2) (for examples of each category see Appendix A). A comprehensive description of the data processing steps related to the ROV imagery is available in Appendix A. The ROV was equipped with a SeaBird SBE 49 CTD that measured temperature, conductivity and pressure. All CTD data were processed with the SBE Data Processing (V7.20g) software, which also calculated depth, salinity and oxygen. The ROV CTD data were also used to characterize the water masses *in situ* using the classification by Emery (Emery, 2003a) (Appendix A).

Table 2.1 Information of the ROV dives from Annan seamount

ROV ISIS Dive	Time spent on seafloor (h)	Analysed transect length (m)	Area sampled (m^2)	Depth range (m)	Temperature range (°C)	Number of species	Total abundance
223	16.18	4100	11890	200-666	6.7-12.2	62	19702
224	15.6	4800	13920	1350-2132	3.3 -4.5	79	3417
225	19.38	5200	15080	2100-2742	2.8-3.4	92	5191
227	18.73	1900	5510	680-1300	4.5-6.5	71	1579

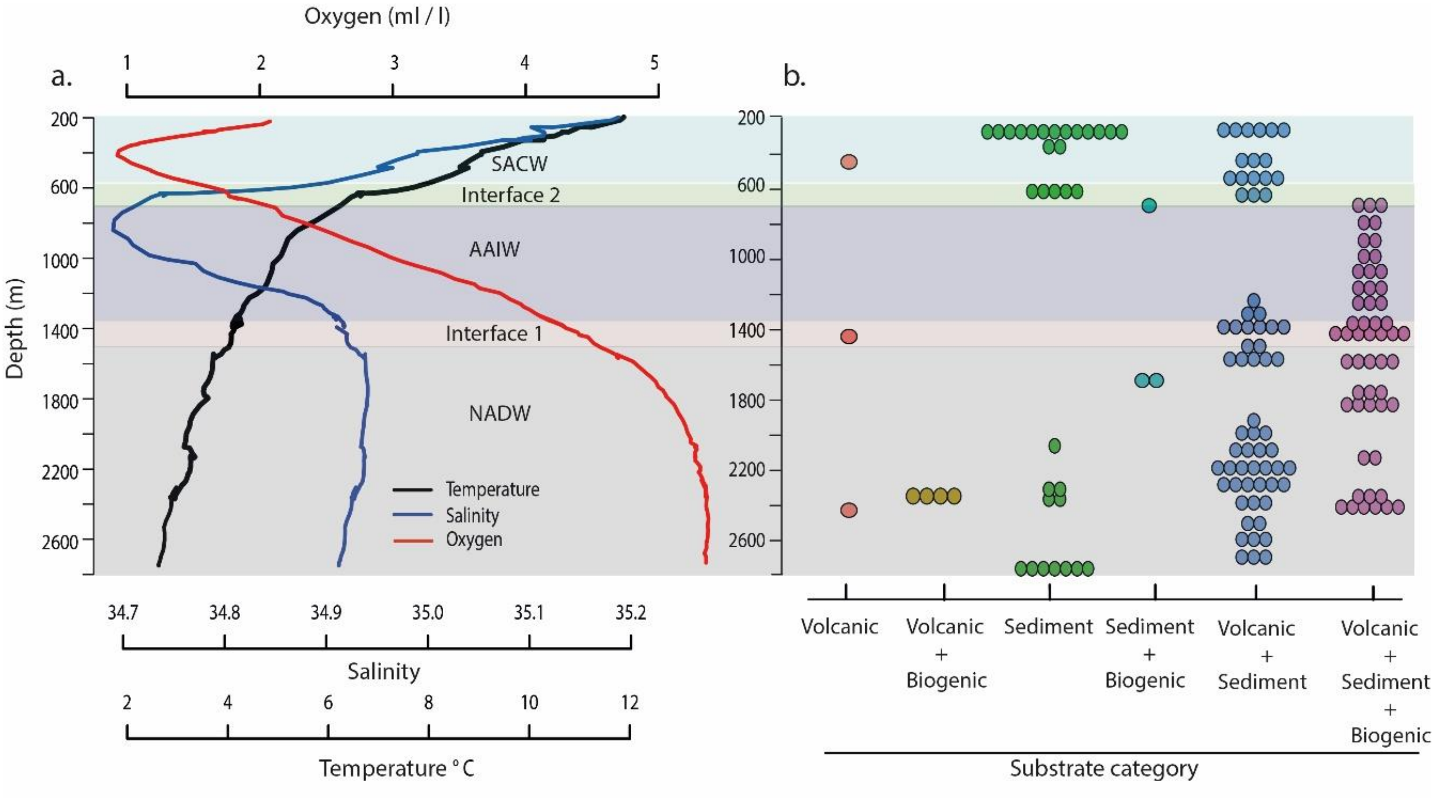


Figure 2.2 Temperature, salinity, oxygen and water mass categories from the ROV CTD (a) along with the different substrate categories across the seamount from the 100 m sample size (b). SACW= South-Atlantic Central Water, AAIW = Antarctic Intermediate Water, NADW = North- Atlantic Deep Water. The interfaces are defined from raw ROV CTD data (Appendix A).

Shipborne multibeam bathymetry data were acquired with the ship's hull-mounted Kongsberg EM-120 echosounder and processed using CARIS HIPS and SIPS (v. 8.1). The data were gridded at 25 m resolution. The bathymetry was used for extracting quantitative descriptors of the seabed terrain (Wilson et al., 2007) (see Appendix A for a detailed description). These included slope, topographic position index (TPI) at two scales (3x3 and 9x9 pixels neighbourhood radius), roughness, aspect (divided in eastness and northness), and three measures of curvature (general, profile and plan) (Jenness, 2012a, 2012b). The species, substrate, temperature, salinity and oxygen, and bathymetry-derived data were then combined by spatial joins in ArcGIS (version 10.2.2). After evaluations of different sample sizes, it was decided to use 100 m and 200 m ROV transect sample lengths, which generated 160 samples and 78 samples, respectively. The finer scale sample size of 100 m was chosen on the basis of maintaining substrate and habitat fidelity whilst capturing enough individuals per sample to be able to perform community analyses. The broader scale of 200 m was used to investigate how strongly spatial scale affected beta diversity patterns and corresponding environmental drivers.

2.3.3 Statistical analysis

Beta diversity analyses were conducted according to the methodology proposed by Legendre & De Cáceres (2013) and Legendre (2014) using the R package 'adespatial'. These approaches allow for i) no prior knowledge of the study area's alpha or gamma diversity to estimate beta diversity, ii) assessment of individual species' and sample contribution to beta diversity and iii) partitioning of the spatial variation and testing of explanatory environmental factors. Prior to the analysis, all species occurring only once throughout the study site were removed because i) the nature of the data collection did not enable verification of their taxonomic identity and ii) they were not deemed to be representatives of the community. Both presence – absence and species abundance data were generated. The former is suitable for the wide depth range covered in this study, while the latter provides an insight to differences in abundance. The data were transformed prior to statistical analyses using the Hellinger transformation, which limits the importance of rare taxa when computing dissimilarities as our survey was a depth transect (i.e. every depth was visited once), which could lead to the generation of false rare species.

The relative Local Contribution to Beta Diversity (LCBD) of each 100 m length sample and the Species Contribution to Beta Diversity (SCBD) were calculated using the function *beta.div* (Legendre and De Cáceres, 2013). The LCBD represents the ecological comparative uniqueness of the sample, and its significance for each sample was assessed through a permutation analysis ($p<0.05$, 999 iterations) testing the null hypothesis that species' distribution is random among sampling units. The SCBD represents the degree of contribution of each species to the overall beta diversity and was calculated on the Hellinger-transformed species matrix.

In order to further understand the ecological processes behind beta diversity, a total beta diversity index was calculated. Total beta diversity was then partitioned into species replacement and richness difference by the *beta.div.comp* function using the Jaccard dissimilarity for presence-absence and species abundance data for abundance difference (Legendre, 2014). This computation provides indices for total beta diversity, species richness/ abundance difference and replacement in addition to distance matrices. These indices determine the dominant process along the spatial gradient, while the matrices can be used to understand how environmental variables affect different components of beta diversity. For this, each matrix was used in a Principal Coordinates Analysis (PCoA) with a Lingoes correction to account for negative eigenvalues. The resulting coordinates, along with the environmental variables, were used as input in forward selection (*forward.sel* function) from which a set of estimated significant environmental variables were used as input explanatory variables in a Distance-based redundancy analysis (dbRDA). The absolute significance of the environmental variables behind the processes depicted by the Jaccard dissimilarity, richness difference and replacement matrices, was assessed with an F-test testing for significance ($p<0.05$, 999 permutations) (Legendre, 2014). Several reiterations of the analysis were conducted in order to avoid correlation between co-variable oceanographic parameters (depth, temperature and oxygen) and terrain variables (broad and fine scale TPI and general, planar and profile curvature). The data sets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

2.4 Results

2.4.1 Overview of Annan Seamount biological communities

Annan Seamount was characterised by abundant and diverse megafaunal communities, generating a record of ~30 000 individual organisms separated into 180 morphospecies. After excluding species with only one occurrence, for reasons previously discussed, 150 morphospecies were used in subsequent analysis. Changes in community composition were apparent across the depth transect and different substrate types, with the following five distinct biological assemblages described in more detail. The summit of Annan at ~ 200 m depth was occupied by mobile benthic communities, mainly the ophiuroid *Ophiotreta valenciennesi*, an unknown white urchin species and the holothurian *Stichopotidae* sp. Below the summit, with increasing depth up to 650 m , the community was dominated by large aggregations of the urchin *Cidaris cidaris*, different species of anemones and the cushion-star *Plinthaster* sp. The depths of 1300 -1500 m harboured extensive multi-species cold-water coral gardens, comprised of species such as *Paragorgia* sp., *Paramuricea* sp. and *Corallium* sp. along with unidentified primnoid and bamboo coral species and associated invertebrates. Several vertical walls and extremely steep slopes were observed, which were also colonized by similar morphospecies of coral, but their respective abundances varied. The deeper part of the study area, from ~ 2300 m onwards, was characterized by sediment plains interspersed by volcanic substrate and dead bamboo coral skeletons. These skeletons occurred on an elevated seabed and were occupied by high abundances of *Anthomastus* sp. (~3300 individuals in 1.5 km distance). The sediment plains, down to ~2730 m depth, were inhabited by a diverse holothurian community, with different species of the *Benthodytes* genus and the Synallactidae family along with *Peniagone* sp. and an unusual morphotype of the *Ellipinion* sp.

2.4.2 Samples and species contribution to beta diversity

The total beta diversity index for Annan Seamount was high, with the value of 0.92 out of the maximum possible value of 1, which occurs when all sites contain different species. The values of the contribution of individuals samples to beta diversity, as calculated from the LCBD analysis, ranged from 0.0009 to 0.007 (Fig. 2.3). The p-values for the significantly higher beta diversity samples ranged from 0.001 to 0.005. At the shallower sites within the SACW, the ecologically unique samples were on mixed substrates (Fig. 2.3), and consisted of feeding aggregations of the asteroid *Plinthaster sp.*, an unknown species of urchin (Urchin white sp.2) and *Ophiotreta valenciennesi* (Fig. 2.3 and 2.4). The latter two species also exhibited large variance across the study site as depicted by the high SCBD values (Fig. 2.5). The significant communities at the interface between SACW and AAIW were sediment communities highly dominated by cerianthid anemones and *C. cidaris* (Fig. 2.3), with the latter, due to urchin aggregations, having some of the highest SCBD values across this study (Fig.2.5). Within the AAIW, and the upper part of the NADW, the significant LCBD sites were highly heterogeneous habitats (Fig. 2.3), hosting urchins on the sediment substrates, and corals and associated fauna attached to dead coral skeletons and large boulders (Fig.2.4). The significant samples at the deeper part of the NADW were sediment communities (Fig.2.3), but contrary to shallow sediment habitats, the distribution of the different species of echinoids and holothurians, such as *Scotoplanes* (seapigs) and *Benthodytes* sp., was mostly sparse. Conversely, *Anthomastus sp.*, which had the overall highest SCBD value, also occurred within the depths of the NADW in large aggregations over 100 m distances (Fig. 2.5). Other species with high SCBD values were *Enallopsammia* sp. and *Metallogorgia melanotrichos* (Fig. 2.5). Specifically, *M.*

melanotrichos was scattered, contributing to a variety of different communities in low abundances throughout the study site.

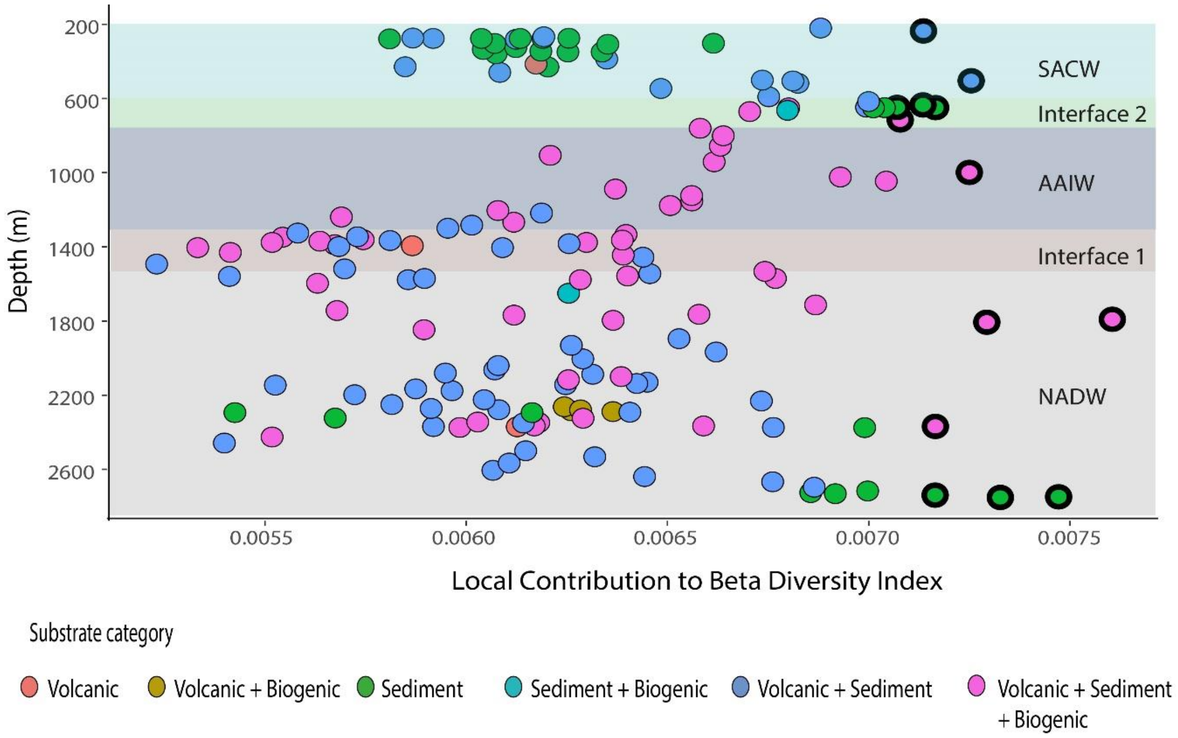


Figure 2.3 The Local Contribution to Beta Diversity Index of the 100 m length samples per substrate and water mass type. The black circles illustrate the significant samples at $p < 0.05$, n=160.

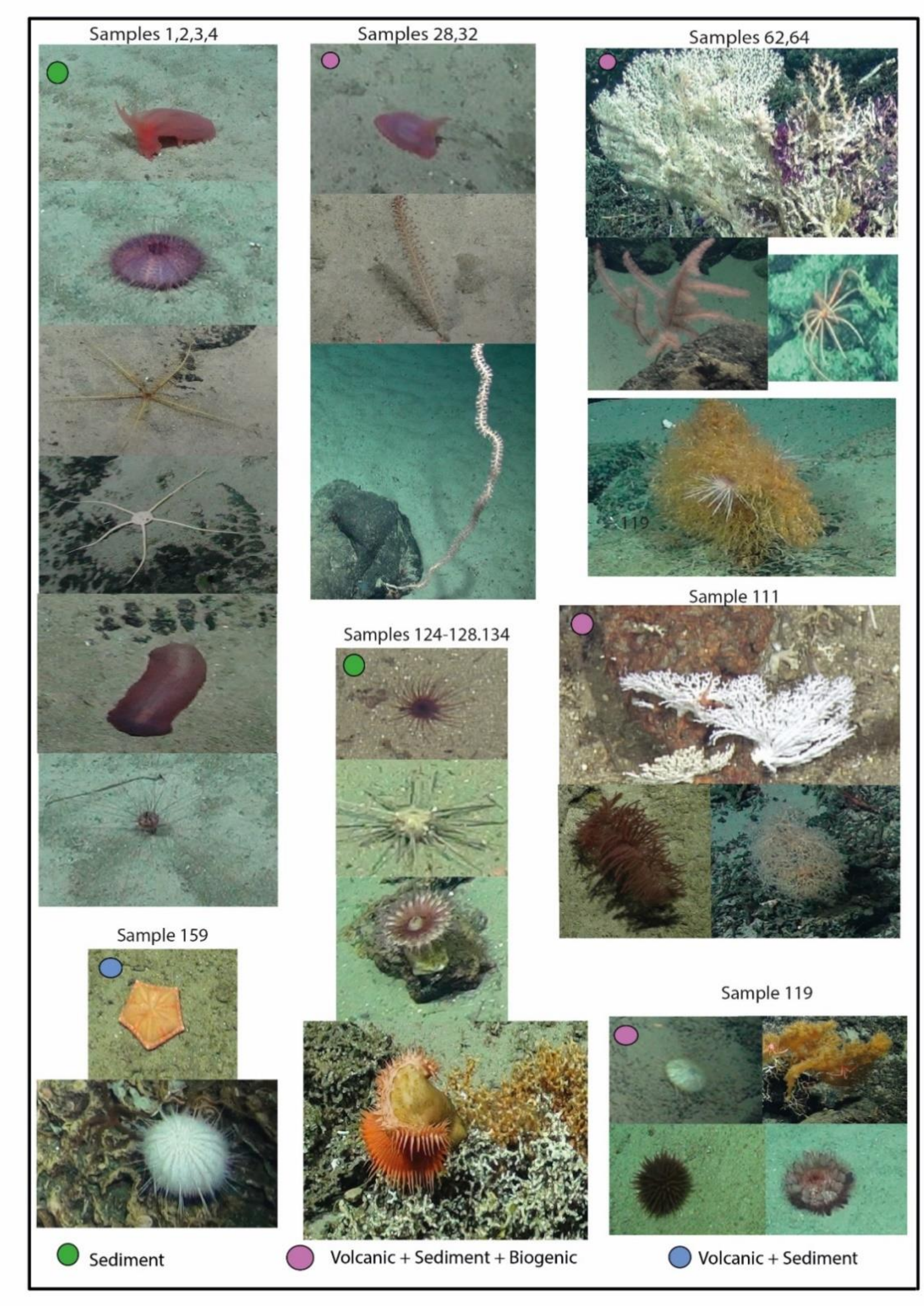


Figure 2.4 Examples of the communities of the significant Local Contribution to Beta Diversity samples with their corresponding habitats. The species names are per sample grouping from left to right and then from top to bottom. Samples 1,2,3,4 – *Peniagone or Amperima* sp., Pink echinothurioid , Comatulidae, *Ophiomusium* sp., *Benthodytes* sp. and *Aspidodiadema* sp.; samples 28, 32 - *Ellipinion* sp., *Funniculina* sp., Isididae whip; samples 62,65 - *Corallium* sp. and *Clavularia* sp., *Parantipathes* sp., Brisingidae, *Acanella* sp.; sample 111 - Stylasterid, *Bathypathes* sp. and Chrysogorgid.; sample 119 – white echinohurioid, *Leiopathes* sp., *Liponema* sp., *Phormosoma* sp.; samples 124-128,134 - brown cerianthid anemone, *Cidaris cidaris*, purple cerianthid anemone, Hormathiidae on *Solenosmilia variabilis*; sample 159 - *Plinthaster* sp. and Urchin white sp.2.

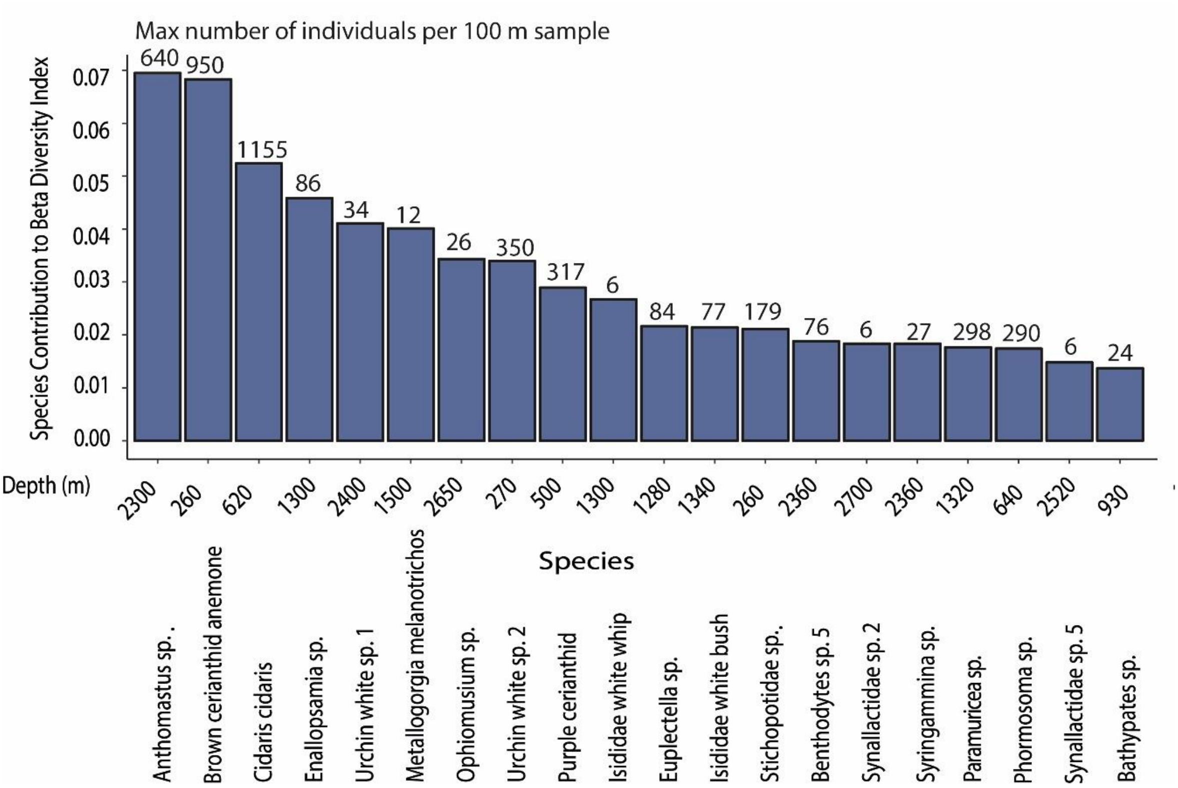


Figure 2.5 The contribution of the top 20 individual species to beta diversity and the maximum number of individuals per 100 m sample and corresponding depth.

2.4.3 Partitioning of total beta diversity

The dissimilarities, in the form of Jaccard dissimilarity, species replacement and richness difference, between samples were extremely high throughout the study transect (Fig.2.6). These patterns were similar at both sampling scales as well as for both presence-absence and species abundance data. Partitioning of the total beta diversity, using presence-absence data, showed the species replacement component to be dominant (~ 68 %), with the species richness difference contributing only ~ 32 %. The species richness difference component was more dominant at ~200 and ~ 500 m water depth (Fig. 2.6). It was also relatively high at ~ 1300 – 1500 m depth, albeit fluctuating rapidly with the species replacement component (Fig. 2.6).

The significant variables explaining the patterns in the Jaccard dissimilarity matrix were water depth and correlated variables (oxygen and temperature), water mass, substrate, slope, eastness and northness (aspects), and broad scale TPI (R^2_{adj}=0.24) (Table 2.2). It is worth noting that temperature, depth and oxygen had the same p and R^2_{adj} - values for this matrix. For the species replacement matrix the significant variables with the highest R^2_{adj} (0.24) were depth, water mass, broad scale TPI and northness (Table 2.2). The species richness difference component was explained purely by water mass in the presence/absence data (R^2_{adj} =0.14). Water mass also affected the species abundance difference, along with substrate (R^2_{adj} = 0.27) (Table 2.2). At both scales the explanatory variables were similar and measures of curvature and surface roughness were not found to influence the different components of beta diversity.

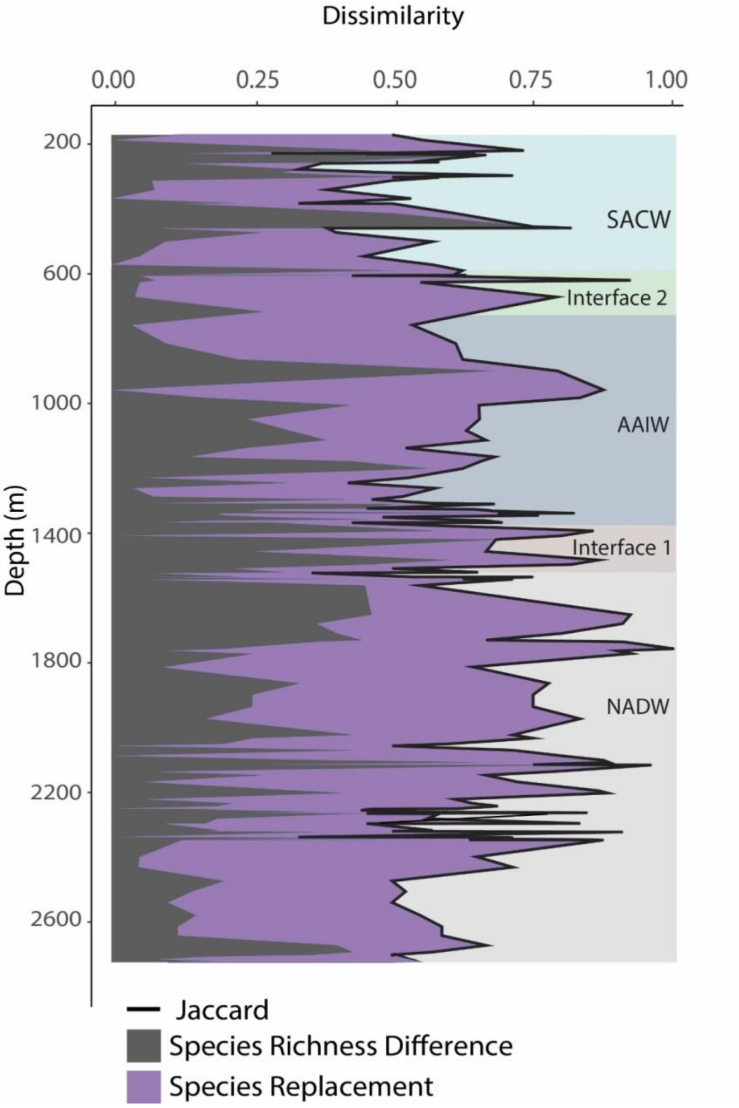


Figure 2.6 The Jaccard based dissimilarity using presence – absence data between each consecutive 100 m length sample showing the relative proportion of species replacement *vs.* species richness difference contribution towards total beta diversity across the depth range. SACW= South-Atlantic Central Water, AAIW = Antarctic Intermediate Water, NADW = North- Atlantic Deep Water. The interfaces are defined from raw ROV CTD data (Appendix A.)

Table 2.2 Results from the Distance-based redundancy analysis (dbRDA) with a forward selection, showing the significant environmental variables ($p<0.05$) affecting the Jaccard dissimilarity, species replacement, species richness/abundance difference using a) presence – absence and b) species abundance data of 100 m length samples (n=160).

a) Presence-absence	R^2_{adj}		Water mass	Substrate	Slope	Eastness	Northness	Broad-scale TPI
Jaccard$_{100m}$	0.22	Depth *p=0.001*	*p=0.001*	*p=0.002*	*p=0.001*	*p=0.004*	*p=0.015*	*p=0.001*
	0.22	Temperature *p=0.001*	*p=0.001*	*p=0.001*	*p=0.003*	*p=0.012*	*p=0.003*	*p=0.001*
	0.22	Oxygen *p=0.001*	*p=0.001*	*p=0.001*	*p=0.008*	*p=0.008*	*p=0.011*	*p=0.001*
Repl$_{100m}$	0.24	Depth *p=0.001*	*p=0.001*	*not sig.*	*not sig.*	*not sig.*	*p=0.007*	*p=0.001*
	0.22	Temperature *p=0.001*	*p=0.001*	*p=0.003*	*p=0.003*	*p=0.003*	*p=0.010*	*p=0.003*
	0.24	Oxygen *p=0.001*	*p=0.001*	*p=0.007*	*p=0.001*	*p=0.001*	*p=0.001*	*p=0.001*
Rich. diff.$_{100m}$	0.14	*not sig.*	*p=0.001*	*not sig.*	*not sig.*	*not sig.*	*not sig.*	*not sig.*
b) Species abundance								
Jaccard$_{100m}$	0.20	Depth *p=0.001*	*p=0.001*	*p=0.001*	*p=0.001*	*p=0.001*	*p=0.018*	*p=0.010*
	0.20	Temperature *p=0.001*	*p=0.001*	*p=0.001*	*p=0.001*	*p=0.001*	*p=0.014*	*p=0.001*
	0.20	Oxygen *p=0.001*	*p=0.001*	*p=0.002*	*p=0.001*	*p=0.002*	*p=0.018*	*p=0.001*
Repl$_{100m}$	0.19	Depth *p=0.001*	*p=0.001*	*p=0.002*	*p=0.001*	*p=0.001*	*p=0.001*	*p=0.001*
	0.19	Temperature *p=0.001*	*p=0.001*	*p=0.011*	*p=0.002*	*p=0.003*	*p=0.010*	*p=0.010*
	0.19	Oxygen *p=0.001*	*p=0.001*	*p=0.008*	*p=0.001*	*p=0.001*	*p=0.001*	*p=0.001*
Abun. diff.$_{100m}$	0.27	*not sig.*	*p=0.001*	0.042	*not sig.*	*not sig.*	*not sig.*	*not sig.*

2.5 Discussion

This study applied recently developed beta diversity landscape metrics to a seamount benthos across a bathymetric gradient. The analysis identified sites with ecologically unique communities (LCBD), and species which showed high variance across the seamount (SCBD), thus contributing to high beta diversity. The decomposition of beta diversity, quantified, for the first time in seamount benthos, the respective proportions of species replacement and species richness difference. Furthermore, this decomposition allowed us to assess the effects of *in situ* depth related parameters obtained by the CTD on the ROV, and relatively fine scale terrain variables, on each beta diversity mechanism.

Total beta diversity at Annan Seamount was high in this study (0.92 out of 1), showing that community level turnover along the depth transect was frequent. The macrobenthos in the coastal areas of the Red Sea exhibits an index of 0.43 (Alsaffar et al., 2017), while the macrofauna and meiofauna in hydrothermal vents only exhibit ~0.36 (Sarrazin et al., 2015) of the maximum total beta diversity of 1. However, the lack of replicate transects across the large Annan seamount restricts drawing generalisations about seamounts typically having higher beta diversity than other habitats. The significant LCBD samples above ~ 600 m depth, had highly dominant species present, which also had large SCBD values, such as *Cidaris cidaris* (Fig. 2.5). While this urchin occurs on dead coral substrates in addition to sediments, *C. cidaris* was found to form large aggregations in soft sediments, which were flagged as significant LCBD sites (Fig. 2.3). Histological studies on their gonads revealed that the urchins were mature and aggregating to spawn (Wadge, 2015). Previous observations of *C. cidaris* aggregations suggested that these are for both reproductive and feeding purposes and form irrespective of the presence of predators (Stevenson et al., 2015). This detailed information available on one species highlights that temporal biological interactions are likely to be important in driving local beta diversity by producing ecologically unique communities.

The majority of the species contributing towards beta diversity on Annan Seamount had patchy distributions, often characterised by high abundance over a limited depth range resulting in high variance (Fig.2. 5). Conversely, a previous study in Taney Seamount attributed faunal turnover to the rarer species, which were suspected to have a narrower depth range while abundant fauna would be expected to have a wider depth range (McClain and Lundsten, 2015). The contrasting results might arise from different methodological approaches as McClain and Lundsten (2015) applied a log- transformation for data normalisation, giving more importance to rare taxa. Differences could also arise from seamounts being variable in terms of their morphology and summit height, which in turn affects productivity, potentially leading to ecologically distinct beta diversity patterns (McClain and Lundsten, 2015; Rowden et al., 2010a). However, results from streams and lakes support our findings, by showing that abundant species occupying an intermediate number of sites contribute most to beta diversity (Heino and Grönroos, 2017; Vilmi et al., 2017). The abundant fauna in the present study were often confined to an optimal environmental niche, where they thrived, dominating their respective communities causing visual zonation patterns. A compressed depth range for megafauna has been previously linked to intrinsic mechanisms, such as competition for smaller prey, opportunistic species outcompeting others, or the local availability of food parcels (Rex, 1977, 1981).

Partitioning of beta diversity on Annan Seamount shows that it is dominated by species replacement (68%), with differences in species richness only accounting for 32% of the total beta diversity (0.92). A dominating replacement component along a depth-gradient has also been found in asteroids and holothurians in the Porcupine Seabight and Porcupine Abyssal Plain (Wagstaff et al., 2014). The majority of the explanatory variables used in this study were correlated with changes in the different beta diversity components. Dissimilarity between samples was influenced by the oceanographic variables, depth, temperature and oxygen, the factorial variables of water mass and substrate, in addition to terrain properties such as slope, aspect and TPI. Here we are able to pinpoint that depth and correlated variables have an impact on beta diversity specifically through the species replacement component, likely by creating physiological niches across the seamount. It must be noted, however, that our data set does not contain any replicate transects and different patterns could be present in other locations on the seamount.

Water depth, which is also a proxy for other parameters, influencing community structure is a well-documented phenomena in seamount benthos (McClain et al., 2010; McClain and Lundsten, 2015). It is thought to represent energy availability in the form of temperature and POC flux to the deep-sea (McClain and Rex, 2015). Previous studies on bivalves across depth transects show that replacement is more dominant in productive regions. In lower productivity areas, nestedness, which is a type of species richness difference leading to ordered species loss, prevails (Brault et al., 2013a). Therefore, high species replacement in Annan Seamount could arise from its proximity to a relatively productive region off the west-African coast (Wang et al., 2013). Water masses also influence the species replacement component, which is in agreement with previous work demonstrating that water mass boundaries cause changes in the faunal composition (Bett, 2001; Howell et al., 2002; Tyler and Zibrowius, 1992). A possible mechanism influencing the replacement component could be, therefore, that water masses act as barriers causing genetic divergence resulting in closely related species sorting into depth bands, as seen in octocorals (Quattrini et al., 2017).

The species replacement component was also affected by bathymetric properties, such as TPI and the northness of the seabed. These are both variables that have a more localised effect on the hydrodynamical flow. The aspect of the seabed influences the direction of the hydrodynamical flow and as such changes in this variable could be reflected in the presence or absence of sessile suspension feeders. The direction of the flow could be particularly relevant for large communities of habitat-forming species, such as cold-water corals, which are known to prefer to grow perpendicular to the water flow in order to optimize food capture (Roberts et al., 2009). There are no *in situ* hydrodynamical flow data available, but the main orientation of the ROV dives was south-easterly. As such, northness being associated with the species replacement component, suggests that the analysis has successfully captured communities with differential flow preferences.

The other variable affecting species replacement was TPI, which provides information on whether an area is elevated or has low to no relief in comparison to the surrounding seabed morphology. As such, it also affects which species are present by providing elevation and thus access to currents, or alternatively, seabed depression to those species that require it. Furthermore, the community composition of species replacement, as assessed by species abundance data, was also influenced by slope. This means that slope affects the relative abundances of the species present and as such, the community dynamics. Such differences were also observed from the imagery data, as certain species, such as Isididae whip corals and flytrap anemones, were more abundant on vertical walls and ledges while others, such as *Corallium* sp., *Enallopsammia* sp. and *Paramuricea* sp. preferred more gently sloping sites. Similarly, previous research on Taney Seamount Chain found that species are likely to favor horizontal or vertical surfaces as both extremes had higher faunal density than intermediate slopes (McClain and Lundsten, 2015).

Perhaps surprisingly, none of the individual oceanographic variables linked with the richness difference component of beta diversity, but those variables combined, feed into the factorial water mass parameter. Water masses are a global scale variable with fluctuations in their characteristics over geological time scales. As such, the water mass variable is likely to affect larval transport to the seamount by acting as a connective pathway between deep-sea habitats (Watling et al., 2013) as the dispersal range of deep-sea fauna is relatively large (Baco et al., 2016). Additionally, water mass interfaces have also been proposed to enhance species richness by allowing the co-existence of warmer and colder-origin species (Bett, 2001; Henry et al., 2014). The impact of water masses on the species richness difference component of beta diversity could also be linked to seamount fauna often reflecting the regional species pool (Ávila and Malaquias, 2003; Hall-Spencer and Rogers, 2007; McClain et al., 2009; Samadi et al., 2006) with strong similarities with nearby banks (Howell et al., 2010b) and continental slopes (O'Hara, 2007). The benthos of Annan Seamount is likely to be affected by all these mechanisms, as it lies between a cooler Canary Current and a warmer North-Equatorial Current system, and expands across three water-masses. Therefore, it is likely that other large scale variables, such as currents, along with evolutionary variables, affect the species richness difference component in marine systems.

Additionally, the use of species abundance data revealed that water masses along with substrate affect differences in abundances. As is the case with most seamounts, the substrates encountered were highly heterogeneous, encompassing hard firm volcanic rock, boulder fields, dead coral debris and mixed sediment types. It must be noted, however, that certain substrate types were markedly more common than others and, as such, there is a strong bias towards higher beta diversity indices in certain substrates due to under sampling of others (Fig. 2.2). Despite this, the effect of substrate on the species composition shows that while many of the species in the study occur over a multitude of substrate types, they are significantly more abundant in their preferred substrate type. For example, cold-water corals will grow over dead coral skeletons, rocks, boulders, pavements and outcrops as these all provide a firm attachment point and a degree of elevation into the currents. However, in this study, substantial multispecies coral gardens were seen where there were extensive volcanic plateaus available.

The effect of the substrate on replacement was also obvious at the summit, where zonation took place with ophiuroids dominating large encrusted hard surfaces, cerianthids the soft sediments, and an unknown species of white urchin occurring on top of the large boulders. Conversely, at depth, the soft-sediment communities were diverse and sparse, with a more gradual zonation of different species of holothurians, ophiuroids and xenophyophores, perhaps caused by small-scale sediment characteristics.

Overall, our results show that high habitat heterogeneity combined with the biological (or physiological?) effects of depth increases local biodiversity by providing neighboring areas with different ecological niches. This environmental complexity increases beta diversity and thus local biodiversity by affecting the species composition mostly through the replacement component and to a lesser degree by increasing or decreasing the number of species co-existing. While most of the measured variables showed a highly significant relationship with the beta diversity components, the explained variance remained relatively low throughout the study. This low variance intuitively suggests that these variables only represent a fraction of the environmental drivers behind changes in beta diversity and that noise was introduced to the data by studying a wide range of taxa. The low explanatory power of beta diversity models, however, is common across biomes and is thought to arise from the large influence randomness has on evolutionary and ecological processes (McClain et al., 2012). Furthermore, the lack of coherent information on the basic biology and ecology of the deep-sea benthos (Taylor and Roterman, 2017) makes understanding deep-sea beta diversity patterns challenging across local, regional and global scales. The large knowledge gap also results in difficulties predicting the consequences of anthropogenic activities and predicting recovery timelines (Williams et al., 2010).

The landscape metrics applied in this study, however, provide a useful tool for understanding ecological patterns in the deep-sea. For example, species contributions to beta diversity are expected to change in response to anthropogenic disturbances (Heino and Grönroos, 2017). As such, these indices could provide useful when monitoring and mitigating impacts from habitat fragmentation such as those potentially linked to deep-sea mining. In particular, this study suggests that in order to maintain high beta diversity on seamounts, species replacement and richness difference, should be considered as separate entities, as they appear to be affected, respectively, by local and global environmental parameters. Future work should concentrate on testing whether these patterns hold across wider deep-sea environments, comparing total beta diversity on different seamounts and testing beta diversity patterns of individual taxocenes. The results also indicate the necessity to incorporate quantitative descriptors of the seabed terrain along with large scale-variables, such as POC flux and ocean currents, to future beta diversity analyses.

2.6 Conclusion

This study describes for the first time the biological communities of Annan Seamount. The seamount was characterized by diverse and abundant benthic megafauna, which were used to analyse beta diversity patterns using novel landscape metrics, never before applied to the seamount benthos. Ecologically important sites and communities were distinguished along with highly variant species, which contributed towards beta diversity. Changes in beta diversity are mostly dominated by species replacement with a smaller contribution from changes in species richness difference. Most importantly, this study confirms statistically, for the first time, how changes across an oceanographic gradient and local –scale terrain variables affecting flow regimes, impact beta diversity through species replacement on seamounts. Interestingly, the results demonstrate that beta diversity caused by changes in species richness can be linked with large-scale circulation patterns, which along with substrate, also causes changes in species abundance.

Chapter 3 The biodiversity and spatial distribution of cold water corals on Equatorial – Atlantic Seamounts

Author contributions. This chapter is in preparation for submission to the peer-reviewed journal of Marine Ecology. The author list for this article is: Victorero L., Broad E., Robinson L.F., Taylor M.L, Huvenne V.A.I. L.V. and E.B. prepared the image catalogue, E.B collected the data from ROV imagery under the guidance of L.V., L.V. conducted the statistical analysis and wrote the chapter. L.F.R. was the principal investigator on the RSS James Cook 094 voyage, and along with M.A.T. and V.A.I.H. acquired the data. All authors reviewed the manuscript.

3.1 Abstract

Cold-water corals are one of the most dominant components of seamount fauna. They are widespread across seamount seascapes and there is mounting evidence that they play an ecological role by acting as localised biodiversity hotspots for invertebrates, in addition to providing habitat for a variety of fish species. However, their biological traits, such as longevity, slow growth, and low recruitment rates make them vulnerable to anthropogenic threats, such as trawl fisheries, deep-sea mining, and climate change. In order to manage and conserve these ecosystems effectively, there is a need to fill the gaps in their known biogeographical patterns. Coral biodiversity patterns on seamounts are not well understood due to lack of sampling, with pronounced gaps in the Equatorial Atlantic. To address this, we present new data on cold-water coral diversity and abundance within three seamounts from the tropical Atlantic and describe the coral communities present based on ROV video transects. We also compare the assemblage composition between seamounts and explore possible differences between the environmental settings (bathymetric, oceanographic, and food input) as potential causes for dissimilar communities. Our results show that these sites host ~50-70 morphologically distinct coral species, with richness decreasing east to west, potentially as a response to a decrease in food input. The communities between the seamounts were dissimilar as only 15 species were shared between the three sites, while 25 were unique to a certain site, suggesting that many species have a localised distribution. Comparisons between our species richness results with a published global diversity cold-water coral seamount data set suggests potentially that Equatorial Atlantic seamounts could act as hotspots for cold-water coral biodiversity.

3.2 Introduction

Cold-water corals are a diverse group encompassing Octocorallia (soft corals), Antipatharians (black corals), Stylasteridae (hydrocorals) and Scleractinia (stony corals). In the deep sea, they have been referred to as “animal forests”, since they form reefs, coral gardens, and patches that create shelter for many other species (Buhl-Mortensen et al., 2015). Cold-water coral habitats have been termed of high biological and ecological value since they act as local hotspots of biodiversity and biological activity (Henry and Roberts, 2007). The reasons for this include their complex 3D morphology, which creates a multitude of habitat niches for commensal species by providing shelter and better access to food particles. Therefore, cold-water coral ecosystems, along with sponge grounds, are often described as “ecosystem engineers”, which means that, as a result of their presence and the habitats they build, they can significantly impact the number of species present and the heterogeneity of an area (Jones et al., 1994). Furthermore, these ecosystems are considered to be of high economic value (Foley et al., 2010), since they foster commercial fish species, which tend to occur more frequently and in higher abundances within and in proximity of cold-water coral environments (Costello et al., 2005; Koenig, 2001). Fostering fish species of commercial importance means coral habitats are also threatened by deep-sea bottom trawling, in which they constitute a large portion of the bycatch (Anderson et al., 2017; Clark et al., 2016). As a result, their ecological and economical value makes them ideal biodiversity conservation targets in the deep sea, but in order to develop efficient global management and conservation strategies, an understanding of their biogeographical distribution must be established (Tittensor et al., 2009).

Cold-water corals are one of the most prominent seamount fauna with more coral species recorded from these features than any other invertebrates, making them one of the better studied invertebrate taxa in the deep sea (Rogers et al., 2007; Stocks, 2004). Cold-water corals are suspected to have an affinity for topographic heights, because of the hard substrate availability and the increased productivity regime with strong hydrodynamics supplying them with food particles (Genin et al., 1986). The diversity of corals on seamounts is considered to be relatively high (Rogers et al., 2007) and could be much higher than currently assumed, as highlighted by a recent re-examination of bamboo coral specimens with molecular techniques, yielding 12 new species (Heestand Saucier, 2016).

In an attempt to estimate cold-water coral diversity on seamounts, Rogers et al. (2007) compiled a unique data set producing 3,215 coral species recorded across 184 seamounts. This data compilation shows that the best sampled areas are the seas around New Zealand, the Hawaiian Islands, the North-east and West Atlantic, and western margin of North America (Rogers et al., 2007). The compilation suggests, through accounting for the sampling effort, that the greatest coral diversity occurs in the South-West Pacific followed by the North-East Pacific (Rogers et al., 2007). The high diversity within the Pacific is attributed to dispersion from the shallow coral hotspot of the Indo-Pacific first into the SW Pacific deep-waters and subsequently to NE Pacific (Rogers et al., 2007). The region of the North-East Atlantic initially shows a high number of species, which is attributed to the availability of suitable coral habitat in terms of complex geomorphology coupled with high productivity (Rogers et al., 2007). However, when this region is corrected for sampling intensity, the species richness decreases suggesting that the initial pattern might also be a mere artefact caused by a higher intensity of sampling (Rogers et al., 2007). Despite this attempt by Rogers et al. (2007), estimates of global coral diversity on seamounts are incomplete, since only a small fraction of seamounts has been sampled with pronounced gaps in certain regions (Fig. 1.2, Chapter 1). In particular, the authors point out that within the Atlantic, the tropical Atlantic is one of the most poorly sampled deep-sea regions, with most of the research focused within the North-East and West Atlantic (Rogers et al., 2007). These gaps prevent a sound understanding of cold-water coral biodiversity patterns and wider biogeographical patterns, thus hindering our understanding of the distribution and diversity of cold-water corals, and ultimately leading to less effective management activities in relation to the preservation of biodiversity.

To counter the situation described above, the present study focuses on enhancing our understanding of cold-water coral biodiversity patterns within the Equatorial Atlantic. Here, we present the species richness and abundance from three distinct seamounts based on analyses from ROV video data. We also compare the community assemblages across the three sites, in order to understand the wider spatial distribution of cold-water corals in this region and relate our results to environmental variation between the seamounts.

3.3 Methods

3.3.1 Site description

The three seamounts investigated in this study are located within the Equatorial Atlantic (see Fig. 3.1), which is a transitional region for global circulation. From east to west we studied the following: Annan seamount, located just off the Sierra Leone Rise; Knipovich seamount ~ 800 km further towards the west; and Vayda seamount located ~3500 km away, west of the Mid-Atlantic Ridge. The circulation pattern within this tropical region is westward with Annan seamount being at the meeting point between the Canary Current and the North-Equatorial Current (NEC), with the latter reaching both Knipovich and Vayda seamounts. The bottom water-masses within the region are the Arctic Bottom Water, overlaid by the North Atlantic Deep Water from ~ 3500 m depth (Giresse, 2008). The Antarctic Intermediate Water Mass occurs at depths of 1500 - 500 m and is overlaid by the South-Atlantic Central Water with influence from the North-Atlantic Central Water from the surface (Emery, 2003b).

3.3.2 Data collection and processing

During the RRS James Cook expedition JC094, video footage data was collected using the ROV '*Isis*' Super SCORPIO camera across three dives per site. All the dive transects in the different seamounts are across a depth gradient. Details concerning the setup of the SCORPIO camera are available in Appendix A. The coral fauna was annotated using Ocean Floor Observation Protocol (OFOP, v. 3.3.7a). A detailed annotation methodology is available in Appendix A. The video annotations of the corals and other invertebrate fauna associated with the corals were made by designating taxa to the highest taxonomic resolution possible based on visual assessment using species catalogues, voucher specimens collected during the cruise, and consultation with taxonomic experts. The resulting morphospecies are a limitation of this study, as they are likely to result in an underestimation of species richness as they do not account for cryptic species.

The three sites were mapped using the ship's hull-mounted Kongsberg EM-120 multibeam echosounder and data were processed using CARIS HIPS and SIPS (v. 8.1) and gridded at 50 m resolution with the spatial references of World Geodetic System 1984 Universal Transverse Mercator Zone 27 N (Annan), 26 N (Knipovich), 22 N (Vayda). At this stage the coral occurrences were mapped in ArcGIS based on the georeferenced OFOP annotations on top of the ROV Ultra-short baseline (USBL) track. Transects were first divided into 1 m long samples. The bathymetry was used to extract quantitative descriptors of the seabed terrain (Wilson et al., 2007), to be used in investigating the geomorphological setting between the coral fauna of each seamount. The variables derived included slope, fine-scale topographic position index (TPI), rugosity, surface area, aspect (divided in eastness and northness), and general curvature. They were generated using Jenness Enterprises' Spatial Analyst Extension and Land Facet Corridor Tools by calculating each variable from the 50 m pixel resolution basemaps and extracting its value for each sample's midpoint. The coral occurrences were combined with the bathymetric data by using the spatial joins function in ArcGIS (version 10.2.2). The oceanographic data acquired from the CTD casts were combined with the coral occurrences and bathymetric data based on the depth values acquired from the bathymetry.

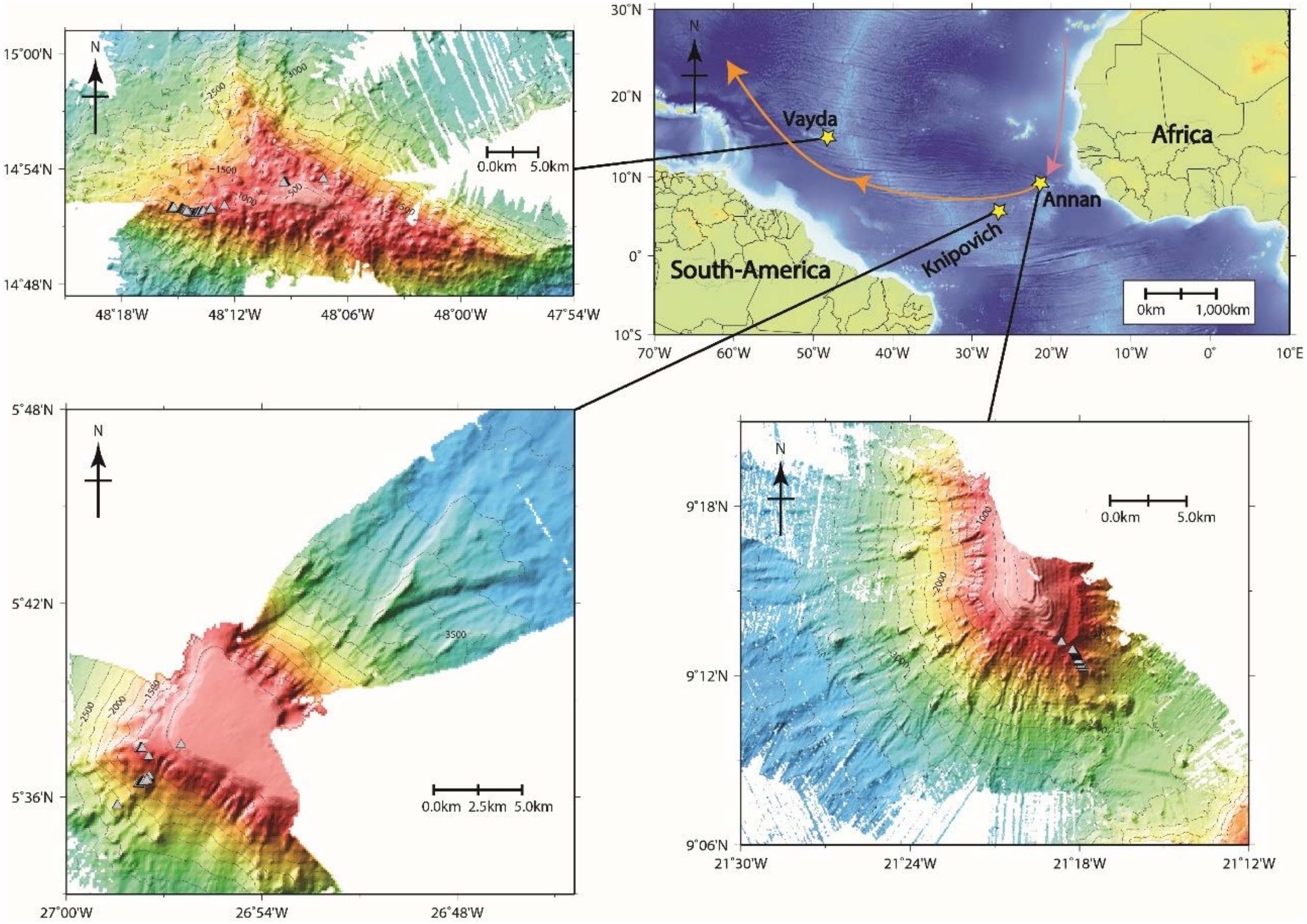


Figure 3.1 Map of Annan, Knipovich and Vayda seamounts showing the location of the cold-water corals (grey triangles) with bathymetry of 50 m pixel resolution. In the inset map pink arrow represents the Canary Current and orange arrow represents North-Equatorial Current.

For the purpose of community comparisons, we focused our analysis between 1000 -2000 m depths, since each seamount has extensive coral fauna occurrences within this depth thus allowing comparisons of patterns of biodiversity between the seamounts. In total there were 65 coral species occurring within this depth band. The 1 m length samples which were within 50 m proximity of each other were assigned to correspond to the same coral assemblage. Isolated singular coral occurrences that were further then 50 m from neighbouring coral occurrences were thus excluded at this stage and they are not included in the multivariate analysis of the communities (but the total number of species are presented in Table 3.1.). Since the coral assemblages were of different extents, the smallest patch size of corals was measured, which was 15 m long. In order to optimise the number of samples per assemblage and thus reduce data loss while maintaining habitat fidelity, it was decided to use a sample size of 10 m. More details on data collection from the transects are available in Appendix A. The corresponding environmental data were averaged across the segments of 10 m length. This generated 79 samples (of 10 m of coral assemblage coverage) for Annan, 64 samples for Knipovich and 183 samples for Vayda seamount.

Particulate Organic Carbon

In order to gain an insight towards the input of food supply in each of the seamounts, particulate organic carbon (POC) samples were collected. Pre-combusted and Milli-Q rinsed GF/F filters were used to filter 2-4 litres of seawater on board, sampled from the CTD niskin bottles. The sampling strategy consisted of taking samples at the surface and then every ~ 300, 400, or 800 m intervals until the base of the seamount was reached. POC analysis was conducted following a similar method as described in Lourey et al. (2004). In short, frozen filters were decarbonated with HCl for 48h and left to dry at 50 °C. The filters were not weighted prior to usage, hence the filters were dry weighted prior to analysis. The analysis was conducted on a Carlo Erba NA 2500 elemental analyser in-line with a VG PRISM III isotope ratio mass spectrometer at The University of Edinburgh. There was a technical issue with the mass spectrometer, in which two samples from Annan seamount were analysed together. The following equations were applied to the Elemental % Composition obtained from the analysis to obtain a final POC flux.

$$Weight\ Correction = \frac{Elemental\ \%\ Composition}{Dry\ Weight\ (mg)} * 1.00\ (mg)$$

$$POC\ Flux\ (\mu g\ l^{-1}) = (Weight\ Correction * Dry\ Weight\ (mg)) \div 100 * 1000 * Filtered\ Water\ Volume\ (l)$$

The surface productivity patterns obtained here were also checked against chlorophyll and POC satellite data to avoid the bias introduced by snapshot sampling (Appendix B).

3.3.3 Statistical analysis

Species richness and total abundance for the three sites were calculated in R. For the purposes of the following multivariate analysis, we converted the data set into presence – absence data, as recommended by Borcard et al. (2011) for comparisons across large spatial scales. The statistical analysis comparing the biological cold-water coral assemblages from the three seamounts were done in PRIMER (version 7). The similarity distance matrix between samples was constructed using the Bray-Curtis dissimilarity index, which was subsequently used in the Analysis of Similarity (ANOSIM), which is suitable for non-parametric data, to test for significant differences between seamounts and to obtain an R value. The ANOSIM R ranges between 0 and 1, with values closer to 0 indicating more variability within the fauna from the same seamount than with the fauna of another seamount, while 1 means high dissimilarity between the communities from different seamounts. The results are visualised using a Nonmetric Multidimensional Scaling – ordination. With the aim of pinpointing which morphospecies contributed most to any significantly dissimilar communities between the seamounts we used SIMPER. We also performed ANOSIM on the normalised environmental data set using the Euclidean distance to investigate whether the environmental settings were dissimilar between the sites and subsequently produced boxplots of the range of values for each environmental variable. A sampling bias was explored during the data exploration phase, as there were more samples in Vayda seamount. However, the depth range was the same and the area surveyed consistent between all sites. Despite this, we accounted for the sampling imbalance by rarefying the number of samples to 64 (the number of samples on Knipovich) and randomly generated this number of samples from Annan and Vayda seamount. However, this did not change the statistical analysis results and we present the results with both data sets in Table 3.2.

3.4 Results

3.4.1 Description of the cold-water coral communities

This study shows that seamounts within the Equatorial Atlantic have a diverse and abundant cold-water coral fauna, with a total of 122 morphologically distinct coral species recorded throughout the study. The Annan coral communities are characterised by *Enallopsammia rostrata*, a variety of bamboo corals, primnoids, and different species of *Corallium*. Extensive multispecies coral assemblages occurred between the depths of 1300 – 1500 m, with the most dominant species being *Paragorgia* sp., *Paramuricea* sp. and *Corallium* sp. with many large specimens (> 60 cm). A large coral assemblage dominated mainly by *Paramuricea* sp. was also observed. The geomorphology of this seamount consisted of steep slopes and vertical habitats, which also had abundant coral fauna and associated invertebrates. An interesting observation of the coral communities is that there are only a few occurrences of *Madrepora oculata* and *Solenosmilia variabilis*, which are commonly observed in the NE Atlantic. Knipovich seamount also had abundant communities of *Enallopsammia rostrata*, *Paramuricea* sp., in addition to occurrences of *Acanella* sp. growing together with thickets of stony corals. In addition, here we found many white branching Isididae – corals (*Keratoisinidae* sp. white). Similar to Annan seamount, Knipovich also had some vertical habitats (Fig. 3.2) and overall the main coral areas appeared to occur over a small knoll-type feature. Vayda seamount had a coral garden formed by large pink Isididae specimens (*Keratoisinidae* sp. pink) and also an abundant community of white Paragorgiidae corals (Fig 3.2. c.3). The latter were unfamiliar to the taxonomic experts we have approached and thus potentially a new species. Many specimens of the *Iridogorgia* genus were observed, with some of them being identified as *Iridogorgia magnispiralis*, while others are tentatively identified as the *Iridogorgia bella* and *splendens*. The Vayda coral assemblages were often accompanied by an abundant sponge fauna, either growing directly on dead coral skeletons or occurring on the hard substrate in close proximity of the corals. Similar to the other two seamounts, a few isolated stony coral thickets were observed. Both Annan and Vayda had abundant soft coral assemblages of the genus *Anthomastus*. It must be noted that one of the challenges in characterising the coral fauna within this project, is the relatively high number of Plexauridae species across all sites and this particular group is notoriously challenging since there is a lack of taxonomic expertise.

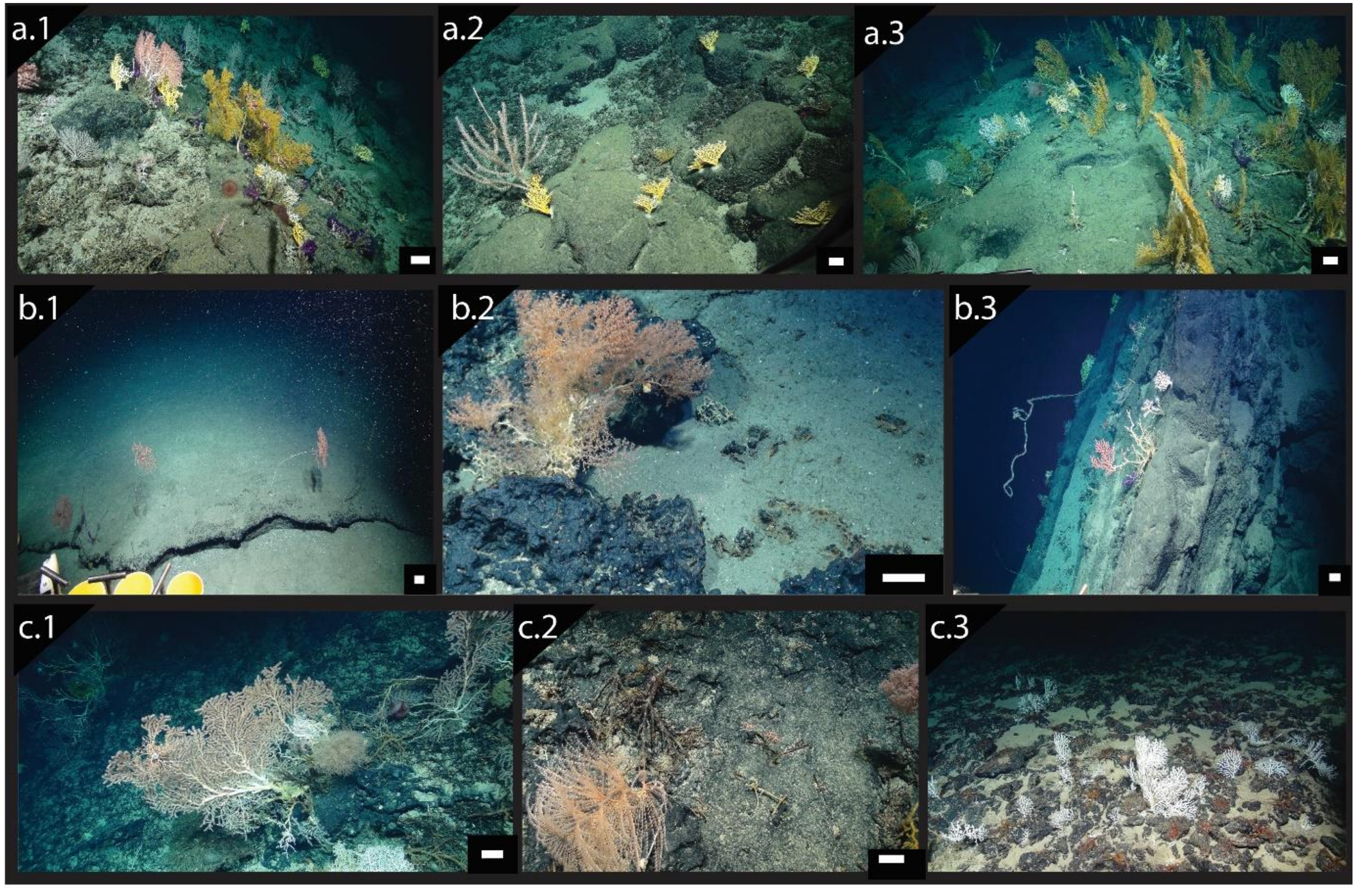


Figure 3.2 Examples of the cold-water corals species from the three seamounts (a –Annan, b- Knipovich, c – Vayda).

3.4.2 Comparison of the biodiversity patterns

Species richness varied across seamounts, with the highest number of coral species and associated species present at Annan seamount and lowest at Vayda seamount (Table 3.1). Of the 65 species used in the comparison between the 1000-2000 m water depths, 15 of the species were shared between all sites, 25 between two sites and 25 were unique to one of the seamounts. Knipovich and Vayda seamount had similar numbers of coral and associated species. Conversely, total abundance was highest at Vayda seamount and lowest on Knipovich. It must be noted that the patterns observed here potentially suffer from a sampling bias as the ROV data were collected in an opportunistic fashion meaning the video transects were not stratified or randomised per seamount. Comparisons between the seamount communities with the ANOSIM test showed a significant pattern (p=0.001, R= 0.42 or 0.46, Table 3.2). Since the R value of this test ranges between 0-1, with the latter meaning more dissimilar communities, the results can be interpreted only as a modest dissimilarity between the communities (Fig. 3.3).

The most dissimilar coral communities were those occurring on Annan and Vayda seamounts, which are accordingly the furthest distance apart, with Knipovich communities being somewhere in the middle in comparison to the neighbouring seamounts. Results from the SIMPER analysis (Appendix B) illustrate that the differences in communities arise from Annan seamount having an abundant population of the stony coral *Enallopsammia rostrata*, bushy bamboo corals, and *Corallium* sp., while Vayda frequently has *Metallogorgia melanotrichos*, *Paramuricea* sp. and different Chrysogorgid species. Knipovich seamount, which sits between the other two sites appears to have mixed communities, with records of both *Enallopsammia rostrata* and *Metallogorgia melanotrichos*, in addition to hosting *Clavularia* sp., which is regularly present on all seamounts.

Table 3.1 Comparison of the number of species, associates and total abundance between the three seamounts within the Equatorial Atlantic based on ROV-video footage, with a) using all the data generated across each seamount and b) the rarefied (n=64) data set between 1000- 2000 m depth. The temperatures without brackets are derived from the ROV CTD and those with brackets correspond to values from the CTD instrument

Seamount	Annan	Knipovich	Vayda
a)			
Coral species richness	70	53	48
No. of associated species	97	88	89
Total abundance	9 000	6 000	12 160
Analysed transect length (m)	16 000	11 424	17 160
Area sampled (m^2)	46 400	26 275	48 048
b)			
Coral species richness	45	37	33
Coral abundance	2 569	1 442	843
Analysed transect length (m)	790	640	1 830
Area surveyed (m^2)	2 291	1 472	5 124
Temperature range (°C)	4.3-9.2 (3.5-5.2)	3.9-4.3 (3.6-4.9)	4.3-5.4 (3.6-5.6)

Table 3.4 Results from ANOSIM comparing compositional differences between the seamount communities using the rarefied data (n=64) . The values in brackets represent any results that were different when using the whole data set. Permutations=999.

	R Statistic	Significance Level
Global Test	0.42 (0.46)	0.001
Pairwise tests between seamounts		
Annan, Knipovich	0.33 (0.35)	0.001
Annan, Vayda	0.58	0.001

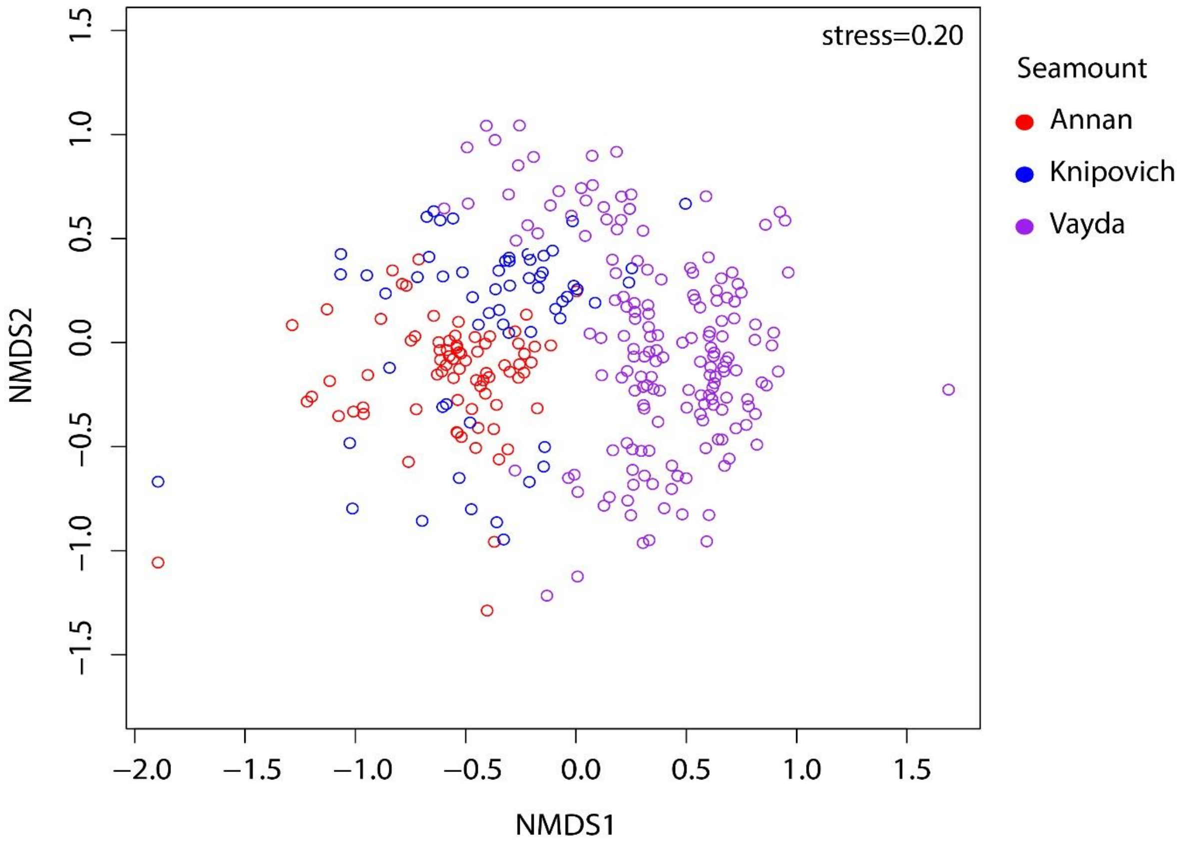


Figure 3.3 Non-metric multidimensional scaling ordination plot based on a Bray- Curtis dissimilarity matrix of cold-water coral species showing only modest differentiation between the community compositions from different seamounts using the whole data set.

The environmental settings of the seamounts in the areas of coral assemblages were compared in order to see whether differences in the coral communities can be attributed to differing abiotic settings. The ANOSIM results using oceanographic and bathymetric data showed the sites were significantly different in terms of their environmental settings (p=0.001, R=0.51), and the boxplots for showcasing the range of each parameter per seamount are available in Figs. 3.4 and 3.5. In particular, Annan seamount appears to be markedly different to the other two sites with higher TPI values, which are interpreted as areas which have relatively high elevation in relation to the surrounding seabed. These are most likely the vertical habitats present at this site, which can be seen in the bathymetry as terraces (Fig. 3.1). Another apparent difference is that on Vayda seamount the coral assemblages occur slightly deeper than at the other two sites, which could be a sampling artefact caused by the limited field of view of the ROV footage, since there is hard substrate available at shallower depths. The oceanographic plots (Fig. 3.5), however show that Vayda has slightly higher oxygen values than the other two sites. However, the main difference between the seamounts is the variation in POC input and hence food availability with an increasing offshore distance resulting in lower POC values (Fig. 3.6). Annan seamount has much higher food availability in comparison to the other two sites, which have similar POC values in comparison to each other. In particular Annan seamount has high POC values between the 1000 -2000 m depths, where large areas of coral gardens occurred. Additionally, another interesting feature of Annan seamount is similar POC values within the range of 75-90 µg/l in the surface waters above the seamount and in the seamount base (Fig. 3.6).

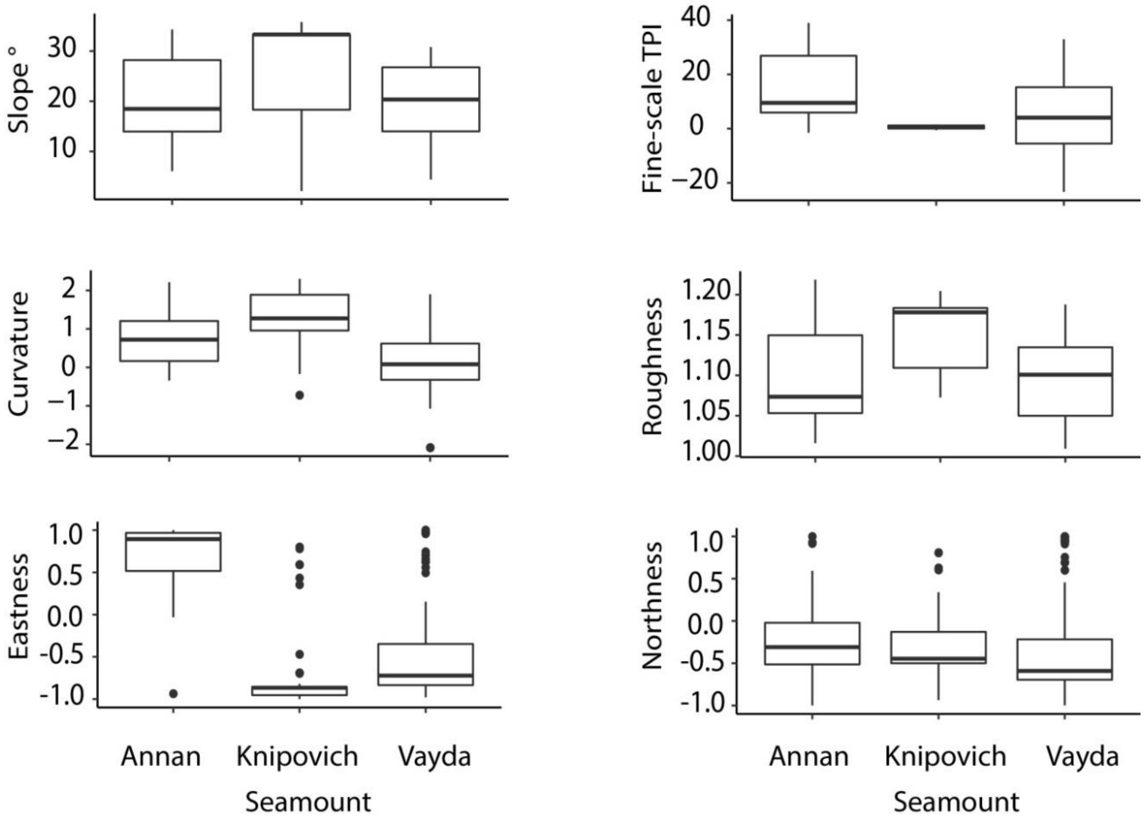


Figure 3.4 Boxplots highlighting the range of values for bathymetric parameters at locations of coral communities. The dots outside the box represent outliers. Annan n=79, Knipovich n=64 and Vayda n=183.

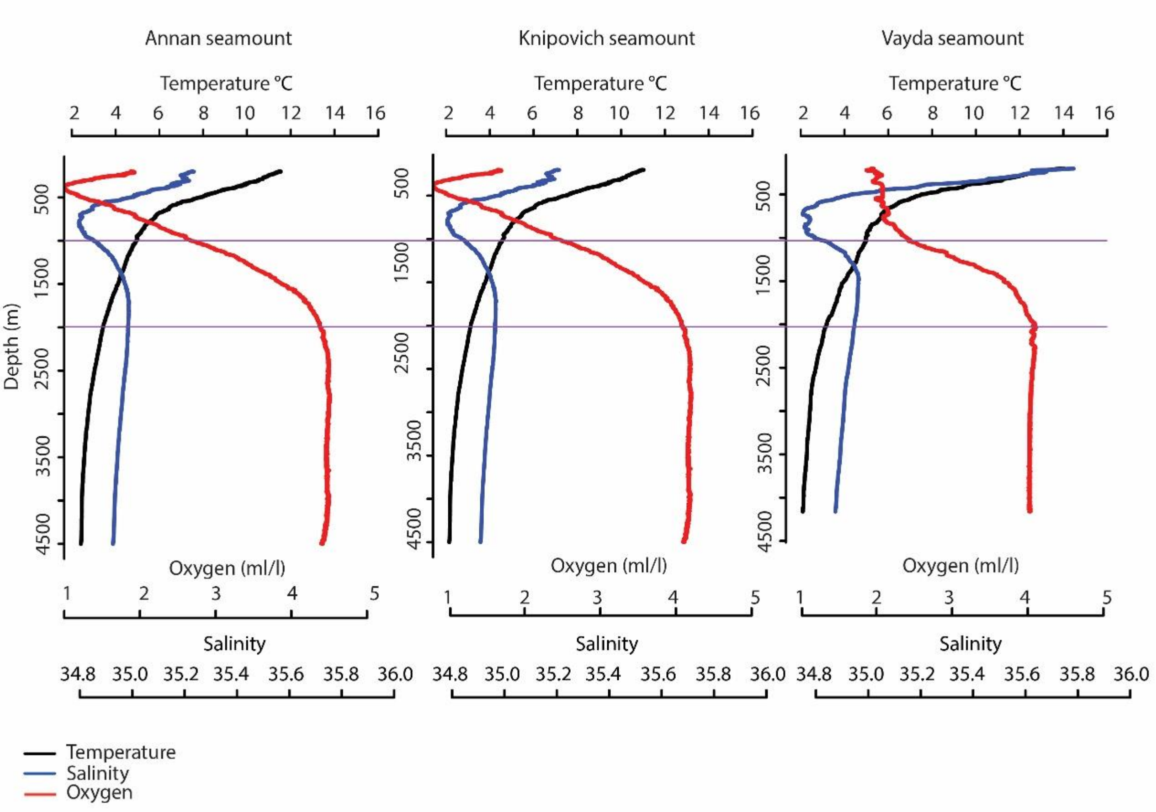


Figure 3.5 The oceanographic profiles from the summit to the base of the three seamounts based on CTD casts. Purple lines indicate the depth band of 1000- 2000 m, from which the coral communities were compared between the seamounts.

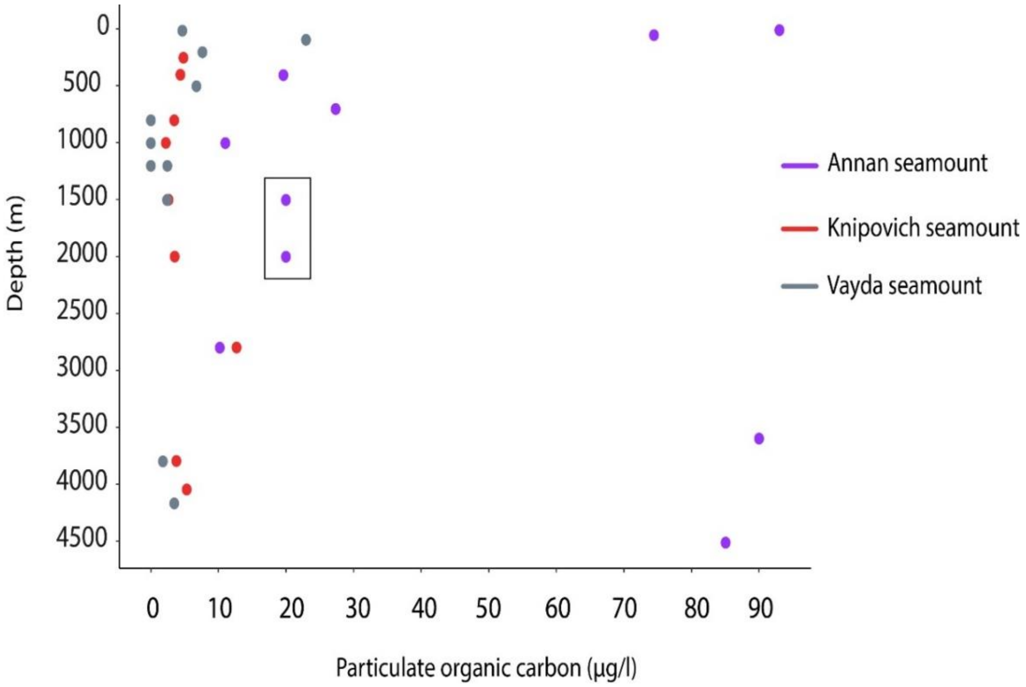


Figure 3.6 The particulate organic carbon measured in the water column next to each seamount. Annan N=10, Knipovich N=9, Vayda N=11. The grey box represents two samples which were analysed together due to a malfunction of the mass spectrometer.

3.5 Discussion

This study describes the coral fauna from Annan, Knipovich, and Vayda seamounts across the Equatorial Atlantic. The data collected from ROV video footage revealed that all three sites contain a diverse and abundant cold-water coral fauna, such as gorgonian and antipatharian corals. As the communities present are described in detail in the results section of this study, in this section we will focus on the peculiarities in relation to other regions and seamounts. An interesting observation from surveying these previously unexplored seamounts, is that the tropical seamounts had a very limited amount of *Solenosmilia variabilis* and some *Madrepora oculata* specimens, but all three sites had abundant *Enallopsammia rostrata* - colonies. In comparison the first two species are very widespread and highly common within the North-Atlantic (Davies and Guinotte, 2011b), with the transects across all three seamounts covering the appropriate temperature range for the occurrence of these scleractinian species (*Solenosmilia variabilis* : 3.3–14.5°C, *Madrepora oculata:* 1.8-15 °C in the Atlantic Ocean (Keller and Os'kina, 2008). The presence of *Madrepora oculata* and *Enallopsammia rostrata* in our data set leads to a disagreement with results from habitat suitability models, which for these species, show low habitat suitability in the areas of our sites, despite the algorithm having the ability to incorporate seamounts larger then > 1 km across (Davies and Guinotte, 2011). The authors describe that *Enallopsammia rostrata* is mostly found in areas with limited particular organic carbon input. However, in the present study, this species occurs frequently and in high abundances on all the sites and hence across a variety of productivity regimes. The widespread *Lophelia pertusa*, which is common in the North-Atlantic, was absent from our records. In particular this species could be expected to occur on the shallower parts of Annan seamount as there are records of *Lophelia pertusa* off the western coast of Africa (Davies and Guinotte, 2011), and therefore it's absence might be due to lack of sampling,. However, it is worth noting that *Lophelia pertusa* is also absent from the well-studied Tropic seamount, which is located 1600 km to the west, south of the Canary Islands (Murton, 2016), but here its absence could be linked with the fact that most of this seamount lies below a 1000 m water depth. Furthermore, habitat suitability models show that *Lophelia pertusa* is mostly restricted to the NE Atlantic and South Eastern North-American coast and that overall seamounts provide less suitable habitats for this species (Davies and Guinotte, 2011). Interestingly, some of the species occurring in this study appear to be shared with the cold-water coral fauna from the Hawaiian Islands, such as bamboo coral species, which are yet to be described (Watling, pers. communication) in addition to *Iridogorgia magnispiralis* and *Iridogorgia bella* (Watling, pers. communication).

The number of cold-water coral species found within our study sites can be deemed high in comparison to the species richness of other seamounts as assessed by Rogers et al. (2007). It must be noted that the comparisons are tentative as the sampling effort between the current regional study and the Rogers et al. (2007) global study is not standardised. Furthermore, the global seamount cold-water coral data set relies heavily on samples collected with mobile sampling gear, such as trawls, and this type of gear has been shown to under sample corals in comparison to imagery based techniques (Williams et al., 2015, see also Mortensen et al. 2008: Table 1 and 2). With these caveats in mind, the global database compilation shows that seamounts off western-Africa have an estimated 35-42 coral species, while in our study Annan seamount has 70 species. This number rivals some of the highest coral species richness values found across the 184 seamounts in the Rogers et al. (2007) data set and resembles values found in the region of the NE Pacific and Hawaiian Islands. The number of species for Knipovich (53) and Vayda (48) are also high, in particular in comparison to seamounts closest to Vayda. These seamounts, originally only host 1-9 coral species, but when corrected for the low sampling effort, they are likely to have high diversity (Rogers et al., 2007), thus falling in agreement with what our results suggest for the seamounts in the present study. The potential high overall diversity of cold-water corals within the equatorial region, which can be observed in both data sets, could arise from it acting as a boundary area, where different circulation paths and water masses converge, transporting a diverse set of larvae from both North and South Atlantic. Alternatively, there is also an evolutionary explanation for high tropical diversity, in which regions such as the tropical West Atlantic, are hypothesized to have served as diversification epicentres, pumping diversity to the surrounding Atlantic deep sea (Briggs, 2003; Jablonski, 1993).

Comparisons between the coral assemblages from the three seamounts showed that the two seamounts furthest apart (Annan and Vayda) had the most dissimilar communities. Interestingly, the communities from the Knipovich seamount were equally dissimilar to the other two sites, despite its geographical proximity to Annan seamount. However, the ANOSIM R value depicting dissimilarity falls within the medium spectrum, suggesting that there is a certain degree of similarity between the coral communities across this tropical region, with 15 species shared between all sites and 25 species shared between two sites. This similarity is caused by species which have a wide distribution, such as *Metallogorgia melanotrichos*, *Enallopsammia rostrata* and *Iridogorgia magnispiralis*, often occurring on many seamounts and seamount-like habitats in different oceans (Davies and Guinotte, 2011; Glover et al., 2018). Conversely, previous studies comparing seamount biota have found striking differences between the community composition of adjacent seamounts, or chains of seamounts (de Forges et al., 2000). In our study there are 25 coral species which can be deemed unique to one of the three sites. This lack of species overlap between seamounts suggests that for some species there is the potential for a localised distribution or that the resulting patterns are caused by a sampling artefact. The latter option would be generated by the limited sampling effort of 1 to 2 ROV transects per seamount conducted in this study, with a limited field of view over a patchwork of benthic habitats. This artefact can only be resolved through future sampling, but meanwhile the prospect of a localised occurrence of certain species, in this example from the Isididae and Antipatharian orders, has potential implications for their conservation, as recruitment between seamounts is poorly understood, yet it forms a pivotal point in management and conservation scenarios of coral ecosystems.

The reasons for the potential dissimilarity of coral communities between the sites, in particular between Annan and Vayda seamounts, could perhaps arise from both historical and contemporary processes. When comparing the bathymetric settings of the habitats where the corals occur, there are some distinct differences for example in the topographic elevation index (Fig. 3.1 and 3.4). For example, on Annan seamount, there is a set of vertical habitats, which appear to be colonized by different communities than those occurring on more gently sloping sites (Victorero et al., 2018). Such habitats are likely to affect both the number of species and the community composition, thus causing the slight dissimilarities seen here. Furthermore, on Knipovich the corals occur slightly deeper and on top of a knoll (Fig. 3.1), suggesting that the species found within this small geomorphological feature might be ones particularly well adapted to elevated current speeds. However, the most striking difference between the sites is the input of food particles as measured by the POC sampling, which provides a snapshot into the productivity regime. Here, we see a much higher POC input over Annan seamount in the 1000 -2000 m depth band (Fig. 3.5). An examination of surface chlorophyll and POC concentrations from satellite data verifies a higher productivity regime in Annan seamount (Appendix B), which is located in close proximity of a productive region off the west coast of Africa (Wang et al., 2013). The enhanced productivity could potentially explain the higher species richness here, since higher rates of productivity have also been previously affiliated with higher species richness in the deep sea (Woolley et al., 2016). An extension of this reasoning is that the summits of these sites are at markedly different depths, which is thought to affect the assemblage composition of the benthic fauna through the variation in physicochemical characteristics affecting the colonisation of fauna (Rowden et al., 2005). While in this study we have tried to circumnavigate the issues caused by comparing communities at different depths by focusing on the 1000-2000 m depth band, the depth of the seamount summit is suspected to influence the overall biodiversity (Clark et al., 2011), with different mechanisms leading to differences in the productivity regime. For example, Turnewitsch et al. (2016) found that POC export was elevated over a tall seamount with a summit depth of ~105 m, which is attributed to tidal dynamics bringing nutrients upwards leading to brief periods of enhanced primary productivity, with subsequent export of the particles into deeper water. Similarly, seamounts with summits just below the photic layer have been suggested to accumulate the maximum amounts of zooplankton due to their vertical migration to intermediate depths (Genin, 2004). These are both possible mechanisms that can be linked to Annan seamount, which has a much shallower summit then the other two seamounts.

3.6 Conclusion

This study provides the first description of the cold-water coral fauna from three seamounts across the poorly sampled Equatorial Atlantic. Our results show that these seamounts harbour diverse and abundant cold-water coral fauna, with the community composition changing from east to west, which is attributed mainly to changes in POC input. The initial results from these three seamounts suggest the tropical deep-sea might harbour high cold-water coral species richness, and thus provides new insight into the landscape of cold-water coral diversity within the Atlantic Ocean. The data set presented here indicates that future studies should explore this region more thoroughly, in order to improve the understanding of coral biogeography, leading to more efficient management of these vulnerable marine ecosystems.

Acknowledgements

The data collection for this work was funded by the ERC Starting Grant projects CACH (grant no. 278705). The authors would like to thank the crew, technical staff and science party of the RSS James Cook 094 TROPICS research expedition and particularly Shannon Hoy for processing the bathymetry. L.V would like to thank Sian Henley for supervision during the POC analyses. We would also like to extend our gratitude to Jaime Davies, Tina Molodotsova and Les Watling for their taxonomic expertise. V.A.I.H was funded by the ERC Starting Grant project CODEMAP (grant no. 258482). M.L.T. was funded by the NERC DeepLinks project (NE/K013513/1). L.V is funded by the Southampton Partnership for Innovative Training of Future Investigators Researching the Environment (SPITFIRE, a NERC Doctoral Training Partnership – grant number NE/L002531/1).

Chapter 4 Ecological communities and drivers of biodiversity within the transverse ridge of the Vema Fracture Zone

Author contributions. This chapter is in preparation for submission to the peer-reviewed journal of Frontiers in Marine Science. The author list for this article is: Victorero L., Sym E., Robinson L.F., Taylor M.L, Huvenne V.A.I. L.V. and E.S. prepared the image catalogue, E.S. collected the data from ROV imagery for her MSci thesis under the co-supervision of L.V., L.V. conducted the statistical analysis and wrote the chapter. L.F.R. was the principal investigator on the RSS James Cook 094 voyage, and along with M.A.T. and V.A.I.H. acquired the data. All authors reviewed the manuscript.

4.1 Abstract

Fracture zones (FZ) are major deep-sea features which off-set the mid-ocean ridge axes and are to date one of the least explored types of deep-sea habitat. Our knowledge of their biology and ecology, and their potential role as biogeographical pathways between ocean basins, remains speculative. Here we investigate the transverse ridge habitats within the Vema FZ based on 55 h of ROV-footage across the summit, flank, and deep slope and we present the first biological characterisation of these habitats. The ridge habitats range from sediment plains, over volcanic plateaus to vertical walls and pinnacles. These habitats were found to host 46,300 individuals across ~8.5 km belonging to 172 different morphospecies. The communities observed include vulnerable marine ecosystems (VMEs) such as cold-water coral gardens consisting of *Enallopsammia rostrata* and sponge gardens of *Poliopogon* sp. The pinnacles were colonised by multi-species coral assemblages, such as primnoids and chrysogorgids. In order to understand patterns of biodiversity and their drivers within the ridge, we modelled changes in species richness and abundance in response to topographic and oceanographic variables. Species richness and total abundance were significantly influenced by depth and both increased in relation to steeper slopes, with species richness additionally being driven by local seabed elevation. Comparisons with other Mid-Atlantic Ridge (MAR) areas suggest that both ridge communities are similar in terms of their species composition, but the Vema transverse ridge communities are more abundant. Our results suggest that Vema FZ would be a strong candidate site to include in future environmental management plans, since it hosts communities that are representative of the non-vent MAR fauna that could be potentially impacted by deep-sea mining.

4.2 Introduction

Fracture zones (FZ) are long linear bathymetric features in ocean basins, resulting from the offset of mid-ocean ridge (MOR) axis segments. They are poorly explored deep-sea ecosystems, with most of the ecological research concentrated on nearby MORs and in particular on hydrothermal vent systems. However, FZs are thought to play a major role in deep-sea biogeographical patterns. Some hypotheses suggest that FZ offsets disrupt along-axis gene flow of certain vent fauna in the MOR system (Van Dover et al., 2002). Or alternatively, that their large topography influences faunal connectivity by acting either as a dispersal barrier or a pathway, for example between the eastern and western parts of the Atlantic (Guggolz et al., 2017). At present, growing mineral exploitation interests, in particular of valuable Seafloor Massive Sulphides (SMS) from hydrothermal vent systems, combined with technological advances in deep-sea exploration, have stimulated scientific interest towards enhancing the overall understanding of MOR areas and associated FZ ecosystems (e.g. NERC transforming fractures – call, SEMPIA workshops). Furthermore, in the future, FZs themselves could be candidate sites for deep-sea mining as they host mineral deposits, which are similar to those occurring on seamounts. These deposits include ferromanganese crusts (Hein et al., 2003; von Stackelberg and Beiersdorf, 1991) and nodules (Devey et al., 2018).

The Vema Fracture Zone is one of the largest FZs across the Mid-Atlantic Ridge (MAR) and the main focus of the present study. It is one of the major FZs that have been proposed as Areas of Particular Environmental Interest (APEI) in response to the administration of exploration licences by the International Seabed Authority (ISA) for a total of 300,000 km^2 across the MAR (Dunn et al., 2018). The APEIs are essentially no-mining zones capturing a diverse set of habitats and faunal communities of ecological importance aiming to maintain connectivity within the larger system, which is/will be under localised physical disruption i.e. mining. The APEI designation is strategic and together these areas form a network, thus contributing towards the larger regional environmental management plans (EMPs), which have the overarching aim of protecting biodiversity and thus ecosystem function (Lodge et al., 2014). The network should therefore be representative of the benthic habitats and associated ecosystems, in order to be effective under different scenarios of mining impacts, which are yet to be quantified (Lodge et al., 2014). Previous APEIs designations, such as those in the Clarion-Clipperton Zone, relied on biophysical surrogates, such as nodule abundance, particulate organic carbon flux to the benthos and bathymetry, since there was a lack of detailed data on the benthic fauna (Dunn et al., 2018).

Similarly to previous APEI designations, the proposed designation of Vema FZ relies mostly on physical characteristics, such as it being a major conduit for Antarctic Bottom Water flowing from the western to the eastern basin (Morozov et al., 2015), the presence of a clam species, which is found in vents and seeps (Krylova et al., 2010), and its strategic location fitting into a broader APEI network maintaining connectivity (Dunn et al., 2018). Previous biological research on Vema FZ is limited, with only macro- and meiofaunal communities on the nearby abyssal plains having been recently characterised (Riehl et al., 2018). To date there has been no description of the communities and biodiversity patterns from the bathymetrically complex hard-substrate areas such as the transverse ridge. These areas are likely to host communities that could be representative of those occurring on the MAR and in closer proximity to SMS deposits, and thus within the spatial extent of mining impacts.

This study has two aims; the first is to describe the habitats and ecological communities from the Vema transverse ridge for the first time, thus presenting a rare detailed insight into the benthic communities of a potential APEI, prior to its designation. Our results will provide a platform from which to discuss whether Vema FZ is a valuable potential APEI from an ecological perspective, for example by being representative of other non-vent MAR ecosystems. The second aim of the study focuses on understanding the spatial distribution of biodiversity across the ridge and how it is shaped by oceanographic and terrain descriptors, which could be used as biophysical surrogates in future studies of the current site.

4.3 Methods

4.3.1 Site description

The Vema FZ, in the Equatorial-Atlantic, extends a total of 2500 km across the Mid-Atlantic Ridge. Surface flow over this area is influenced by the North Equatorial Current (NEC) flowing westward, creating the southern part of the subtropical gyre (Bourlès et al., 1999). The Vema FZ acts as a conduit for the coldest and densest bottom waters flowing from the western to eastern Atlantic basin. These include the Antarctic bottom water (AABW) at depths below 4000 m (Demidov et al., 2011), overlaid by the North Atlantic Deep Water (NADW) up to ~ 1200 m and the Antarctic Intermediate Water (AAIW) flowing up to depths of 800 m depth (Morozov et al., 2010). The transform valley comprises the Vema transverse ridge, which offsets the MAR by 320 km to the left (Fig. 4.1). This ridge is one of the highest within the MAR system and is very narrow being <30 km wide at the base (Kastens et al., 1998).

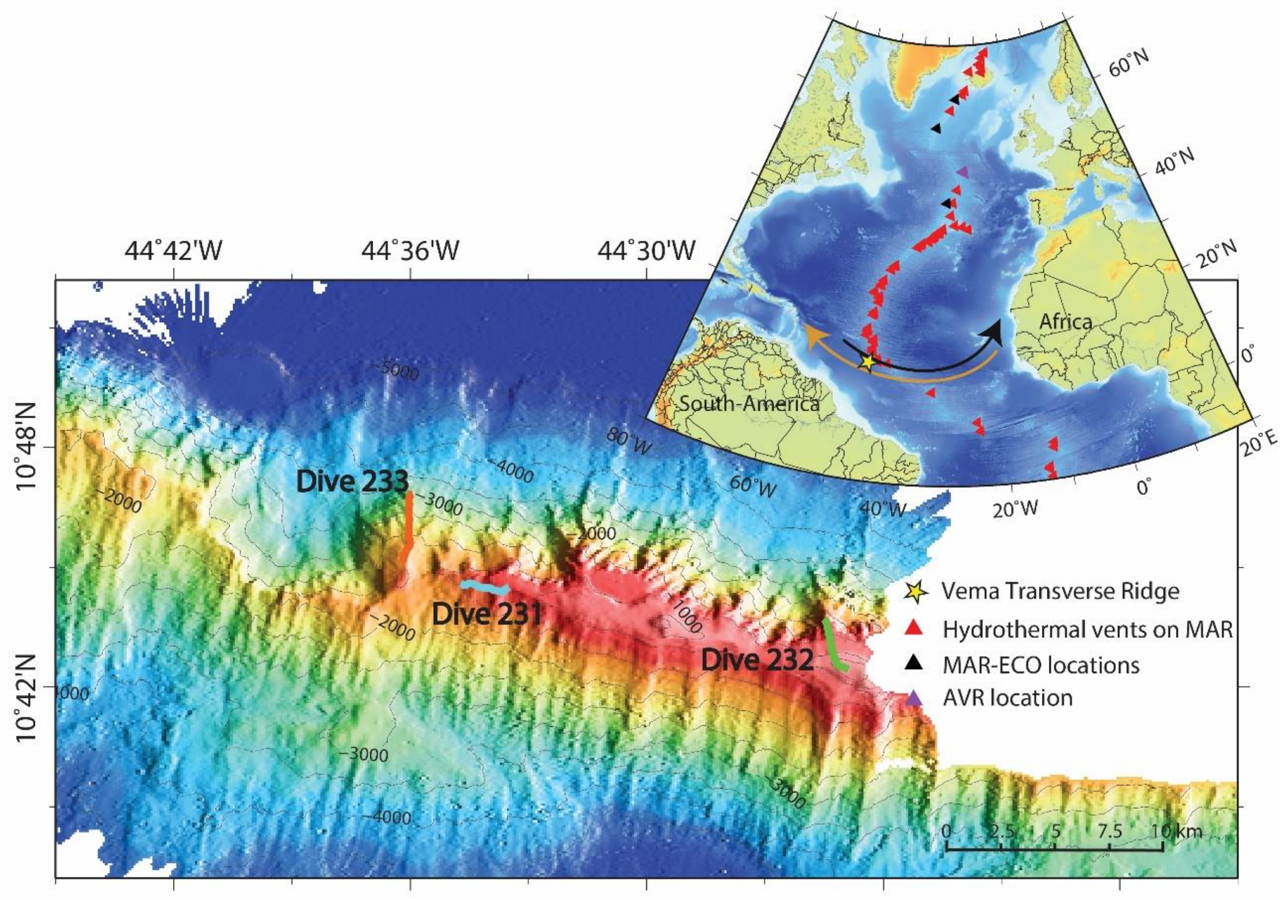


Figure 4.1 Map of the eastern section of the transverse ridge within the Vema Fracture Zone showing the location of the ROV dive tracks. The inset map shows the location of hydrothermal vents on the Mid-Atlantic Ridge (MAR) based on the InterRidge Global Database of Active Submarine Hydrothermal Vent Fields (Beaulieu, 2015). The inset map also shows the location of previous studies on MAR faunal communities; location of the MAR-ECO project (Mortensen et al., 2008) and Axial Volcanic Ridge (AVR)– coral study (Morris et al., 2012). The direction of the main surface current (NEC=North-Equatorial Current, orange arrow) and the direction of bottom water transport (Antarctic Bottom Water, North-Atlantic Deep Water, black arrow) are indicated on the inset map.

Three million years ago the ridge was a tectonic island at sea-level or above before subsiding to its present depth range of ~500-5000 m (Kastens et al., 1998). Therefore, this part of the Vema FZ is considered a paleoisland and is thought to have played an important role in the connectivity for fauna between the central American and African continents (Palmiotto et al., 2017). While much oceanographic and geological research has been conducted over the Vema FZ, the biological communities and habitats on the ridge appear to have only been visited by the RRS *James Cook* in 2013 as part of the ERC-funded Tracing Oceanic Processes using Corals and Sediments expedition (TROPICS).

4.3.2 Data collection

The ROV *Isis* generated in total 54.35 hr of video footage in three transects across the summit, flank, and deep slope of the Vema ridge covering a total of ~ 8.6 km and a 600-2985 m depth range (Table 4.1) (Fig. 4.1). The video footage was used to identify and count benthic fauna > ~3 cm, and annotate and classify the substrates. The substrate categories were defined as 1) hard (volcanic plateaus, pinnacles and other complex extensive hard substrate geomorphologies and carbonate platforms), 2) soft (sediment, ripples), 3) soft and hard (a mixture of the previous two), 4) biogenic (dead coral framework), 5) biogenic and hard, 6) debris (coral and shell rubble mixed with sediment), 7) boulders, cobbles, and pebbles with sediment. A detailed description of the data processing steps related to the ROV imagery is available in Appendix A. The ROV was fitted with a SeaBird SBE 49 CTD that measured temperature, conductivity and pressure, and the data were processed with the SBE Data Processing (V7.20g) software.

Table 4.1 Detailed information from each ROV dive in the Vema Transverse Ridge

ROV ISIS Dive	Feature	Time on seafloor (h)	Length of sampled transect (m)	Area sampled (m2)	Depth range (m)	Temperature range (°C)	Number of species	Total abundance
232	Summit	17:03	3000	7800	570-1310	2.8-4.4	104	26,637
231	Flank	18:27	2700	7020	1100-1500	4.4 -5.2	80	15,784
233	Deep slope	19:51	3600	9360	1580-2940	4.8 - 7.1	106	3,879

The ridge was mapped using the ship's hull-mounted Kongsberg EM-120 multibeam echosounder and data were processed using CARIS HIPS and SIPS (v. 8.1) and gridded at 50 m resolution. The bathymetry was used to extract quantitative descriptors of the seabed terrain (Wilson et al., 2007) to be used in the statistical analysis described below. The variables included slope, topographic position index (TPI) at three scales (3x3, 6x6, 9x9 pixels neighbourhood radius), rugosity, surface area, aspect (divided in eastness and northness), and general curvature (Jenness 2012a, 2012b). The species, substrate, temperature, salinity, and bathymetry-derived data were combined by their spatial location (spatial joins) in ArcGIS (version 10.2.2). The ROV transects were then post-hoc divided into 100 m sample lengths, which generated 93 samples. This sample size was chosen on the basis of maintaining substrate and habitat fidelity whilst capturing enough individuals per sample to be able to perform statistical analyses. Furthermore, this sample size also enables result comparison with previous work from other sites visited during the same research expedition (Victorero et al., 2018) and with previous studies of the MAR fauna (Morris et al., 2012).The number of communal morphospecies between the transverse ridge and the other data sets presented in this thesis (Annan, Knipovich and Vayda seamounts) were also recorded, in order to assess whether there could be shared fauna between the sites, potentially indicating connectivity.

4.3.3 Statistical analysis

In order to understand how oceanographic and topographic variables influence the different biodiversity metrics (i.e. species richness, abundance) within the ridge, we employed generalised additive models (GAMs). GAMs provide a semi-parametric modelling framework, which has proven effective for ecological data sets comprising non-linear relationships between the response and explanatory variables (Guisan et al., 2002). The underlying assumption of GAMs is that the functions are additive, and the relationship between the mean of the response variable and the smoothed explanatory variables is obtained through a link function. The GAMs were fitted using the mgcv-package with the Maximum Likelihood smoothing parameter estimation method in R (Wood, 2011) (R Core Team, 2016). The optimal model structure was chosen using backward selection by sequentially removing the highest non-significant term and refitting the model until all terms left were significant. Model validation consisted of producing diagnostic plots iteratively throughout the modelling process (gam.check function) and by plotting model residuals against explanatory variables. The distributions chosen were quasi-Poisson with a log link for species richness (the variance exceeded the mean only slightly) and negative binomial with a log link for abundance (the response variable was overdispersed). Multicollinearity of explanatory variables, which can result in unstable parameter estimates within the models, was assessed using Variance Inflation Factors (VIF). VIF values for each parameter were estimated with the corvif- function from the AED-package with each round excluding the variable with the highest VIF- value, until all variables were below the cut-off point of 3 indicating lack of multicollinearity (Zuur et al., 2010). Therefore, rugosity, surface area, finer-scale TPI, and temperature and oxygen were excluded from the analysis through an iterative process. The substrate variable was also omitted from the final analysis, because of a disparity in the number of samples from each different substrate category. For example, hard substrate with biogenic material was sampled over 67 times while plain sediment only twice. Spatial autocorrelation was accounted for by having the depth of the middle point of each 100 m sample as an explanatory parameter in the models. This was verified through evaluating the patterns of the residuals with and without this parameter in spline correlograms against distance (spline.correlog –function) (Bjørnstad and Falck, 2001).

4.4 Results

4.4.1 Ecological description of the habitats and communities

The summit habitats of the Vema transverse ridge, located at ~ 570 m, consisted mainly of coral debris with sediment. These habitats were occupied by abundant shrimp and squat lobster *(Eumuninidae* sp.) communities and the occasional crab (Fig. 2a). From the ROV video, particles in the water column are visible and it appears as if there is a relatively high amount of marine snow falling on to the summit seabed. Going deeper from the summit, the substrate changes into carbonate platforms at ~ 600 m water depth. These substrates also host shrimps, but are characterised by stylasterid coral fields (Fig. 2a). The stylasterids were ~1- 2 cm in size and below the threshold of 3 cm. They were often visible only when they occurred in high abundances, which meant that they could not be reliably annotated throughout the videos, and were therefore excluded from the statistical analysis. The carbonate platforms also have occasional sponge species and the sediment pools occurring around them were home to ceriantهid (burrowing) anemones. These communities are typical and occur frequently throughout the sloping portion of the dive down to ~ 1000 m. Along this portion of the dive, we also observed many specimens of *Acanella* sp. living in the sediment, which became more common with depth and with a gradual change in the substrate (Fig. 4.2a). There are high abundances of *Acanella* sp. down to 1300 m with peak abundances of 130 individuals over a 100 m distance. The *Acanella* communities thrive in habitats characterised by sediment and dead coral framework. With increasing depth, volcanic rock became more common on the slope, in the form of complex geomorphologies, such as terraces and large boulders, hosting diverse cold-water coral assemblages. The species observed include white *Corallium* sp., *Paramuricea* sp., *Iridogorgia magnispiralis* and *Iridogorgia bella*, *Metallogorgia melanotrichus* and *Enallopsammia rostrata*. Some vertical habitats were also colonised by chrysogorgids, primnoids and isidids. Several large fan–shaped *Madrepora oculata* matrices were also observed, growing vertically in a slightly downward orientation. There was a particularly large *Maderepora oculata* specimen measuring over 2.8 m in length and 1.3 m in width, potentially being one of the biggest specimens observed to date (Fig. 4.2c).

The flank habitats of the ridge were surveyed over 1100 – 1500 m depth and were overall characterised by abundant crinoid communities. The shallower part consisted of a gentle slope, which was either carbonate or just covered with a thin sediment layer. Here, yellow stalked crinoids (Hyocrinidae –family?) were dominant with up to 1000 specimens over a 100 m distance. *Acanella sp.* - corals were also present, belonging to the same morphospecies to those occurring on the deeper part of the summit dive.

There were several morphospecies from the Antedonoidea and Atelecrinidae families. These crinoids occurred on the sloping carbonate surfaces, with coral debris and also on the dead coral framework (Fig. 4.2d). A gradual zonation was observed between the different species in terms of their relative abundances. An area of sediment patches with coral debris were inhabited by *Halipteris* sp. seapens (Fig. 4.2e). The exposed volcanic substrates had the occasional individual cold-water coral species, such as *Paragorgia* sp., *Bathypathes* sp., Isididae bamboo whips, and *Enallopsammi*a *rostrata.* Eventually, the latter became dominant with hundreds of specimens creating a single species coral garden at ~ 1300 – 1400 m. Some of the dead *Enallopsammia rostrata* skeletons were colonised by demosponges (Fig. 4.2c). Additionally, *Enallopsammia rostrata* were observed to have commensal crinoids attached to their branches, which also occurred on the sponges colonising the dead coral skeletons (Fig. 4.2c). At the deeper end of the dive, at ~1500 m depth, there was a boulder field, where again abundant crinoid communities from the Anteonoidea family were dominant.

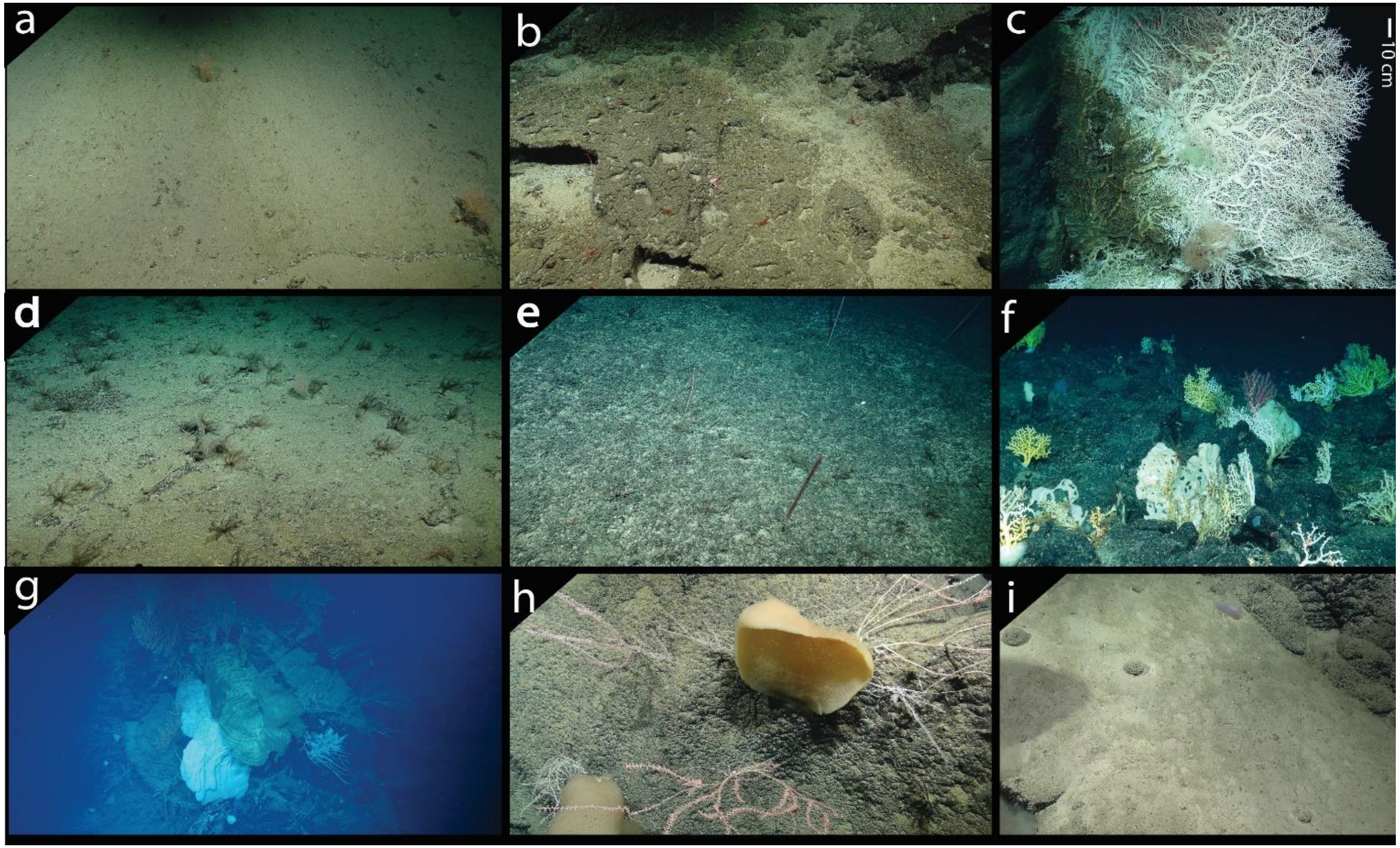


Figure 4.2 Example of different habitats from the transverse ridge ; summit; a) *Acanella* sp., b) *Eumunidae* sp. and Stylasterid corals on carbonate platforms, c) a close up of a *Madrepora oculata* matrix growing vertically, flank; d) Atelecrinidae - crinoids, e) *Halipteris* sp. –seapens on coral debris, f) *Enallopsammia rostrata* coral assemblages and dead skeletons with demosponges , deep slope; g) a large Rosellidae (*Chonelasma* sp. ?) sponge, h) *Polipogon* sp. and Isididae corals, i) Xenophyophores and a *Synallactidae* – holothurian. Scale bar shown when ROV lasers were available.

The deep slope survey exhibited the most complex geological morphology encountered on the ridge. The shallowest part of the transect, up until ~ 1600 m depth had relatively low abundance of fauna in comparison to other areas within this transect. These habitats comprised a rock slide with boulders, pebbles, and cobbles on a slope infilled with sediment. More stable, heterogenous volcanic rock, in the form of pinnacles were often observed. One of these pinnacles at the depth of ~2400 m had a large *Chonelasma* sp. sponge (Fig. 4.2g). Around this sponge, there were thriving coral colonies, mainly of Isididae. The pinnacles at ~ 2600 m depth had a vertical wall with one side covered with a primnoid coral species and the other side without any visible fauna. Conversely on another wall, we saw abundant multispecies coral communities comprising of Isididae, primnoids and chrysogorgids along with some sponges. Deeper, at ~ 2670 m, the complex volcanic rock was covered by an abundant sponge garden composed of *Poliopogon* sp. (Fig. 4.2h), bamboo corals, and stylasterids. The deepest part of this transect had sediment patches among the volcanic rock with fauna such as Isididae corals, xenophyophores, and Synallactidae holothurians at ~2700 m (Fig. 4.2i).

4.4.2 Biodiversity patterns

The observed species richness on the ridge consisted of 172 morphospecies, with 46,300 individuals over the total distance of 8.5 km. The transverse ridge shared 36 morphospecies with Annan and Knipovich seamounts, and 23 morphospecies with Vayda seamount. The latter two are likely to be underestimates of shared species as they are based on annotations of coral taxa and associated fauna. The statistical analysis revealed a significant relationship with the environmental variables for the biodiversity metrics. Species richness was found to have a significant relationship with depth, slope, and broad scale TPI (all p-values <0.001, $R^2_{adj}=0.65$, deviance explained 64.7%) (Fig. 4.3). Both slope and broad scale TPI influenced species richness positively in a linear fashion with highest number of species in steep areas and/or in areas which were elevated in comparison to the surrounding seafloor (Fig. 4.3). The relationship of species richness with depth was more complex, showing a distinct peak at intermediate depths (~1300 m), at an intermediate slope (20°) with the community consisting of a variety of sponges, corals, and asteroids. Species richness is lower at depths of 2000 m, but shows an overall increase with deeper depths (Fig. 4.3).

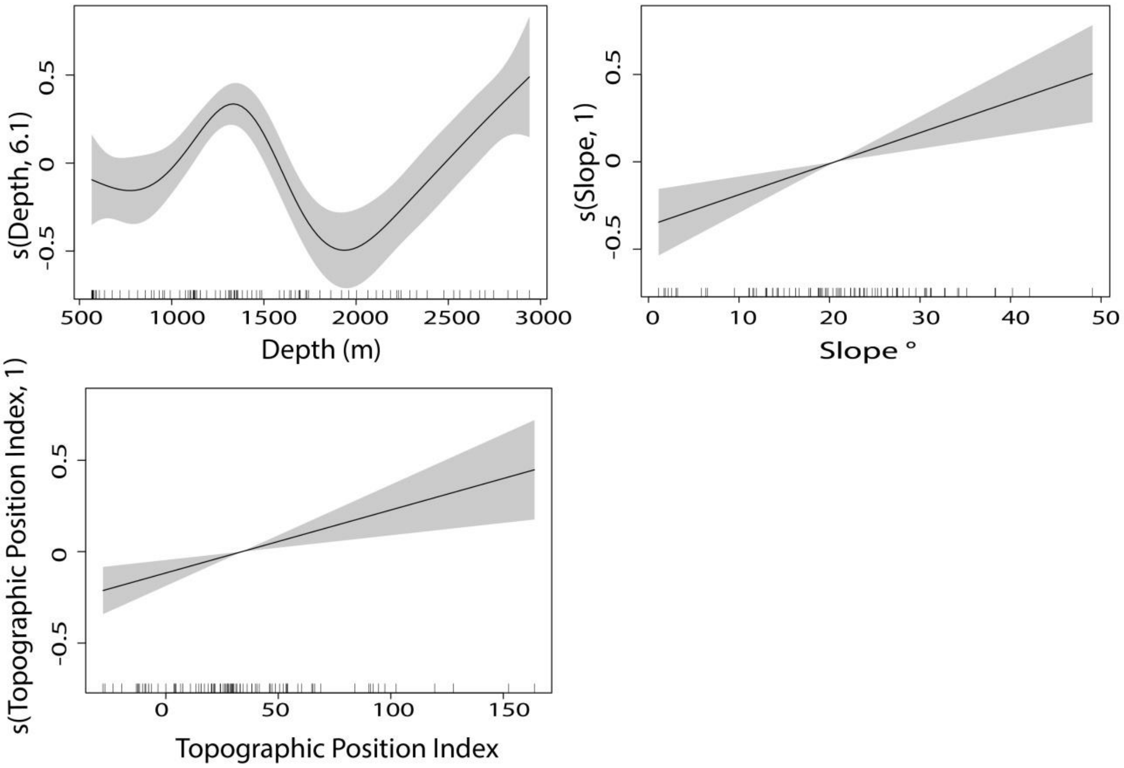


Figure 4.3 The relationship between the smoothed terms of the significant ($p<0.05$) explanatory variables and species richness from the General Additive Models. The black line represents the relationship between the predictor (y-axis) and response (x-axis) and the grey shading illustrates +/-2 standard errors. The x- axis shows values for the predictor variable and the y-axis represents the smoothing spline function, with the estimated degrees of freedom (EDF) for each smoothed term. An EDF of 1 represents a linear relationship and the higher the EDF, the less linear the relationship is. The vertical lines at the bottom of the x-axis represent observations. The results presented at the link scale (log).

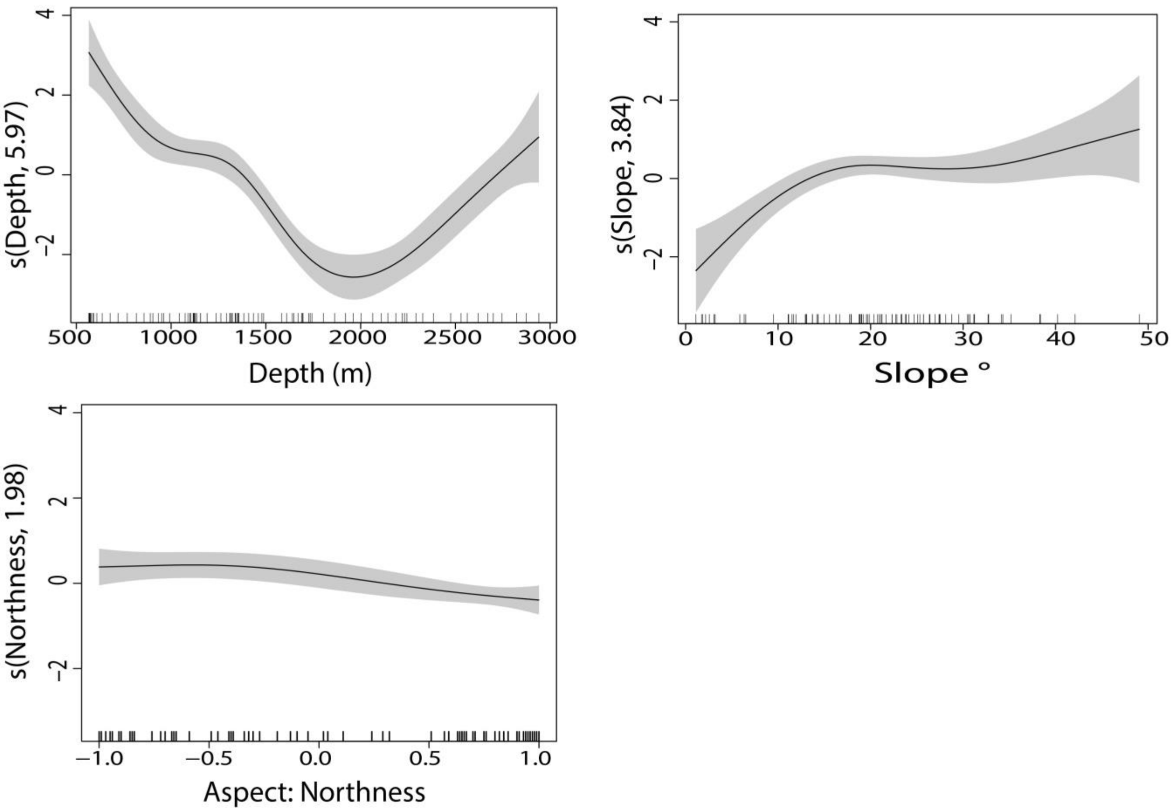


Figure 4.4 The relationship between the smoothed terms of the significant ($p<0.05$) explanatory variables and total abundance from the General Additive Models. The black line represents the relationship between the predictor (y-axis) and response (x-axis) and the grey shading illustrates +/-2 standard errors. The x- axis shows values for the predictor variable and the y-axis represents the smoothing spline function, with the estimated degrees of freedom (EDF) for each smoothed term. An EDF of 1 represents a linear relationship and the higher the EDF, the less linear the relationship is. The vertical lines at the bottom of the x-axis represent observations. The results presented at the link scale (log).

Similar variables also governed changes in the total abundance of fauna with depth (p-value < 0.001), slope (p-value <0.001), and the northness aspect of the slope of the seabed (p-value <0.003) significantly influenced the abundance patterns (R^2_{adj} =0.57, deviance explained 72%) (Fig. 4.4). Higher megafaunal abundances were associated with steeper slopes, with slopes above 15° showing a relatively constant pattern of faunal abundances. The northness of the seabed slope shows a relatively uniform pattern, with only a small increase at -0.5 radians suggesting that southward facing areas could have slightly higher abundances. It must be noted, however, that GAM p-values are only approximate and the significance of this term could be a sampling artefact as vast portions of the ROV tracks are orientated towards a northward aspect while the graphical output lacks major patterns (Fig. 4.4). Higher abundances at ~600 m depth occurred on intermediates slopes (20°) with the assemblages dominated by *Munida* sp. (squat lobsters) and stylasterid sp. occurring on a more southward facing seabed. An increase in abundance can also be seen around the depths of 1100-1500 m, because of prevalent crinoid fields and gardens of *Enallopsammia rostrata*. The lowest total abundance occurred at ~2000 m depth, which coincides with lowest species richness, with only an occasional specimen of *Anthomastus* sp. and *Paramuricea* sp present. Following this, total abundance, similarly to species richness, increases again around ~ 2400 m depth with the community becoming dominated by a variety of corals from the Isididae and from the *Chrysogorgia* genus; this is likely to be associated with the complex geomorphology found at the deepest part of the ROV transects, such as the pinnacles.

4.5 Discussion

4.5.1 Ecological communities of the Vema Transverse Ridge and representability of MAR communities

Transverse ridges are spectacular features, which are often associated with large fracture zones providing complex heterogeneous geomorphological surfaces. Therefore, it is not coincidental that this site appears to host ecologically similar benthic communities to other topographically complex deep-sea features that are better characterised, such as seamounts, continental rises, and canyons. Specifically, the transverse ridge habitats include vertical walls, outcrops, biogenic substrates, carbonate platforms, sediment plains, and boulder fields. These habitats were found to host a variety of Vulnerable Marine Ecosystem (VME) taxa, such as the *Enallopsammia rostrata*, *Madrepora oculata*, *Metallogorgia melanotrich*os, *Stylasteridae* sp., and black coral patches, deep-sea sponge aggregations and seapen fields of the *Halipteris* sp. These type of ecosystems have been determined to be vulnerable to physical disruption because of their biological traits, such as longevity, low fecundity, and lack of ecological resilience (NEAFC, 2015).

In order to assess the representativeness of the Vema transverse ridge versus other non-vent MAR ecosystems, we compared our faunal records to those from more northern parts of the MAR, characterized by the MAR-ECO project (see Fig. 4.1 for locations). This project covered an area ranging from the Icelandic EEZ to the northern boundary of the Azorean EEZ, which is now subsequently regarded as a single VME unit by ICES (ICES, 2013). Direct faunal comparisons between our study and the MAR-ECO surveys are difficult, because of the lack of high-resolution taxonomy and standardisation of methodologies, which is typical of ROV-based deep-sea studies. Nonetheless, limited comparisons based on the species list from the MAR-ECO project, show that the coral species occurring on the transverse ridge are similar to the fauna found in the MAR. The shared species between include *Madrepora oculata*, with the other coral fauna presented in the MAR-ECO species list identified to a coarse taxonomic resolution (Mortensen et al., 2008). These include a variety of different morphospecies, which are a variety of primnoid sp., *Anthomastus* sp., *Iridogorgia* sp., *Paramuricea* sp., *Paragorgia* sp., *Acanella* sp. and *Chrysogorgia* sp. (Mortensen et al., 2008).

Similarly, the holothurian species list from the MAR-ECO project reveals shared genera with the morphospecies from the transverse ridge. These include *Benthodyte*s, *Peniagone*, *Synallactes,* and *Amperima* (Gebruk, 2008). Further comparisons with the northern MAR fauna are available from a cold-water coral study on the Axial Volcanic Ridge, with the manuscript providing images of the more common coral species (Morris et al., 2012). The morphospecies presented by Morris et al. (2012) include *Iridogorgia magnispiralis*, *Anthomastus* sp., *Paragorgia* sp., *Bathypathes* sp. and similar looking Isididae and chrysogorgids. The Axial Volcanic Ridge study examined 274 h of ROV footage across the depth range of 2600 -3600 m, describing in total 20 coral species, with a maximum of 59 individuals observed over a distance of a 100 m (Morris et al., 2012). Our results vastly exceed these numbers with 43 coral species recorded throughout the study, with peak abundances of 4472 individuals of stylasterids and 497 individuals of *Enallopsammia rostrata* over the distance of a 100 m. However, if we restrict the comparisons to only the overlapping depth band between the two studies, (2600 – 3000 m), Morris et al. (2012) presents 17 coral species, while we find 21 species, with higher peak abundance (>600 of stylasterids over 100 m distance). The faunal similarities to the other MAR studies must be interpreted cautiously, but there is a prospect that the transverse ridge fauna could potentially be an extension of the MAR fauna and therefore could be considered a representative ecosystem of the non-vent MAR communities.

Many of the benthic fauna occurring on the transverse ridge are also found on seamounts in the Eastern Equatorial-Atlantic, such as the Annan Seamount (Victorero et al., 2018), Knipovich and Vayda Seamount (Chapter 3) and Tropic Seamount (Murton, 2016). The shared fauna, which ranged from 23 to 36 morphospecies, could be a consequence of the eastward flow passing Vema and influencing the Eastern-Atlantic basin, reaching the Sierra Leone Rise, the Cape Verde ridge and the Canary Basin (McCartney et al., 1991). The shared taxa potentially suggests that this FZ could be one of the connective pathways across the MAR by acting as a stepping stone between the western and eastern Atlantic basins. Studies on the macrofauna from the abyssal plains on either side of the Vema FZ also imply that for many species the Vema FZ enables gene exchange across the MAR (Bober et al., 2018; Brandt et al., 2017; Guggolz et al., 2017). Coral dating from the transverse ridge also shows that coral species, such as *Madrepora oculata* and *Enallopsammia rostrata*, have occurred here for at least ~ 36 500 ± 1300 and ~ 16 000 ± 600 years, respectively (Robinson, pers. communication). Therefore, our results indicate that Vema FZ is likely to meet the APEI criteria on the basis that 1) it hosts ecologically significant communities, such as VMEs, 2) could be a representative of the MAR ecosystem, because of similarities between the communities in the northern MAR and 3) there is some degree of evidence through recent studies that it might play a role in connectivity and biogeographical patterns across the Atlantic basin.

4.5.2 Environmental drivers of biodiversity on the Vema Transverse Ridge

The environmental drivers assessed within this study comprise remotely acquired parameters, which are often used as a proxy for biodiversity within other deep-sea ecosystems (e.g. Robert et al., 2014; Roland Pitcher et al., 2012). Ideally, these proxies would be used to predict biodiversity patterns in larger areas across the ridge, but the limited coverage of the ROV transects would result in biased predictions. Therefore, we focus on using environmental proxies for explaining the observed patterns instead, which can be useful for future studies on FZ and for confirming similarities with other topographically complex habitats. Our results show that the most parsimonious model explaining patterns in species richness included the seabed depth, slope, and broad-scale local elevation (TPI). The effect of depth on species richness has been linked to energy availability (Rex et al., 2005; 2006). For example, large-scale diversity patterns in molluscs are though to reflect historical events and productivity gradients (Rex et al., 2006), while diversity patterns of ophiuroids have been directly linked to increased POC flux to the seabed (Woolley et al., 2016). Similarly, in polychaetes, both species richness and abudance show a positive relationship with POC flux (Stuart et al., 2017). The relationship between species richness and abundance of the megafauna in response to depth in our study, however, is relatively complex. We observe heightened species richness and abundance at intermediate depths of ~1300 m with a pattern of increase in both variables towards the deepest sites (Fig. 4.3). These depths correspond to areas of habitat-forming species, such as corals and sponges and at the deepest sites, there are complex geomorphological features, such as pinnacles where vertical habitats were colonised by a variety of coral taxa. Therefore, it is most likely that there is sufficient food input to allow these habitat-forming species to thrive, which in turn creates local hotspots of species richness and increases the number of individuals in different parts of the ridge. Additionally, the effect of the deeper features, such as the pinnacles, can be seen in our model, with the overall pattern of steeper sites sustaining both a higher number of species and leading to overall higher total abundances of megafauna (Fig. 4.3 and Fig. 4.4).

Species richness also showed a positive linear relationship with the local elevation of the seabed. The sites that are more elevated in comparison to neighbouring habitats were often colonised by filter-feeding assemblages, such as crinoid fields and assemblages of habitat-forming species, such as cold-water corals, which benefit from better access to currents (Rengstorf et al., 2014). Studies on seamounts have also recognised the importance of slope and local elevation of the seabed governing the distribution of benthic filter-feeders and corals through alterations of the flow regime and amplification of currents (De la Torriente et al., 2018). Similarly, biodiversity studies from canyons show positive relationships between species richness or abundance and steeper slopes (Robert et al., 2014). Furthermore, variability of these seabed properties have been shown to increase species turnover in the megabenthos and hence affect the number of species present across an environmental gradient (Victorero et al., 2018). It must be noted, however, that the biodiversity patterns illustrated by our results are limited by the small sampling area, in particular on the northern side of the transverse ridge. Despite this limitation, the three transects do cover different biophysical landscapes as seen through the depth and slope gradients and provide a starting point for future ecological studies, which aim to explore different benthic communities and biodiversity metrics along similar features to the Vema transverse ridge.

4.6 Conclusions

This study represents the first biological data set available from the transverse ridge within the Vema Fracture Zone. Our results show that the ridge supports diverse and abundant deep-sea megafaunal communities, including VME taxa. The distribution of biodiversity metrics shows that species richness is governed by factors that vary with depth and increases with topographic heterogeneity represented by the seabed slope and local elevation. Total abundance is highest at the summit of the ridge, but similarly to species richness, can be seen to peak at the steep deep slope habitats. This detailed data set contributes evidence towards the consideration of Vema FZ as a part of a network of APEIs across the MAR. Our results suggest that the transverse ridge communities are ecologically significant, could be representable of non-vent MAR communities, and could contribute towards connectivity and wider biogeography between the two sides of the Atlantic.

Acknowledgements

The data collection for this work was funded by the ERC Starting Grant projects CACH (grant no. 278705). The authors would like to thank the crew, technical staff and science party of the RSS James Cook 094 TROPICS research expedition and particularly Shannon Hoy for processing the bathymetry. We would also like to extend our gratitude to Andy Gooday, Andrey Gebruk, Jaime Davies, Tina Molodotsova, Chris Kelly and Les Watling for their taxonomic expertise. V.A.I.H was funded by the ERC Starting Grant project CODEMAP (grant no. 258482). M.L.T. was funded by the NERC DeepLinks project (NE/K013513/1). L.V is funded by the Southampton Partnership for Innovative Training of Future Investigators Researching the Environment (SPITFIRE, a NERC Doctoral Training Partnership – grant number NE/L002531/1).

Chapter 5 Synthesis

5.1 Scientific contributions

This study provides the ecological characterisation of three seamounts and one ridge based on 275 h of ROV video footage covering approximately ~ 40 km, with 109 261 organisms annotated across ~ 450 morphological species. It provides a contribution towards seamount ecology in a region where deep-sea exploration is scant (Fig. 5.1.), and in a deep-sea ecosystem which remains largely unexplored (with 0.04 % of seamounts scientifically sampled (Kvile et al., 2014)). This project has used a combination of methods, integrating habitat mapping techniques to obtain information on the benthic environment and the overlaying water-column and numerical ecology to understand species-habitat interactions.

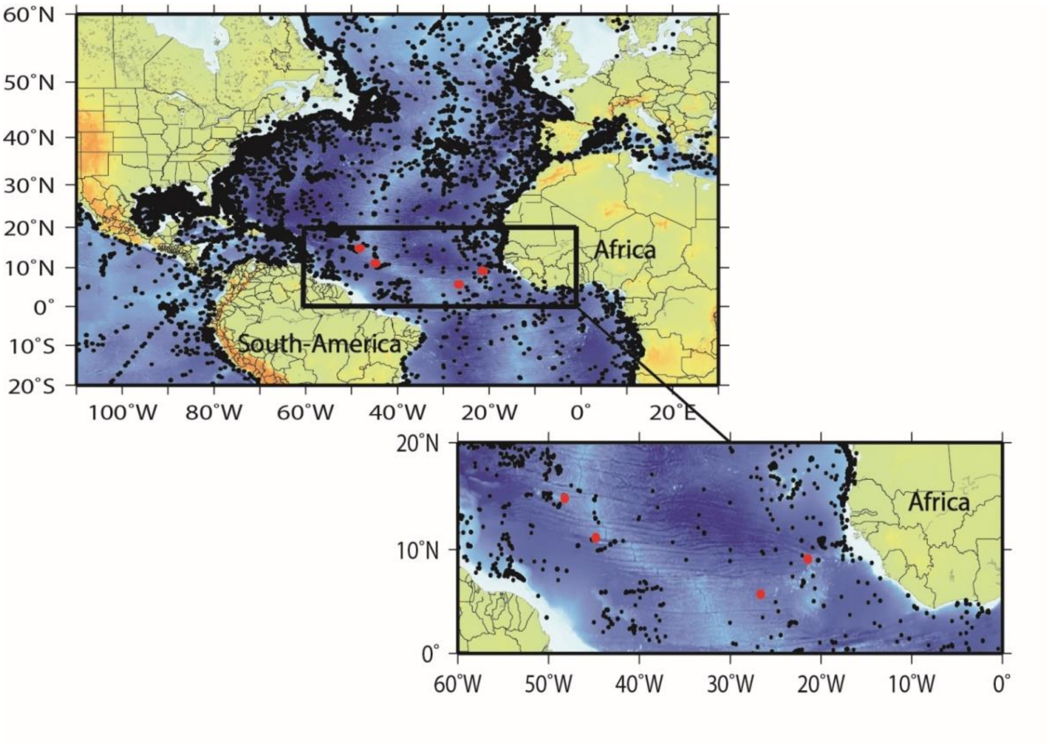


Figure 5.1 Deep-sea sampling within the Equatorial Atlantic. Data obtained from OBIS (2018).

The main scientific findings of each chapter are as follows:

Chapter 2

The aim of this investigation was to fill gaps in the understanding of seamount beta diversity by breaking down beta diversity components. This study was able to successfully pinpoint unique assemblages and species with the highest variance, thus contributing most to elevating seamount beta diversity. Furthermore, a particularly important contribution to seamount ecology was achieved by partitioning beta diversity into ecological sub-processes; species replacement and species richness difference. The partitioning provided a framework for testing hypotheses of beta diversity in relation to spatially varying environmental parameters. The findings lead to the conclusion that beta diversity on seamounts is mainly caused by species replacement, which in turn is linked to oceanographic and terrain variability. Changes in species richness are less prevalent, but still an important component of beta diversity on seamounts and are linked to large-scale oceanographic circulation.

Chapter 3

The purpose of this research was to describe and compare cold-water coral fauna from three seamounts within the relatively unknown deep-sea region of the Equatorial- Atlantic. The new data collected indicates that overall this tropical region harbours a high number of coral species on seamounts in comparison to a previously published global data set. The possible explanations include the region acting as a biogeographic crossroad between the northern and southern Atlantic fauna, caused by the dynamic ocean circulation and mixing of water masses from different origins. An overall reduction in species richness from the eastern-most seamount towards the western seamounts can be seen, potentially as a consequence of decreased food input. The results from this study contribute another piece of the puzzle towards understanding the patterns of cold-water coral biodiversity in the Atlantic and thus contribute towards the biogeography, the management and the conservation of these vulnerable ecosystems.

Chapter 4

This study provided an insight into the biological communities and biodiversity patterns of the transverse ridge within the Vema Fracture Zone. This insight is particularly timely, as a vast portion of the Vema FZ has been proposed as an Area of Particular Environmental Interest (APEI), thus contributing towards a network which can aid in the conservation of the Mid-Atlantic Ridge (MAR) communities from the physical disruptions arising from deep-sea mining. The transverse ridge was found to host an array of Vulnerable Marine Ecosystems (VMEs) such as cold-water corals and sponge gardens, in addition to a wide array of other invertebrates. Spatial patterns in species richness and abundance were governed by the complex geomorphology of the ridge, including vertical habitats, and the water depth, similarly to other deep-sea ecosystems. Finally, the results highlight ecological and environmental similarities with the seamounts investigated in this thesis, and across wider MAR deep-sea communities. Such similarities suggest that transverse ridges could contribute towards biogeographical connectivity between the eastern and western side of the Atlantic. The high resolution biological data set produced here adds evidence towards the potential designation of Vema FZ as part of the APEI network across the MAR.

5.2 Ecological contributions towards the field of seamount research

Seamounts are often termed biodiversity hotspots, despite inconclusive evidence for this. The hotspots characteristic, which is plausible at least for some seamounts, has been argued to arise from either high species co-existence or high species turnover (beta diversity) in a heterogeneous landscape (McClain et al., 2010). The findings of this thesis suggest that it is the latter process, which is likely to govern the patterns of biodiversity on seamounts. The high species turnover, in particular caused by the ecological processes of species replacing each other in response to changes in the environment, suggests that this is the main process, which increases the number of species occurring on the scale of an individual seamount. The ecological process of changes in the number of species is still occurring, but if the system was dominated by coexistence of species, this parameter would be expected to contribute more towards the overall beta diversity. Another paradigm challenged is the contribution of rare species to beta diversity. Previous research with methodological differences has argued that it is the rare taxa which drives beta diversity patterns on seamounts, because of their narrow depth range (McClain and Lundsten, 2015). Instead my findings demonstrate that species which show the highest variance across the study site contribute most to beta diversity and these are often species which occur in high abundances over a limited area.

Previous ecological theories have proposed that the tropical Atlantic deep-sea sustains high diversity, stemming from evolutionary processes (Briggs, 2003). Here, by providing a novel coral data set from the tropical Atlantic and comparing this to a previously published global data set of number of cold-water coral species on seamounts, such patterns can be evaluated. While the comparisons are limited due to differences in methodologies, the Equatorial Atlantic seamounts appear to have much higher coral species richness in comparison to the northern North Atlantic. The number of coral species presented in this thesis rivals the values of the deep SW Pacific, which is considered to have high richness because it is influenced by the coral hotspots of the Indo-West Pacific. Future sampling in the seamounts of the Equatorial region will be able to test if higher species richness of the megabenthos is indeed a typical pattern of this area.

The shared coral taxa between the seamounts, which are bathed by the same surface currents and water masses suggests that the seamounts studied here are not isolated islands. Previous studies have found that differences in taxa between seamounts vary according to the geographic distance, with seamounts in geographical proximity having similar species. However, the differences between the coral fauna of the seamounts cannot be purely attributed to geographic distance. The two seamounts furthest away, Annan and Vayda, were most dissimilar, but Knipovich was equally similar to Annan and Vayda, sharing species with both sites, despite being closest to Annan.

Additionally, the shared taxa between the other sites and Vema Fracture Zone suggests that all these sites could act as trans-Atlantic stepping stones. In particular, Vema Fracture Zone could have a specifically important role in connectivity, not only because of it being the major trans-Atlantic pathway for bottom-water transport which can transport larvae, but also because it is likely to receive larvae dispersing along the MAR, a dispersal pattern seen in a variety of hydrothermal vent fauna (Mullineaux et al., 2018; van der Heijden et al., 2012). The fauna; similarities between the communities from the different sites suggests that these seamounts could act or have acted as stepping stones, but it must be noted that shared taxa does not necessarily represent modern connectivity, which can only be confirmed by genetic work on the specimens collected during the research expedition.

5.3 Contributions towards spatial management and conservation efforts

This thesis supplies new data for various management purposes, such as those related to deep-sea mining and to the conservation of biodiversity in the high seas. The insight into the biodiversity and ecological communities of the Vema Transverse Ridge can aid in the International Seabed Authority's (ISA) management and conservation efforts related to mining impacts on the Mid-Atlantic Ridge. The ecological communities of Vema FZ were characterised independently and prior to the proposed APEI designation, but our results are in good agreement with hypotheses related to Vema's role in connectivity and of potentially being a representative of non-vent MAR communities. Therefore, the ecological communities and biodiversity patterns described from the transverse ridge can contribute to local-scale information towards the ISA's regional environmental management plan. Similarly, the results showing high cold-water coral diversity in the Equatorial-Atlantic, come at a time when there are growing interests and pressure to protect biodiversity in international waters with the UN drafting a high seas biodiversity treaty (Wright et al., 2016). With a wealth of deep-sea discoveries underway, this thesis has paved the way towards beta diversity characterisations of seamount benthos, which are highly applicable to spatial management and towards future explorations in the dynamic oceanographic region that is the Equatorial-Atlantic.

5.4 Technical contributions

An important technical contribution towards the understanding of beta diversity on seamounts was achieved, but there is also methodological development, which should be highlighted and considered in future studies. Previously beta diversity studies in the deep sea have focused on two ecological processes; species replacement and nestedness (ordered species loss) using what is termed the Baselga –method (Brault et al., 2013a,b; McClain et al., 2012, 2016; McClain and Rex, 2015; Stuart et al., 2017; Wagstaff et al., 2014). Nestedness, which is a subtype of species richness difference, describes species in one site being a strict subset of species in a richer site (Baselga, 2012; Legendre, 2014). However, if the species in common between two sites equals 0, the richness difference is not nestedness and as such there is no reference in the data for ecological processes leading to nestedness. It is worth noting this mathematical distinction, because it leads to differences in interpreting the underlying processes that produce observed beta diversity patterns (Baselga and Leprieur, 2015). Thus it is recommended that deep-sea ecologists consider carefully which process they are analysing and whether the communities are truly nested across the study site.

5.5 Limitations of the work

The main limitations of this work relate to the lack of replicates of video transects and the coarse resolution bathymetry data available. The lack of replicate transects across such large spatial scales and depth ranges, which are typical of seamount habitats, leads to a wide range of uncertainties. These include introducing a bias into the observed biodiversity metrics caused by the limited exploration of the study area's landscape, which can subsequently prevent drawing generalisations or even lead to misunderstandings on how biodiversity is spatially structured along benthic habitats. In addition, the limited field of view, which is typical of ROV surveys, leads to the generation of presence only data as the estimation of absences is unreliable, since the organisms that are being annotated could be present just outside the camera's field of view, an issue that can be augmented by the lack of replicate transects. Furthermore, the lack of replicate transects also prevents predictive modelling of the biodiversity patterns encountered and of the distribution of the different habitats across the seamount.

The resolution mismatch between data sets, which are caused by using coarse resolution bathymetry with ground-truth ROV data, in which the typical field of view is only a few meters, leads to a typical scaling issue in habitat mapping exercises. In this study, the best resolution bathymetry available was 25 m pixel size on Annan seamount, but for the other sites the pixel resolution was 50 m at best. This coarse bathymetric resolution prevents capturing the high habitat heterogeneity present on seamounts, and thus the high habitat variability, which can range from sediment plains to outcrops across different spatial scales. Additionally, the habitat characterisations used in this study lack backscatter data (as it was of poor quality), which is useful for deriving sediment classes making substrate interpretations more objective and cohesive and also complementing substrate annotations obtained from ROV video. Fine-scale bathymetry of the seamount terrain across the areas where ROV dives take place, are becoming more common, which will enable to truly test hypotheses across many bathymetric variables at different scales when modelling different ecological processes, communities, species and biodiversity metrics.

Another limitation, which is intrinsically linked with seabed imagery, is the low taxonomic resolution of the studies. While robotic vehicles provide a real asset for studying biodiversity in the deep-sea in a non-invasive way, the footage produced inherently misses certain size-classes of the community and also makes it difficult to identify cryptic species and rare or rarely seen species or infauna. In addition, there is a trade-off between running statistically robust video transects, sampling specimens and making the research programmes generating the data cost-effective. The annotation scheme also introduces another source of uncertainty into the biodiversity patterns established within this study. The software for video annotations used within this study has not been developed sufficiently, especially when comparing it to image annotation software, such as the online tool BIIGLE 2.0 (Langenkämper et al., 2017), which was released half-way through our study. In a practical sense, the new software enables randomisation of video segments, provides an image catalogue that is linked to the annotations thus visualising specimens which have been identified as a certain morphospecies and allowing easy transfer of seabed footage between different annotators. Future projects using ROV data should therefore explore the possibility of extracting images from the video footage and using a more sophisticated software which would allow the previously described issues to be overcome.

5.6 Future work and directions

The current body of work can be developed in many fashions. One of particular interest would be to pursue beta diversity studies by examining and comparing spatial patterns and drivers of beta diversity within a seamount and the neighbouring seafloor. This approach would generate a wealth of information allowing to assess the real importance of seamounts along abyssal plains as hotspots of beta diversity. Additionally, analysing changes in species richness differences along a spatial gradient from the seamount, would allow evaluating and quantifying the importance of the seamount as a dispersal centre for neighbouring habitats and to test other ecological hypotheses, such as seamounts as biomass hotspots. Going even further, it would be of extreme value to collect spatio-temporal data sets from seamounts since there is growing evidence that they are dynamic systems (Rogers, 2018 and references within). Spatio-temporal data sets would enable analyses on which communities have changed in a unique way in terms of species composition, providing an insight in the processes affecting temporal beta diversity. These analyses would also hold great value in terms of understanding the effects of human impacts on the deep-sea benthos over time and assessing the resilience of different communities.

Comparisons between the seamounts within this study were possible, in particular for conspicuous taxa, such as cold-water corals, but it must be noted that such comparisons are not without limitations, as the data quantity available across similar depths and habitats was low, with no repeat transects. A similar challenge in terms of comparisons arose from finding studies on seamounts/ridge systems from other regions to compare our results to, because of a lack of uniform sampling schemes between studies. In the future, it is apparent that improvements in video transect methodology collected by ROVs should be pursued, for example by the development of a best practice for collecting data (stratified sampling designs, collecting transects with different aspects, the angle of the camera, set spatial extent at least for some of the transects etc.) as suggested recently by Woodall et al. (2018).

A formalized protocol in sampling would truly allow many paradigms related to seamount ecology to be addressed with strong statistical confidence and provide a platform for genuine comparisons. However, the existing global data sets should not be forgotten and should be revisited. With constant developments in spatial analytical tools, such as methods allowing assessment of the completeness of biodiversity data sets across different spatial scales (Soberón et al., 2007), these primary biodiversity data sets have unraveled potential in future biodiversity studies. Another useful practical development involves establishing collaborative relationships with fellow imagery annotators from other institutions in order to swap portions of imagery data to ensure repeatability of annotations for quality assessments. These collaborations would allow consistency and comparability between seamount studies, particularly when using software, such as BIIGLE, in which several annotators can share species catalogues and annotations online in real time. Such collaborations would also allow scientists to regularly view a large array of the seamount benthos beyond their own study areas, thus contributing to an enhanced overall understanding of seamounts and biogeographical patterns.

Appendix A Data acquisition and processing

1.1 Data collection from Remotely Operated Vehicle (ROV) imagery

Video from the Super SCORPIO camera on the ROV was used for annotations. This camera was mounted on a fixed bracket on the starboard side of the centre line of the vehicle, had a laser harness (two lasers 0.1 m apart parallel to the focal axis), and a resolution of 1920 x 1080 HD. Two more cameras mounted on pan-and-tilt modules were used to support the identifications from the SCORPIO. Once on the seabed, cameras were white balanced to obtain optimal video quality. Video annotations were performed using Ocean Floor Observation Protocol (OFOP, v. 3.3.7a), which enables georeferenced faunal observations using the ROV's ultra-short baseline (USBL) navigation system (Huetten and Greinert, 2008). The ROV was also equipped with an altimeter and a depth sensor. To obtain statistical consistency all annotations were limited to sections where the ROV stayed within an altitude of 1-2.5 m above the seafloor; above this, identifications became difficult. Estimated field of view for the transects per seamount were calculated by generating randomly 30 time stamps and measuring the lasers within these image frames for each 2 h .mov video file and averaging across all records. The estimated average field of views were 2.9 m for Annan, 2.3 m for Knipovich, 2.6 m for Vema and 2.8 m for Vayda with the array of values reflecting the terrain differences between the sites. The minimum size of organisms recorded was ~3 cm. The video annotations were made by designating taxa to the highest taxonomic resolution possible based on visual assessment using species catalogues, the use of voucher specimens collected during the cruise, and consultation with taxonomic experts, whose identities are available in the acknowledgment sections of each chapter. Additionally, since there are no regional species guides available for the tropical Atlantic deep-sea, the following species guides were used primarily for guidance to be able to assign a correct and consistent morphological species grouping during the annotation processes. These include the online repositories of Benthic Deepwater Animal Identification Guide (NOAA), SERPENT Media Archive (Jones et al., 2009) and the Catalogue of Atlantic Deep-Sea fauna (Howell et al., 2017). The majority of identifications in this study are tentative. As such, the resulting morphospecies restrain the study and are likely to result in an underestimation of diversity, as they do not account for cryptic species or smaller megafauna. This is, however, the most tractable methodology when using ROV imagery data, which is a widely used approach in deep-sea research (Durden et al., 2016). Substrate was initially annotated using the habitat classification for seamount landscapes (Auster et al., 2005), which resulted in three main substrate types with subclasses. The volcanic habitats, which included mainly rocky plateaus, walls, ledges and large boulders, the sediment habitats which included gravel, sand

and ripples and the biogenic habitats, typified by dead coral skeletons. As these often occurred simultaneously in our study sites, they were combined to make six substrate categories; 1) volcanic, 2) volcanic and biogenic, 3) sediment, 4) sediment and biogenic, 5) volcanic and sediment, 6) volcanic, sediment and biogenic. An additional substrate class was introduced for the Vema transverse ridge, where carbonate platforms were common. The substrate, species and CTD data were then imported into ArcGIS (version 10.2.2) for spatial analyses, in which they were joined to environmental variables based on location. Prior to this step, the CTD data set was manipulated in the following fashion. Since there was no oxygen sensor on the ROV CTD, but there was an oxygen sensor attached to the CTD rosette, these oxygen values were matched with the ROV CTD salinity and temperature data based on depth.

1.2 Bathymetry data

When acquiring bathymetry using the EM-120 system, the swath width was around 3.5-5 times the water depth and the beam angles were kept around 60° - 65° port and starboard. The resulting bathymetry provided basemaps with the spatial reference of World Geodetic System 1984 Universal Transverse Mercator Zone (UTM) 27 N for Annan (25 m resolution), UTM 26 N for Knipovich (50 m), UTM 23 N for Vema and UTM 22 N for Vayda. In ArcGIS, the Ultra-short baseline (USBL) track was cleaned and the inherent noise caused by USBL jumps smoothed using the Editing and Cartography Tools. Transects were first divided into 20 m long samples for Chapter 2 and 4 and in 1 m samples for Chapter 3, in order to subsequently generate a variety of sample sizes. The bathymetry-derived variables were generated using Jenness Enterprises' Spatial Analyst Extension and Land Facet Corridor Tools (Jenness, 2012a, 2012b) by calculating each variable from the 25/ 50 m pixel resolution basemaps and extracting its value for each sample's midpoint. As previously described, these variables were matched with the species, substrate and CTD data based through spatial joins.

Table 1. Ranges used for water mass and interface classification from the ROV CTD. Core water mass parameters are per Emery (2003). Interfaces were defined when depth, temperature and salinity values were not all simultaneously within the core values.

Water mass	Depth (m)	Temperature (°C)	Salinity (ppt)
NADW	2500 - bottom	1.5-4	34.8-35
Interface 1	1550-1320	4.1-4-4	35-34.9
AAIW	1500-750	2-6	33.8-34.8
Interface 2	750-600	6-7.9	34.7-34.9
SACW	500 - surface	5-18	34.3-35.8

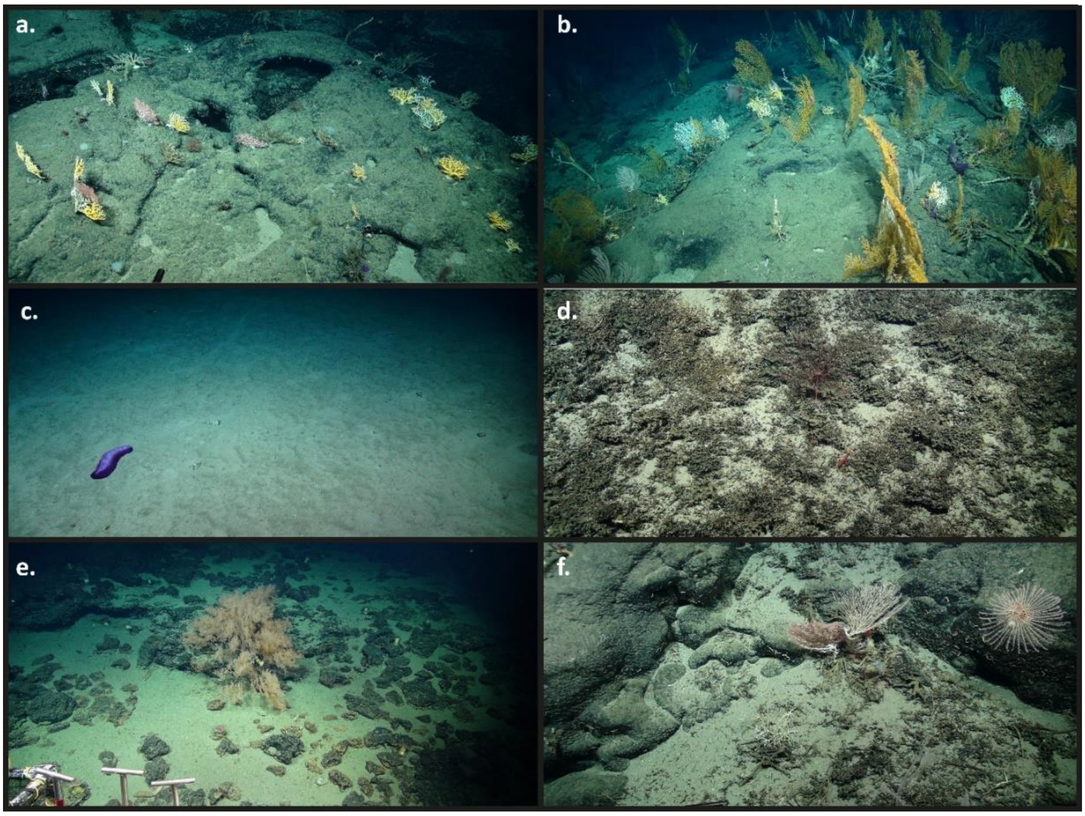
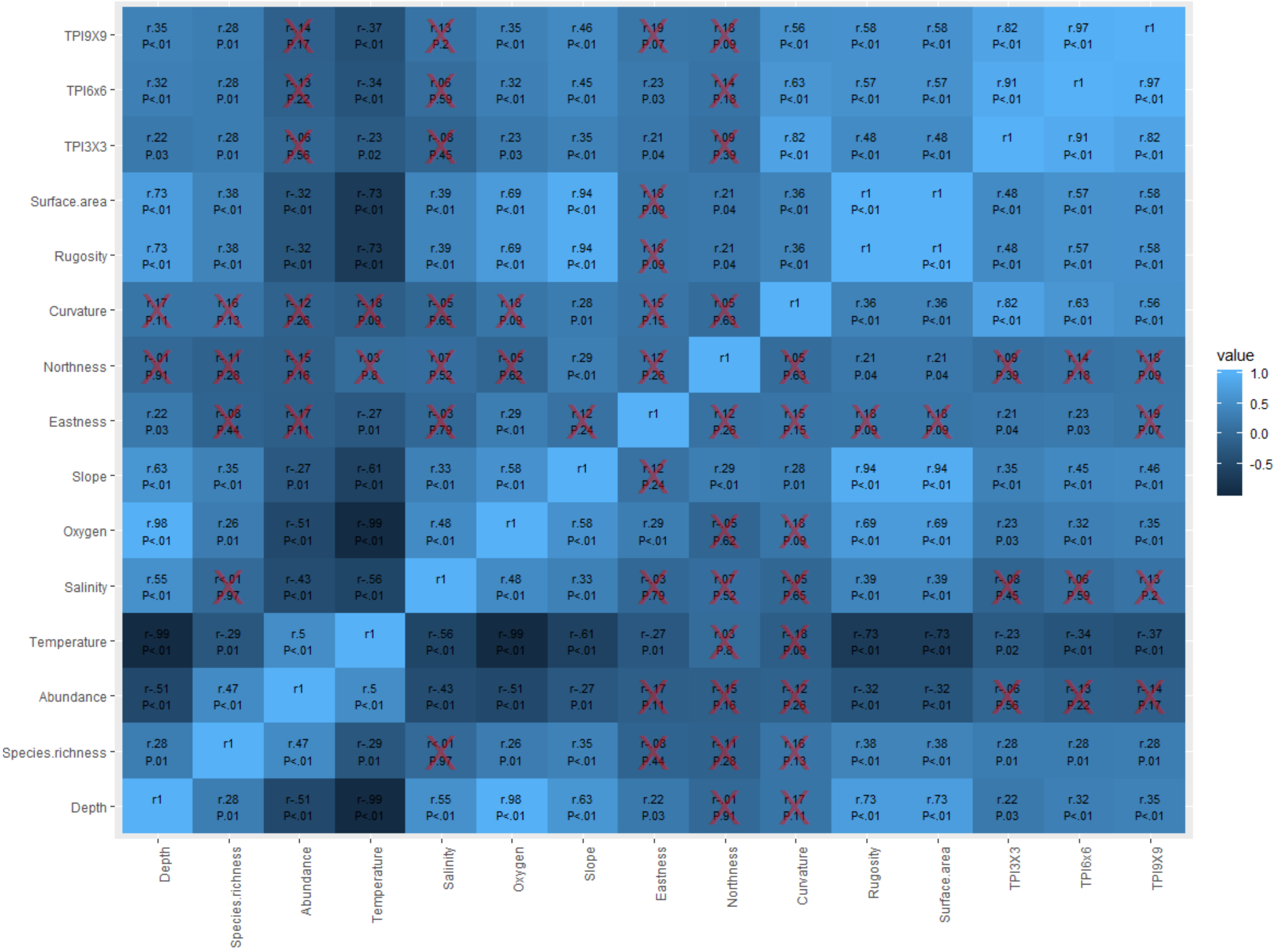


Figure 1. Example of the substrate classes used in the annotations from top left a. volcanic substrate with cold-water corals *Corallium* sp. and *Enallopsamia* sp., b. volcanic and biogenic with a *Paramuricea* sp. dominated coral garden attached to dead coral skeleton, c. sediment with the holothurian *Benthodytes* sp., d. sediment and biogenic with a Atelecrinidae crinoid, e. volcanic and sediment with the black coral *Leiopathes* sp. and holothurian *Stichopotidae* sp., f. volcanic, sediment and biogenic with cold-water corals *Corallium* sp. and *Iridogorgia* sp.

Appendix A

1.3. Details on the analytical rationale

In order to avoid including collinear variables into the same model run, collinearity of environmental variables in each environmental data set was visualised with heatmaps using Spearman rank-order correlation, which can identify monotonic relations. The information generated from the heatmaps guided the decicion making process of which covariables to include in each modelling iteration to avoid collinearity. In addition to the heatmaps, the corvif- function (Zuur et al., 2010) was also applied in the case of using general additive models as described in Chapter 4 to identify multicollinearity. For example, common colinear parameters in this context include depth, tempereture, oxygen and salinity from the CTD data and the bathymetry-derived variables TPI at different scales (Figure 2.).



	Depth	Species.richness	Abundance	Temperature	Salinity	Oxygen	Slope	Eastness	Northness	Curvature	Rugosity	Surface.area	TPI3X3	TPI6x6	TPI9X9
TPI9X9	r.35 P<.01	r.28 P.01	✗ r-.14 P.17	r-.37 P<.01	✗ r.13 P.2	r.35 P<.01	r.46 P<.01	✗ r.19 P.07	✗ r.18 P.09	r.56 P<.01	r.58 P<.01	r.58 P<.01	r.82 P<.01	r.97 P<.01	r1
TPI6x6	r.32 P<.01	r.28 P.01	✗ r-.13 P.22	r-.34 P<.01	✗ r.06 P.59	r.32 P<.01	r.45 P<.01	r.23 P.03	✗ r.14 P.18	r.63 P<.01	r.57 P<.01	r.57 P<.01	r.91 P<.01	r1	r.97 P<.01
TPI3X3	r.22 P.03	r.28 P.01	✗ r-.06 P.56	r-.23 P.02	✗ r-.08 P.45	r.23 P.03	r.35 P<.01	r.21 P.04	✗ r.09 P.39	r.82 P<.01	r.48 P<.01	r.48 P<.01	r1	r.91 P<.01	r.82 P<.01
Surface.area	r.73 P<.01	r.38 P<.01	r-.32 P<.01	r-.73 P<.01	r.39 P<.01	r.69 P<.01	r.94 P<.01	✗ r.18 P.09	r.21 P.04	r.36 P<.01	r1 P<.01	r1	r.48 P<.01	r.57 P<.01	r.58 P<.01
Rugosity	r.73 P<.01	r.38 P<.01	r-.32 P<.01	r-.73 P<.01	r.39 P<.01	r.69 P<.01	r.94 P<.01	✗ r.18 P.09	r.21 P.04	r.36 P<.01	r1	r1 P<.01	r.48 P<.01	r.57 P<.01	r.58 P<.01
Curvature	✗ r.17 P.11	✗ r.16 P.13	✗ r-.12 P.26	✗ r-.18 P.09	✗ r-.05 P.65	✗ r.18 P.09	r.28 P.01	✗ r.15 P.15	✗ r.05 P.63	r1	r.36 P<.01	r.36 P<.01	r.82 P<.01	r.63 P<.01	r.56 P<.01
Northness	✗ r-.01 P.91	✗ r-.11 P.28	✗ r-.15 P.16	✗ r.03 P.8	✗ r.07 P.52	✗ r-.05 P.62	r.29 P<.01	✗ r.12 P.26	r1	✗ r.05 P.63	r.21 P.04	r.21 P.04	✗ r.09 P.39	✗ r.14 P.18	✗ r.18 P.09
Eastness	r.22 P.03	✗ r-.08 P.44	✗ r-.17 P.11	r-.27 P.01	✗ r-.03 P.79	r.29 P<.01	✗ r.12 P.24	r1	✗ r.12 P.26	✗ r.15 P.15	✗ r.18 P.09	✗ r.18 P.09	r.21 P.04	r.23 P.03	✗ r.19 P.07
Slope	r.63 P<.01	r.35 P<.01	r-.27 P.01	r-.61 P<.01	r.33 P<.01	r.58 P<.01	r1	✗ r.12 P.24	r.29 P<.01	r.28 P.01	r.94 P<.01	r.94 P<.01	r.35 P<.01	r.45 P<.01	r.46 P<.01
Oxygen	r.98 P<.01	r.26 P.01	r-.51 P<.01	r-.99 P<.01	r.48 P<.01	r1	r.58 P<.01	r.29 P<.01	✗ r-.05 P.62	✗ r.18 P.09	r.69 P<.01	r.69 P<.01	r.23 P.03	r.32 P<.01	r.35 P<.01
Salinity	r.55 P<.01	✗ r<.01 P.97	r-.43 P<.01	r-.56 P<.01	r1	r.48 P<.01	r.33 P<.01	✗ r-.03 P.79	✗ r.07 P.52	✗ r-.05 P.65	r.39 P<.01	r.39 P<.01	✗ r-.08 P.45	✗ r.06 P.59	✗ r.13 P.2
Temperature	r-.99 P<.01	r-.29 P.01	r.5 P<.01	r1	r-.56 P<.01	r-.99 P<.01	r-.61 P<.01	r-.27 P.01	✗ r.03 P.8	✗ r-.18 P.09	r-.73 P<.01	r-.73 P<.01	r-.23 P.02	r-.34 P<.01	r-.37 P<.01
Abundance	r-.51 P<.01	r.47 P<.01	r1	r.5 P<.01	r-.43 P<.01	r-.51 P<.01	r-.27 P.01	✗ r-.17 P.11	✗ r-.15 P.16	✗ r-.12 P.26	r-.32 P<.01	r-.32 P<.01	✗ r-.06 P.56	✗ r-.13 P.22	✗ r-.14 P.17
Species.richness	r.28 P.01	r1	r.47 P<.01	r-.29 P.01	✗ r<.01 P.97	r.26 P.01	r.35 P<.01	✗ r-.08 P.44	✗ r-.11 P.28	✗ r.16 P.13	r.38 P<.01	r.38 P<.01	r.28 P.01	r.28 P.01	r.28 P.01
Depth	r1	r.28 P.01	r-.51 P<.01	r-.99 P<.01	r.55 P<.01	r.98 P<.01	r.63 P<.01	r.22 P.03	✗ r-.01 P.91	✗ r.17 P.11	r.73 P<.01	r.73 P<.01	r.22 P.03	r.32 P<.01	r.35 P<.01

Figure 2. An example of assessing collinearity between environmental variables and response variables using the Vema Fracture Zone data set. Red crosses in the heatmap indicate non-significant relationships.

The scale of the analyses varied between chapters. For the Annan Seamount data set the samples were originally 20 m long and this scale was used to extract the bathymetry-derived variables, which were joined to the species data through spatial join as described above.

Mantel's multivariate correlograms were used to examine the structure of the spatial autocorrelation of the data using the function mantel.correlog in the vegan-package (Borcard et al., 2011). Figure 3. shows the results from the Mantel's correlogram analysis for the Annan seamount benthic data set, illustrating that significant spatial autocorrelation is present throughout several distance classes. The Moran's I analysis (package ape, function Moran.I), which assesses how related the values of a variable are, based on their spatial location (Bocard et al., 2011), was applied on the species richness of Annan seamount. This also showed the presence of significant spatial autocorrelation. These patterns are caused by environmental and ecological processes, which occur beyond the scale of our sampling scheme. With this information in mind, we adopted statistical methodologies that would be able to analyse our data despite the lack of independence between our samples. The final transect scales were therefore chosen on the basis that there were enough individuals per samples (with a target number of more than ten individuals) while also capturing the patchy habitats present on a seamount. Therefore, the samples were scaled up to 100 m which was deemed to be an appropriate compromise to the aforementioned prerequisites (Chapter 2) and 200 m, in order to assess whether the results were applicable across different spatial scales. The same 100 m sample length was also applied on the Vema Fracture Zone data set in chapter 3, which allows comparisons in any future work between the data sets of this study and also other data sets which have used 100 m long samples.

In chapter 3, the sample length was 10 m long. Figure 3. provides an illustrative example of how the cold-water coral community data set was assembled. Individual coral occurrences which were further then 50 m from a neighbouring occurrence were omitted and the assemblages were subsequently divided in to 1 m segments in order to obtain corresponding environmental data. After this, the distance of the shortest cold-water coral patch was measured and was found to be 15 m long. In order to make use of the highest quantity of data, the sample size was scaled to 10 m by joining 1 m segments from the same community together.

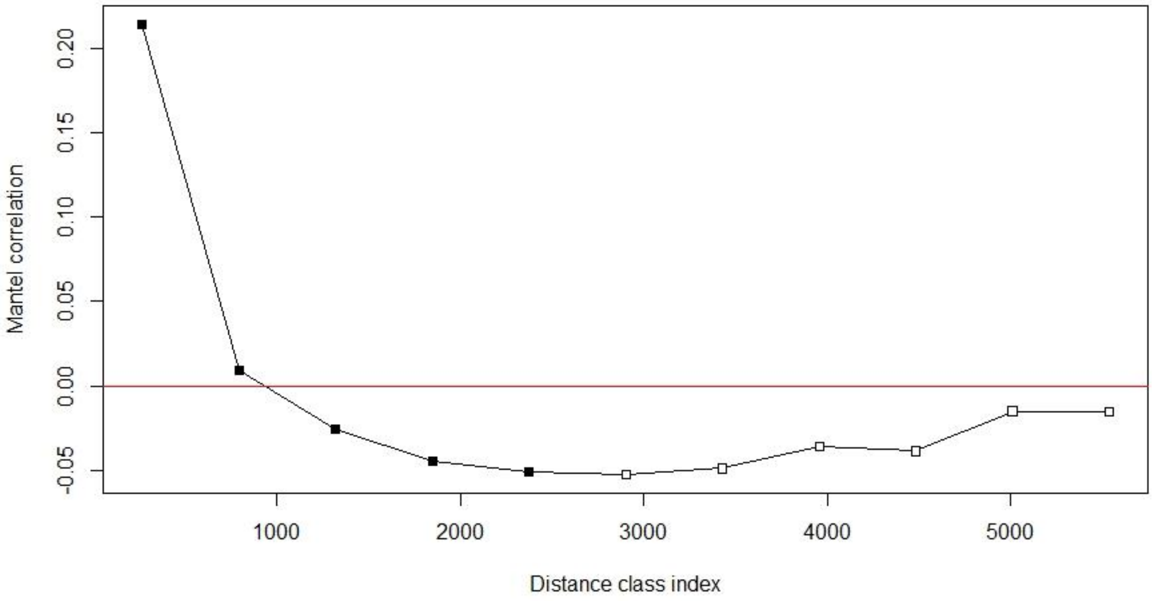


Figure 3. A Mantel's multivariate correlogram using the Annan seamount data set. The black squares represent significant multivariate spatial autocorrelation. The distance class index is shown in meters.

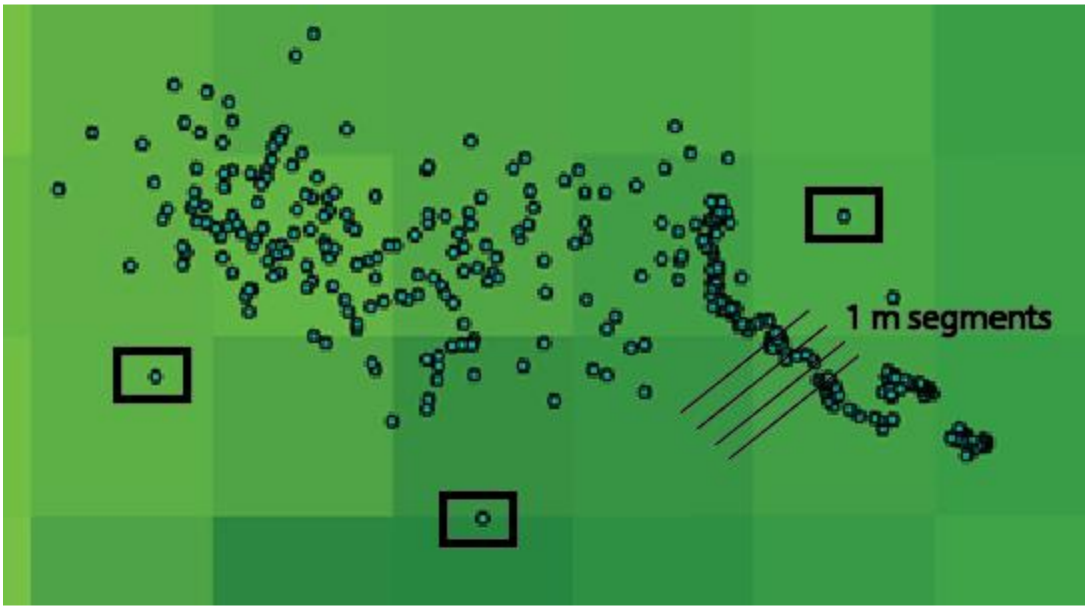


Figure 4. An example of cold-water coral assemblages, with the dots representing occurrences of cold-water corals. The boxes represent individual coral occurrences, which had more than 50 m of distance to their nearest neighbour and which were thus excluded from the community analysis. The transects were divided into 1 m segments and for each segment the corresponding environmental data was extracted.

1.4. Data products

The produced data matrices per chapter include a species data set in which samples are in rows and species in columns along with an environmental data set. As such, this thesis has produced benthic invertebrate data sets for Annan Seamount, Vema Fracture Zone and a cold-water coral data sets from Annan, Knipovich and Vayda seamounts. The environmental data has the corresponding environmental variables, which were acquired through spatial joins, in columns. All the data produced during this thesis will be available open-access following the release of the manuscripts. The data will be deposited in the Ocean Information Biogeographic System (OBIS, http://iobis.org) platform, under the data set name of Tracing Oceanic Processes using Corals and Sediments (TROPICS). The imagery data generated during this thesis has been added to the unified morphospecies image reference catalogue for the North-Atlantic, which will be an open access data base (Howell et al., 2019, in prep). Density estimates of the VME taxa found across the seamounts have been submitted separately to the Deep-Ocean Stewardship VME working group in order to be used in further analyses, workshops and synthesis publications.

Appendix B The results from SIMPER analysis depicting which coral morphospecies contribute towards dissimilar communities between the seamounts.

Groups Annan & Knipovich

Average dissimilarity = 71.35

	Group Annan	Group Knipovich				
Morphospecies	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Bamboo white bush	0.8	0.06	5.42	1.47	7.6	7.6
Corallium sp. pink polyps	0.75	0.3	4.63	1.06	6.49	14.09
Clavularia sp.	0.65	0.84	3.63	0.74	5.08	19.17
Metallogorgia melanotrichos	0.29	0.42	3.59	0.83	5.03	24.21
Acanthogorgia sp.	0.46	0.38	3.44	0.9	4.82	29.03
Paramuricea sp.	0.46	0.16	3.24	0.86	4.54	33.57
Enallopsammia rostrata	0.94	0.58	3.21	0.77	4.5	38.08
Primnoid Calyptrophora sp. 1	0.52	0.03	3.18	0.98	4.45	42.53
Chrysogorgia sp. pink	0.23	0.33	2.88	0.75	4.04	46.57
Leiopathes sp. light brown	0.1	0.34	2.87	0.71	4.03	50.59
Corallium sp. white polyps	0.37	0.2	2.85	0.77	4	54.59
Acanella sp. 3	0.29	0.23	2.71	0.73	3.8	58.39
Bamboo sp. white bush 2	0.04	0.33	2.45	0.65	3.43	61.82
Paragorgia sp.	0.29	0.22	2.4	0.75	3.36	65.18
Corallium sp. pink 2 (bushy)	0.3	0.02	1.86	0.65	2.6	67.78
Bamboo Lepidisis sp. white straight	0.19	0.06	1.73	0.51	2.42	70.2

Groups Annan & Vayda

Average dissimilarity = 83.84

	Group Annan	Group Vayda				
Morphospecies	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Enallopsammia rostrata	0.94	0.16	6.63	1.39	7.91	7.91
Bamboo sp. white bush	0.8	0.07	5.77	1.41	6.88	14.79
Corallium sp. pink polyps	0.75	0.04	5.74	1.26	6.85	21.64
Metallogorgia melanotrichos	0.29	0.69	4.93	0.97	5.88	27.52
Clavularia sp.	0.65	0.33	4.21	0.93	5.03	32.54
Paramuricea sp.	0.46	0.57	4.15	0.88	4.95	37.5
Chrysogorgia sp. pink	0.23	0.57	4.05	0.96	4.84	42.33
Primnoid Calyptrophora sp. 1	0.52	0	3.28	0.97	3.91	46.24
Acanthogorgia sp.	0.46	0.07	3.04	0.87	3.62	49.86
Corallium sp. white polyps	0.37	0.19	2.92	0.75	3.48	53.34
Bamboo Lepidisis sp. white straight	0	0.34	2.42	0.65	2.89	56.23
Paragorgia sp.	0.29	0.1	2.25	0.63	2.68	58.92
Iridogorgia magnispiralis	0.13	0.23	2.11	0.61	2.51	61.43
Bamboo Acanella sp. 3	0.29	0	2.06	0.59	2.46	63.89
Corallium sp. pink 2 (bushy)	0.3	0	1.88	0.64	2.24	66.12
Paranthipathes sp. brown	0	0.27	1.79	0.58	2.14	68.26
Bamboo Lepidisis sp. pink spiral	0.06	0.2	1.78	0.51	2.12	70.38

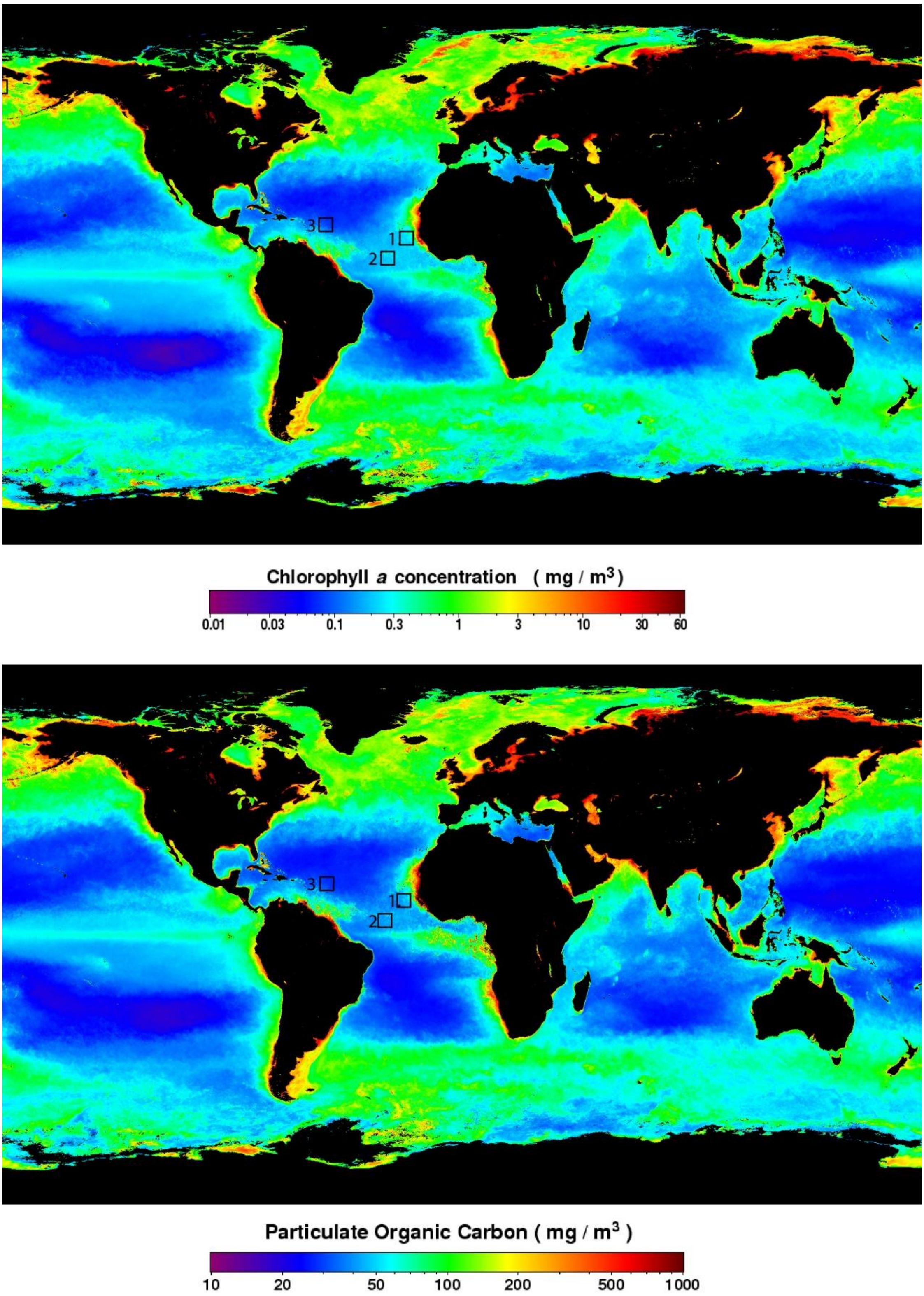
Groups Knipovich & Vayda

Average dissimilarity = 79.94

	Group Knipovich	Group Vayda				
Morphospecies	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Clavularia sp.	0.84	0.33	5.96	1.1	7.46	7.46
Enallopsammia rostrata	0.58	0.16	5.61	0.99	7.02	14.48
Metallogorgia melanotrichos	0.42	0.69	5.17	0.94	6.47	20.95
Paramuricea sp.	0.16	0.57	5.17	1	6.46	27.41
Chrysogorgia sp. pink	0.33	0.57	4.84	0.96	6.05	33.46
Leiopathes sp.light brown	0.34	0	3.38	0.68	4.23	37.69
Acanthogorgia sp.	0.38	0.07	3.37	0.75	4.21	41.9
Bamboo sp. white bush 2	0.33	0	3	0.64	3.75	45.65
Corallium whites sp.	0.2	0.19	2.87	0.62	3.6	49.25
Bamboo Lepidisis sp. straight white	0	0.34	2.84	0.67	3.56	52.81
Corallium sp.	0.3	0.04	2.7	0.64	3.38	56.18
Iridogorgia magnispiralis	0.11	0.23	2.42	0.61	3.03	59.22
Paragorgia sp.	0.22	0.1	2.34	0.58	2.92	62.14
Bamboo Lepidisis sp. white spiral	0.08	0.24	2.32	0.6	2.9	65.04
Paranthipathes sp. brown	0	0.27	2.08	0.59	2.6	67.64
Bamboo Acanella sp.3	0.23	0	1.93	0.52	2.42	70.06

Appendix B1 A composite satellite image of chlorophyll and particulate organic carbon for the year 2013.

Acquired from https://oceancolor.gsfc.nasa.gov/cgi/l3 using Aqua MODIS satellite



Appendix C A peer-reviewed publication during PhD studies

Out of sight, but within reach: A Global History of Bottom-Trawled Deep-Sea Fisheries from >400 m depth

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Author Contributions. LW and CN conceived the study. LV, LW and MP analysed and interpreted the data. LV prepared the figures. LV and LW prepared the animation. LV and LW drafted the text and all authors revised and approved the final version of the manuscript.

Published in Frontiers in Marine Science

Abstract

Deep-sea fish species are targeted globally by bottom trawling. The species captured are often characterized by longevity, low fecundity and slow growth making them vulnerable to overfishing. In addition, bottom trawling is known to remove vast amounts of non-target species, including habitat forming deep-sea corals and sponges. Therefore, bottom trawling poses a serious risk to deep-sea ecosystems, but the true extent of deep-sea fishery landings through history remains unknown. Here, we present catches for global bottom trawling fisheries between years 1950-2015. This study gives new insight into the history of bottom trawled deep-sea fisheries through its use of FAO capture data combined with reconstructed landings data provided by the *Sea Around Us* Project, which are the only records containing bycatches, discards and unreported landings for deep-sea species. We illustrate the trends and shifts of the fishing nations and discuss the life-history and catch patterns of the most prominent target species over this time period. Our results show that the landings from deep-sea fisheries are miniscule, contributing less than 0.5 % to global fisheries landings. The fisheries were also found to be overall under-reported by as much as 43 %, leading to the removal of an estimated 25 million tonnes of deep-sea fish. The highest catches were of Greenland halibut in the NE Atlantic, Longfin codling from the NW Pacific and Grenadiers and Orange roughy from the SW Pacific. The results also show a diversification through the years in the

species caught and reported. This historical perspective reveals that the extent and amount of deep-sea fish removed from the deep ocean exceeds previous estimates. This has significant implications for management, conservation and policy, as the economic importance of global bottom trawling is trivial, but the environmental damage imposed by this practice, is not.

Introduction

The history of global fisheries is one of full- or over-exploitation, with a few exceptions (Pauly and Zeller, 2016). One of the most controversial fishing practices known to date is bottom trawling, which can be dated back to as early as 1376, when concerns and complaints were raised by fellow fishermen about a new destructive and wasteful fishing habit (Roberts, 2010). The extension of bottom trawling to the deep-sea occurred in the second half of the 20th century, prompted by technological advances and a decline in shallow water fisheries (Koslow et al., 2000). The fisheries industry, particularly in Europe, North America, and the former Soviet Union, pushed into ever deeper water in search of more fish. In many cases, these fisheries were promulgated on the high seas where there were few, if any, regulations (Bensch et al., 2009). Many of those fisheries, especially those targeting seamounts have been shown to be “boom and bust” fisheries, and lasting from less than a decade to a couple of decades (Clark et al., 2007) before they are no longer economically viable.

The deep sea is an ecosystem different from that of shallower water. Here organisms, including fish, generally live for long times, have low fecundity, mature at older ages, and have lowered metabolism and slow growth. Drazen and Haedrich (2012) found that for 41 shallow and deep dwelling fish species with sufficient life history data, there was a consistent trend of increasing longevity, decreasing fecundity, and decreasing potential rate of population increase with depth. In addition, deep-sea fish may be more vulnerable to the fishery by aggregating on seamounts for mating or taking advantage of trapping of vertically migrating nekton by seamount topography (Morato and Clark, 2007). Such is the case of the Orange roughy, where fisheries, in order to be economically viable, have targeted spawning and feeding aggregations (Clark, 1999; Roberts, 2002). It is, therefore, likely that deep-sea fisheries could easily and rapidly, over-exploit fish species living on seamounts and ridges, or along the continental slopes of the world.

Fishing in the deep is difficult, and requires large vessels with very heavy gear in order to reach species living at depths of as much as 2000 m. Deep-sea fishing vessels are often of 80 to 100 m length, weighing in at 2000 gross tonnes or more. In some distant water fisheries, the vessel may be much larger and house crew and capabilities for processing and freezing the catch while at sea. Deep trawl gear is usually in the form of an otter trawl which uses metal “doors” that can weigh up to 5000 kg in order to get the net to the bottom and keep the net mouth open while being pulled across the seafloor. The trawl can be very wide, with total distance including the sweeps, bridles and ground gear amounting to 80 – 200 m. The ground gear of a deep-sea trawl is equipped with steel bobbins and/or stiff rubber discs that are designed to allow the net to move over rough bottom without getting “hung up” (Clark and Koslow, 2007). This equipment guarantees that bottom trawling is the most efficient fishing method in the deep-sea, but also the most destructive as it permanently removes the benthic habitats, typically comprising long-lived habitat-forming species, such as deep-sea corals and sponges (Clark et al., 2016). To date, no recovery over decadal time scales have been observed in seamounts targeted by bottom trawling (Williams et al., 2010).

Deep-sea fisheries have been summarized in general terms (Priede, 2017), for specific species (Shotton, 2016) and parts of the ocean, such as seamounts (Clark, 2009b), FAO fishing regions, or for relatively short periods of time (Bensch et al., 2009). However, a comprehensive historical analysis of bottom trawled fisheries describing the major trends with data beyond that provided by FAO, is currently missing. The purpose of this study is to produce a more complete global history of those fisheries promulgated with bottom trawl gear primarily below 400 m. This is achieved by complementing the data set produced by the FAO for the period of 1950 to 2015 (FAO 2017), with unreported landings, bycatch and discards data for the period of 1950 to 2014 from the Sea Around Us Project. We document the history of the species targeted, the countries involved, and the parts of the global ocean that have supported these fisheries and highlight shifts in their patterns through the years covered by the data. In addition, we pinpoint discrepancies between the two data sets to show that the fishing pressure encountered by certain species has not been accounted for in current conservation efforts, which is potentially leading to the mismanagement of deep-sea trawl fisheries.

Methods

When we started this study, there was no comprehensive compilation of fish species caught as part of the deep-sea fisheries of the world (Bensch et al., 2009). Therefore, we developed a list of fish species caught primarily by deep-sea bottom trawling either as target species or bycatch, using records from EU Annex 1 and 2, FishBase (Fishbase.org), the fisheries literature, and from the compilation by Priede (2017) (Table 1). This list of demersal species was reviewed by independent experts to be sure we had not overlooked any species known to be taken, at least in moderate to large numbers, primarily by bottom trawling. A small number of species within this list are also caught with a longline, along with bottom trawling and there is no differentiation between catches by gear types. Global capture data (in tonnage) for species was extracted from the Food and Agriculture Organization of the United Nations (FAO) capture data set using FishstatJ (v. 3.01) for the years 1950 – 2015. As the FAO data only includes the capture landings reported by national governments, a set of estimated unreported capture data for the same species for the years 1950 – 2014 was provided by the Sea Around Us Project (www.seaaroundus.org) at the University of British Columbia. The reconstructed catch data includes species for which FAO did not require reports in the past, as well as unreported landings and discards generated by deep-sea fisheries (Zeller et al. 2017). Both data series were also used to calculate the number of species caught per year.

The Sea Around Us reconstructed capture data is estimated using a seven-step methodology developed by Zeller et al. (2007) and recently modified and detailed in Zeller and Pauly (2016). The method includes sourcing data from reporting entities, in particular FAO, but also local agencies, identification of sectors not covered in the official reports, finding additional sources of information searching literature and archives, developing data anchor points in the time series, and consulting local experts to fill in the data gaps, then interpolating between anchor points for missing data components. Lastly, the uncertainty associated with each reconstruction is quantified.

Deep sea fish species exhibit a continuously changing range of life-history traits with depth (Drazen and Haedrich, 2012). In order to make catch levels more comparable, we divided our list of deep-sea species into two groups. The shallower group comprises slope species that inhabit depths of ~ 200 – 400 m. These species typically mature faster and have higher fecundity resulting in life history characteristics that are more closely allied with species of the continental shelf. As such they provide more productive fisheries with higher magnitude of catches and will be considered in a future paper. The second group, which is the main focus of this study, comprises species living and being caught mostly by bottom trawls below 400 m.These species exhibit more typical deep-sea traits such as slow growth, late maturation and low fecundity, and by comparison have lower weights of catches. Data handling and analysis was conducted in the software “R” (R Core Team, 2016) or with Microsoft Excel®.

Long-term patterns of catch by country was illustrated using the Density Equalizing Cartogram routine implemented in the ‘Cartogram geoprocessing tool’ in ArcGIS (v. 10.2.2). This routine uses a diffusion-based method (Gastner and Newman, 2004) and changes the shape of each polygon (in this case, country) in a manner that reflects the amount of an attribute (catch) associated with each polygon. The final product is a world-map of countries altered according to their deep-sea fishery catch in relation to that of all other countries. We constructed a cartogram for each year from 1950 to 2016.

We added a color gradient to the cartograms to give an indication of the magnitude of catches for each year. In the country analysis, we treated the data for Russian Federation and that of USSR as a single country whereas those formerly in the Soviet Union have their own entries in the FAO database after they became independent. Cartograms were generated separately for the two depth groups using both the reported data from FAO and the reconstructed total estimated catch. The cartograms for the 200 – 400 m depth group will be reported in a future paper.

Results

Global, Regional and Country Specific Trends

The total amount of deep-sea fish caught was ~ 14 million (FAO) and ~ 25 million tonnes (FAO + SAUP) through the historical period of 1950-2015 (Table 2, a). Unreported landings and discards contributed almost equally to the discrepancy between the two data sets (Table S1). Deep-sea bottom-trawled fisheries account for less than 0.5% of the global estimated catch of all fisheries. The first large-scale deep sea fishery catches are from 1956 by the Soviets who, based on reconstructions, discarded an estimated ~ 84,000 t of Greenland halibut in the Northeast Atlantic (Tables S1). The discards were potentially bycatch of the more valuable cod and herring fisheries, which were the predominant target species at that time (Garfield, 1959). From here onwards, both reported landings and unreported catch steadily increased through the 1960s, after which there were three major periods of peak catches, reflected more in the total estimated catch than in the reported FAO data (Fig. 1). These peaks represent sudden increases in catch of one or two species, such as Greenland halibut and Longfin codling, whose populations were newly discovered and rapidly exploited (Fig. 2, and supplementary material, cartogram animation). While the early catches were dominated by just a few species from one or two areas, the deep-sea fisheries history becomes more complex adding more species and regions, with large estimated unreported catches between 1985 and 2010 and an estimated ~600,000 t of fish being caught in the early 1970s, late 1980s and early 2000s.

The total reported and estimated catch of each region is presented in Table 2,b, from which it can be seen that four FAO regions are responsible for the majority of landings: the Northeast and Northwest Atlantic, and the Northwest and Southwest Pacific. These areas are more productive and have high amounts of organic matter falling to the deep sea floor (Lutz et al., 2002; Watling et al., 2013) and as such the deep-sea fish populations in those areas are also very productive. The time period between 1975-2000 includes a notable decrease in landings from the NE Atlantic, which is reflected in the FAO data; in this same period there was an increase in the estimated total catch from the SW and NW Pacific fisheries (Fig. 2). Bottom trawled catches in the NW Pacific, however, showed an overall sudden peak followed by a trend to reduction in landings until recently, which is linked to the collapse of the once extremely abundant Longfin codling stocks (Fig. 2). The SW Pacific fisheries rely on aggregating species, such as Orange roughy and Smooth oreo dories found on and around topographic features, such as offshore banks and mid-ocean ridges that provide a great amount of area at fishable depth within the region. However, as fishing grounds become depleted, there is an overall trend of reduction in catches (Fig. 2) with productivity of the fisheries questioned leading to stricter management (Schlacher et al., 2014). For example, catch quotas for the Orange roughy were lowered in the 1990s once scientific evidence emerged showing slow growth, high longevity (Mace et al., 1990) and rapidly declining biomass for some of the stocks (Clark, 2001).

We have illustrated the changing patterns of catch for individual countries in a series of cartograms, one for each year for both reported landings and estimated total catches. The cartograms are presented in Fig. 4, and the remainder have been made into an animation and are included as supplementary material. The FAO cartograms show the pattern of change of landings, first from the North Atlantic, where Greenland halibut, Longnose velvet dogfish, and Blue ling were the mainstay of the fishery. These species were caught in relatively low numbers, with reported landings for the countries being 20,000 t or less. As of 1950 the countries landing any deep-sea fish were Ireland, Norway, and a few other European nations. Through the 1950s and 60s, catches steadily increased, mostly in the North Atlantic as those three species continued to be exploited.

During this period the Soviet Union expanded into deep-sea fisheries. In 1969 Slender armorhead was discovered on the Hawaiian – Emperor Seamounts and in 1970 an estimated 149,820 t were caught (Fig. 4). The Soviet Union was the primary country targeting Slender armorhead, and as a result it is the first country to report total deep-sea fishery landings in the range of 100,000 to 240,000 t. However, there are also records of the Japanese fleet targeting the Slender armorhead fishery during this time with catches of ~30,000 t (Clark et al., 2007). Unfortunately, the FAO and the reconstructed data sets have no record of this and overall provide poor records for the Japanese deep-sea fisheries.

From the late 1970s and through the 1980s other deep-sea fish species were targeted, in particular Orange roughy, Longnose grenadier and other miscellaneous grenadiers (listed by FAO as "Grenadiers *nei*") and by 1990, the Patagonian toothfish. The 1980s and '90s also represent a period where the disparity between reported landings and total catch estimates was the largest. As will be noted below, these two decades saw very large landings of Longfin codling by Russia, and up to 50% under-reporting of Orange roughy by New Zealand, and systematic under-reporting of Greenland halibut being caught in the North Atlantic.

The diversification of countries fishing in the deep sea and of species landings being reported increase, while the trend for under-reporting decreases during the 1990s and into the 2000s. At the same time the global catch numbers decrease to about half of peak values seen in the 1980s. This pattern is correlated with a decrease in landings from the SW Pacific, which consisted mostly of

Grenadiers and Orange roughy, and an increase in catches from the NE Atlantic where the diversity as well as the tonnage of the catch increased (Fig. 2). In the NW Pacific the large reduction in catch, which buoyed the values in the 1980s and ‘90s, was due to the heavy exploitation of Longfin codling. This species was replaced by catches of Grenadiers (mostly Popeye and Giant, although not specifically reported) and Greenland halibut from the Bering Sea.

Comparisons between the FAO records and the reconstructed catches show a steady increase in both data series for the number of species being caught, or at least recorded (Fig. 3). This can be expected in the FAO data series, as a large number of species were not reported in the past, because of different regulation or the species were often grouped under a category of “*nei*”. However, the reconstructions also show an increase in the diversity of species being caught, with an increase of up to 30 species from the 1950s to the modern era, where the data sets converge. This implies that a true diversification in the species targeted is likely and it is not simply an artefact caused by regulations leading to ungrouping of species.

Individual fisheries

The 72 species or species groups being caught primarily with bottom trawls mostly at depths greater than 400 m, their reported (FAO) catch data, and the total estimated catch (FAO+SAUP) are presented in Table 3. In the following section we give more detail about the most fished and vulnerable deep-sea fishery species, the nations who fish them, and landing trends since 1950. Biological information on individual species not specifically cited has been taken from FishBase.org.and all the catch values described here can be found in the supplementary data tables (Table S1).

Greenland halibut (*Reinhardtius hippoglossoides* Walbaum, 1792), also known as Turbot. The species is found in both the North Atlantic and North Pacific Oceans usually at depths of 500-1000 m. This is a very old fishery in West Greenland, NW Atlantic, being fished commercially using line and hooks since the mid-1800s (Bowering and Brodie, 1995). For many years gill nets were used, but after 1966 large trawlers from Poland, German Democratic Republic and the USSR began taking Greenland halibut as trawl bycatch in the Redfish and Roundnose grenadier fisheries. Indeed, in 1966, the reconstructed data series reveals the Soviets discarding up to 47,000 t of Greenland halibut. Canada entered the directed fishery for this species in the mid-1960s (summarized in Bowering and Brodie, 1995), reporting landings of ~80,000 t over the decade. Portugal entered in the 1980s with minor catches and Spain in the 1990s reported landings of ~ 170,000 t. Spain’s dominance in this fishery likely led to the Canada – Spain “turbot war” of 1993 (Haedrich et al 2001).

On the Newfoundland slope, most of the fish caught between 1991 and 1996 were below the size at 50% maturity (Haedrich et al., 2001). This species had, by far, the highest reported landings through the history of the FAO data set (~ 4.89 million tonnes), and also the highest total catches when unreported landings and discards are included (~ 7.64 million tonnes) (Table 3). The greater part of the catch was from the North Atlantic, first from the northeast, and later from the northwest, with smaller numbers from the North Pacific. Only about 60% of the total estimated catches were reported to FAO. In fact, the catches were likely under-reported by more than 75% for 39 of the 66 years considered here (Fig. 5, Table S1). A major difference between the two data sets arises from the reconstructed discard estimates, which amount to a total of 2.5 million tonnes with ~ 1.8 million tonnes assigned to the Soviet/Russian fleet operating within the Barents Sea (Table S1). In the 1990s discards amounted to 350,000 t, of which 200,000 t were by the Russian fleet in the Barents Sea and 80,000 t in the Norwegian Sea. In comparison, the reported landings for Russia only amount to 47,000 t over the whole decade. The large quantities of discards within this period were likely caused by lowered quotas as the Greenland halibut stocks suffered a decline and became regulated in 1992 (Hønneland and Nilssen, 2001; Nedreaas and Smirnov, 2004). The discard estimates made by Jovanović et al. (2008) use discard data between 1996-2006 and assume a similar discard policy for the species throughout the fishery's history potentially leading to an overestimation of the discard values.

Longfin codling (*Laemonema longipes* Schmidt, 1938), also known as Forked hake in Japan, is a deep-water member of the Gadiformes, in the Family Moridae, primarily inhabiting the NW Pacific continental slope from Kamchatka to Hokkaido and into the Okhotsk Sea. Its depth distribution is 80-1830 m, but the most abundant catches are at 800 m depth (Yokota and Kawasaki, 1990). The fishery is promulgated both by Japanese and Russian vessels, the latter sometimes in contract to Japan. Savin (2013) noted that the biomass of the species in the area where the fishery occurs can reach values as high as 360,000 t. The lowest stock values were recorded in 1984 (116,000 t) and 2006 (66,800 t). Savin (2013) noted that the fishery by Russian vessels started in 1974, followed by Japan in 1976. There seems to be no evidence of a fishery for Longfin codling before that. Even so, by the third year, the landings (unreported to FAO) in Russia were approximately 100,000 t. After the establishment of the EEZ by Japan, some Russian vessels were allowed to fish under contract in Japanese waters. For some reason, except for three years (1978-1980), neither country reports catches of Longfin codling under its own name and there are hardly any records of this fishery existing in the FAO database. Instead, the landings are most likely included under the category "marine fishes *nei*" (Alexei Orlov, personal communication). Thus, estimating the actual catches of this species has been difficult and rely heavily on reconstructed records from the Sea Around Us

Project (Fig. 5) and data recorded in Russian fishery reports (Savin 2013). In the end, this species is estimated to have produced about 3.5 million tonnes of fish, making it the second most productive deep-sea fish caught by trawls and causing one of the biggest discrepancies between the reported landings and total catch estimates.

Orange roughy (*Hoplostethus atlanticus* Collett, 1889) has a very wide distribution, from NW and NE Atlantic, throughout much of the eastern Atlantic, south Central Indian, and SW and SE Pacific. It is one of the oldest commercially exploited fish species, reaching more than 100 years of age (Andrews et al., 2009). Orange roughy matures at the age of 20 -35 (Horn et al., 1998) and spawning occurs in dense aggregations around topographic features such as seamounts, and rises as well as along the continental slope (Branch, 2001). These aggregations are fished and provide high catch rates, leading to rapid overexploitation. The long, slow growth and late maturity of this species, coupled with its low reproductive output, makes recovery slow. The first reported landings of Orange roughy occurred in 1977, by foreign trawlers off New Zealand, but the start of the fishery occurred in New Zealand in 1979 (Branch, 2001). In 1980, in the Chatham Rise area, which is the largest and oldest Orange roughy fishery, virgin catches were about 9-10 t/tow (Clark, 2001), but by the late 1990s catches had decreased to 2 – 3 t/tow. Also, in the 1990s the fishery moved out of New Zealand waters to the Louisville Ridge seamount chain where catches varied from 1.4 – 2.7 t/tow. Other Orange roughy fisheries include those off Australia, NE Atlantic in the mid-1980s and 1990s, off Namibia in the 1990s, and off Chile and in the Southern Indian Ocean in the late 1990s (Figs. 3, 5). Virtually all these fisheries are operating on stocks that are less than 30% of virgin biomass, and several have lasted only a few years (Branch, 2001; Foley et al., 2011). The reconstructed data suggests that for this fishery, landings were under-reported by as much as 50 % between the years of 1981-89. Overall, half a million tonnes of unreported Orange roughy have been caught in the period of 1950-2015, mainly by Japan (~225,000 t), New Zealand (~162,000 t) and South-Korea (~35,000 t). The FAO admits its records underestimate Orange roughy catches with trade analysis confirming at least a 30% underestimation in the year 2001 (Lack et al., 2003). Simmons et al. (2016) note that discrepancies in tray weights, conversion factors, and false reporting in order to avoid income tax liability have all contributed to under reporting of Orange roughy from New Zealand waters. Since 1986, the establishment of the Quota Management System, also gave incentive to under report due to quota restrictions and in order to avoid penalties. In the Chatham Rise fishery, after years of reduced TACs (total allowable catches), the stocks have shown signs of recovery (Doonan et al., 2015) and currently, the fishery is certified as sustainable by the Marine Stewardship Council (MSC) with TACs set at ~ 7,000 t/ year. However, to date, the Orange roughy fishery remains contentious, with scientists and non-governmental organizations (NGOs) raising concerns about its sustainability (Watling, personal observation).

Grenadiers (Macrouridae) *nei* (not elsewhere included) is a category consisting of grenadiers, whiptails and rattails, which are not recorded separately, or species that were not recorded separately until relatively recently. There are about 360 species in this group extending over a wide depth range of 110 – 7000 m, making them widespread in the deep sea. Most species are caught as bycatch and are small or not edible so are either discarded or processed as fishmeal. A few of the larger species, with better quality meat, are targeted and their landings are recorded separately by FAO. FAO did not show any landings for Grenadiers *nei*, until 1977, with total landings now reaching 571,000 t, of which ~ 400,000 t has been reported by Russia from the NW Pacific. These commercially targeted fisheries, include species, such as the Giant, Popeye and Pacific grenadier (Tuponogov et al., 2008) , whose landings are not yet recorded separately by the FAO. The Sea Around Us Project estimates the amount of caught but discarded grenadiers to be close to 2.5 million tonnes since 1950 (Fig. 5). These numbers include some species that were discarded in the early years, but became a targeted fishery later, such as Roundnose grenadier. Two million tonnes of discards are assigned within the New Zealand EEZ (economic exclusive zone) mostly from the fishing entities of New Zealand (1 million tonnes) and Japan (0.5 million tonnes). Rattails are a common bycatch product of the Orange roughy, oreo, hoki, hake, ling and arrow squid fisheries and of the scampi trawling (Anderson, 2012; Anderson et al., 2017; Ballara and O'Driscoll, 2015). The bycatch estimates (% of total catch) made by observers on New Zealand vessels are 0.7% for Orange roughy, 6% for hoki and 30% for scampi fisheries of the total catch, with the majority discarded (Anderson, 2012; Anderson et al., 2017; Ballara and O'Driscoll, 2015). The contrasting discard rates between the official records and the reconstructions are potentially caused by the "observer" effect, in which fishing behavior is modified for the better due to the presence of observers (Simmons et al., 2016). The reconstructions also suggest that the discarding of Grenadiers remains relatively high, when taking into account the fact that the catches for target species have notably decreased (Fig. 5).

Roundnose grenadier (*Coryphenoides rupestris* Gunnerus, 1765), is a benthic to benthopelagic species found along the continental slopes and the Mid-Atlantic Ridge of the North Atlantic Ocean typically at 400 – 1200 m depth. Russian trawlers first caught Roundnose grenadiers as bycatch in their cod and redfish fisheries on the Canadian eastern slope (Atkinson, 1995). It was soon suggested, due to the high numbers and high quality of the fish, that a targeted fishery could be developed in the North Atlantic, with the Danish, developing a fishery in the 1980s in the Skagerrak. The highest reported landings peaked in 1971 at 84,000 t, but declined steadily after 1975 (Fig.5). Haedrich et al. (2001) noted that important biological information for this species was not known until after 1975, by which time the fishery had begun to decline. Both the FAO reported landings and Sea Around Us Project estimated total catches show fluctuations in the catch, and from 1986 to 2006 the reported catch was from 78 to 26% of the estimated unreported catch (Fig. 5). The discrepancy between the data sets arise from reconstructed discards from Denmark between early 1990s to 2006, which are estimated to 10,000- 20,000 t per year amounting overall to 350,000 t. This species is a common bycatch and discard in the demersal mixed trawl fisheries in Skagerrak, Kattegat and North Sea (Gibson et al., 2010) with discard rates of 28% in weight in the NE Atlantic. As the juveniles and adults co-exist within the same area, trawls catch small, non-marketable fish, which are discarded at sea (Pawlowski and Lorance, 2009). The decline in stocks led to an agreement between the EU and Norway, setting the TAC to zero since within the Norwegian waters since 2006 (ICES, 2016). Devine et al. (2006) noted that the steep drop in abundance would qualify *C. rupestris* as endangered under IUCN criteria.

Beaked redfish (*Sebastes mentella* Travin, 1951) is an oceanic migratory fish inhabiting the waters of the northern North Atlantic at 300 -1400 m depth. It is worth noting that this fishery has been mixed, especially in early years, with the Golden redfish (*Sebastes marinus*) fishery. This was the second-most landed fish over the 66 years of the FAO database, even though the fishery started in the 1960s, and had landings that were quite modest through the 1960s to 1990s (Fig. 6). Starting in 2000, however, landings increase, reaching 1.4 million t reported to FAO. Iceland and Russia caught the majority of this fish since 2000. The discrepancies between the reported and estimated total catches arise from 275,000 t of reconstructed discards starting from the late 1980s (Fig. 6). The discards are mainly assigned to Iceland (197,000 t) and Norway (76,500 t), despite both countries having discard bans since 1989 and 1987, respectively (Condie et al., 2014). Nakken (1998) reported that high amounts of undersized redfish were discarded prior to the introduction of sorting grids in shrimp trawlers in 1995. Redfish is also a common bycatch of the cod and haddock fisheries in the Barents Sea (Little et al., 2015). The regulations for this fishery include over quota catches being withdrawn from the following year's quota and size limitations, in addition to bycatch limits with undersized fish landed being counted at 50% of the fish's weight against the annual quota (Assessment of the environmental impact of fishing Monitoring and Assessment Series, 2009). Furthermore, temporary and permanent closures of fishing areas can occur when juvenile fish are caught in excess (Little et al., 2015) thus indirectly providing some incentive to discard undersized redfish.

Slender armorhead (*Pentaceros wheeleri* Hardy, 1983), also sometimes known as Pelagic armorhead or Longfin armorhead, is a benthopelagic species of the North Pacific, typically at depths of 400 - 600 m. It forms spawning aggregations on the southern Emperor and northern Hawaiian Ridge seamounts (Boehlert and Sasaki, 1988). The fishery for Slender armorhead followed a classic "boom and bust" pattern, starting with its discovery by Soviet trawlers in 1967 (Humphreys et al., 1984). According to the FAO landings data, the Soviet fleet fished the area until the stock was exhausted in 1977 (Figs. 2, 6). In the second year of the fishery, 145,000 t of fish were reported as landed, with a subsequent peak of 150,000 t in 1973. The catch steadily declined to 200 t in 1977. After years of no landings, fewer than five tonnes per year have been landed from these seamounts over the last decade (Table S1). Humphreys et al. (1984) also cite a series of Japanese works that show Japan having caught between 25,000 and 35,000 t of armorhead from the southern Emperor seamounts from 1970 to 1976. None of these catches are recorded in the FAO database or in the catch estimates reconstructed by the Sea Around Us Project.

Patagonian toothfish (*Dissostichus eleginoides* Smitt, 1898), also known as Chilean seabass, is a benthopelagic species. It is widely distributed around the Southern Ocean, mostly outside the Antarctic Convergence, while its congener, Antarctic toothfish (*D. mawsoni* Norman, 1937) lives mostly on the Antarctic shelf and slope within the Convergence. The Patagonian toothfish is typically found between 50 – 1500 m water depth. The toothfish fishery is both a longline and bottom trawl fishery, with the latter method becoming more common outside Antarctic waters where trawl usage is allowed. The bulk of the catch is from the FAO area in the SW Atlantic, that is, the Argentine shelf, Falkland Islands, and South Georgia, with Pacific, Southeast (Chile slope) and Indian Ocean, Antarctic (Kerguelen Plateau) not far behind. Chile, France, and Argentina, in that order, landed most of the catch. There was a ~ 10% difference in the 1990s between the reported and unreported estimate of total catches (Fig. 6), although Collins et al.(2010) suggest that illegal, unreported, and unregulated (IUU) catches might be under-estimated by as much as 50% in some areas. The unreported landings amount to a total of 125,609 t, half of which were from the Prince Edward Islands in South-Africa. The reconstructions suggest that there were half a dozen nations under-reporting their landings. Some of these, such as Panama, are known for providing flags of convenience for other nations (Bialek, 2003). Since 1999, in response to high IUU fishing, the fishery has been managed using a Catch Documentation Scheme (CDS) by the CCAMLR, in which the fish are tracked from the point of landing and throughout the trade cycle (Bialek, 2003).

Blue ling (*Molva dypterygia* Pennant, 1784) is a benthic, non-migratory species distributed within the NE and NW Atlantic and the western Mediterranean, typically between depths of 350-500 m. It aggregates for mating along the continental slope and on offshore banks and seamounts, which makes it vulnerable for serial depletion (ICES, 2017). Blue ling fisheries have been recorded in FAO landings data since 1950 with landings from Norway and Germany in the NE Atlantic. Faroe Islands entered the fishery in the early 1970s. Peak catches occurred in the 1980s (Fig. 6), after which catches were strongly reduced, partly due to restricting catches to periods when mating aggregations were not occurring, and to management measures reducing total allowable catches in the NE Atlantic. In the NE Atlantic, two of the depleted spawning areas have remained closed since 1993 and since 2003 ICES has advised for no direct fishery and a reduction in bycatch (ICES, 2017).

Longnose velvet dogfish (*Centroscymnus crepidater* Barbosa du Bocage & de Brito Capello, 1864), also known under many other common names, such as Black shark and Deepwater dogfish in Australia, Pailona à long nez in France, and Sapata preta in Azores. This shark is benthic and widespread globally, being found on bathyal ridges and continental slopes at depths between 230 -1500 m, in all oceans, except the western Atlantic, central Pacific and polar waters. In the FAO database, Ireland was the only country reporting landings of this species until 2002 (Fig. 2). Subsequently, France and United Kingdom entered the fishery, with France landing relatively large amounts, as high as 2,460 t in 2010. Estimated unreported landings exceed those reported to FAO by only minor amounts (Fig. 6) due to some discarding of this species.

Discussion

Comparing reported and estimated total landings

This study complemented the FAO records with reconstructed unreported landings and discards from the Sea Around Us Project to estimate more accurate catch levels for deep-sea fisheries. The analysis reveals that overall deep-sea fisheries are likely to have captured ~ 43 % more fish than what was reported to FAO. Specifically, the period between years 1975-2000 was characterized by the highest catches, much of which were not reported to FAO (Fig. 1). Catch data from FAO has often come under attack for being inaccurate at best, and unreliable at worst (Lobo and Jacques, 2017; Pauly and Zeller, 2017; Ye et al., 2017). It should be kept in mind, however, that FAO reports in its database only what is reported to it. For some areas of the world, at various time periods, the "official" landings reported to FAO closely parallel the best in-country records. An example of this is the NE Atlantic since the establishment of the European Union's Common Fishery Policy in 1983. Fish catches are managed through a variety of steps that begin with scientists from member countries contributing information to the ICES advisory working groups, after which total allowable catches (TACs) are designated for each species. The data ICES receives is based on each country's monitoring procedures and can reflect haul data and ship logs monitored by observers. Many countries use shipboard observers to verify catch numbers, but observer coverage is highly variable and spotty between nation, representing sometimes only 5% of the vessel trips (Auster et al., 1996; Lorance et al., 2010). The presence of the observers is known to lead to modified behavior by the fishermen, leading to better, more careful fishing and reporting (Simmons et al., 2016).

When observers are not present it is possible that catch data only reflects what was kept and landed at the dock, with fish that were discarded not being included. The unwanted fish were either not of high enough quality, not large enough, or not of interest or marketability or could not be landed due to restrictions in quotas (Zeller et al., 2017). It is improbable that deep-sea fish, once caught along with tens of thousands of other fish in a trawl net from the cold ocean, then deposited into the hold where the catch is sorted, would survive once returned to the ocean. Therefore, those dead fish should have been part of the catch levels reported, but they were not, although there are efforts now in some areas to record the discarded fish numbers (Pawlowski and Lorance, 2009). Indeed, our results indicate that one of the major discrepancies with FAO records and total estimates, arises from the high amount of discards involved in the deep-sea fisheries, totaling 6 million tonnes over the study period. The high amounts of discards is not unexpected, as bottom trawling is known to generate the highest discard rates in comparison to other fishing gear (Zeller et al., 2017). It is important to record this discard data, because ignoring it and using only landings data to model population dynamics, results in poor stock assessments and biased fishing patterns leading to mismanagement of deep-sea fisheries (Pawlowski and Lorance, 2009).

Another notable discrepancy between the data sets is the number of different species being landed. This difference might be expected as the FAO did not require the reporting of many of these species in the earlier time periods, but the increasing trend is also apparent in the FAO + SAUP data set. This increase in species being landed, especially since the mid-1990s (Fig. 3) suggests that fishing vessels no longer concentrate their efforts on only a few economically viable species. Instead, it is likely that as the most valuable fish stocks are depleted and are more heavily regulated, a broader range of species become targeted and markets developed for them.

It is evident that catch data from both FAO and the Sea Around Us, contains uncertainties. The Sea Around Us Project has engaged multiple teams of people in most fishing countries to try to estimate the unreported catches (Pauly and Zeller, 2016). The method of estimating can vary from country to country, so it is possible that the accuracy of the estimates will also vary according to country. In some areas, for example, the Russian Far East and Japan, estimates for the landings of some fish species were corrected as, we found, during the study, additional literature that indicated more precisely when certain fisheries began. One of the most extreme cases of unreported fish landings concerns the Longfin codling fishery, which as previously described had only minor landings in the FAO database, despite producing 100,000 t in the third year of the fisheries existence (Savin, 2013). Another case illustrating the uncertainty with both the FAO and Sea Around Us data sets, is the absence of landings for Japan’s Slender armorhead fishery within the Hawaiian-Emperor seamount chain, despite records stating catches of 30,000 t (Clark et al., 2007). Despite these limitations, the FAO landings data complemented with the Sea Around Us reconstructions is the only data compilation available for estimating reported and unreported landings and discards for deep-sea fisheries

Ecological consequences of deep-sea trawling

There are two long term consequences of the deep-sea bottom trawl fishery. Bottom trawling enables rapid exploitation of fish species and indiscriminately catches whatever fish are in the path of the trawl. It is also known to physically alter the benthic habitat (Haedrich et al., 2001) by removing or crushing habitat-forming species (Clark et al., 2016; Koslow et al., 2001; Williams et al., 2010). Merrett and Haedrich (1997) make two observations about the management of deep-sea fisheries that are still important today. First, they make the analogy of the distant-water trawler as a “roving predator” (p. 227) seeking prey throughout the world’s ocean. Unfortunately, the predator has evolved far faster than the prey. The first distant-water trawler, the *Fairtry*, was built in the 1950s in England. It was a fully-developed floating fish factory, capable of both catching and processing fish. It became the model for vessels fishing far from ports where normally fish stored on ice would be landed. The capability of the predator to consume large numbers of fish was born, and then kept from extinction by the provision of financial subsidies, at least in some areas, to help allay the enormous costs of operating such large vessels at sea for long periods of time. Of the world’s 13 biggest high seas bottom trawling nations, there is only one (New Zealand), which does not provide subsidies, suggesting that many deep-sea trawl fisheries would have ended much sooner in the absence of subsidies (Sumaila et al., 2010). In view of these developments, Merrett and Haedrich (1997) conclude that “the deep-sea fishery should not be considered a fishery at all. There is a much stronger analogy to a mining operation wherein an ore body is exploited to depletion and then new sources (mines, virgin stocks) are sought” (p. 228).

For many of the target species, recruitment and restoration of populations is a possibility if the level of exploitation is strongly reduced or eliminated, or the exploitation strategy is altered for a number of years, as was the case for Blue ling (Large et al., 2010). On the other hand, several other species have been fished to very low numbers, often in a decade or two. Patterns of depletion are apparent in the Slender armorhead fishery, where the population was reduced to a fraction of its virgin biomass in eight years. Similarly Longfin codling estimated landings were as high as 200,000 t in 1986, and 55,000 t in 1994, and Roundnose grenadier estimated catches were greater than 60,000 t in 2001 but a rapid decline in stocks lead to a moratorium in 2006. We show that considerable fish biomass has been removed from the deep-sea, particularly in certain areas and while we do not understand the consequences of that removal yet, it is likely that the deep-sea ecosystem is being changed. For example, many of these fish species, such as the Greenland halibut, are top-predators within their habitats and removing them could cause trophic cascading as previously seen in cod fisheries (Frank et al., 2005). Others are mid-level predators and their removal may have more subtle consequences related to the removal of biomass that would otherwise recycle in the benthic ecosystem as these fish grow, reproduce and die.

Appendix C

The impact of trawling goes beyond the capture of fish populations since the benthic fauna gets removed from the seabed, thus comprising a large fraction of the bycatch (Anderson and Clark, 2003; Probert et al., 1997). The routine use of trawls in these fisheries results in considerable environmental modification, loss of habitat structure, and reduction of biodiversity, especially on seamounts (Clark et al., 2016). In addition, where these fisheries occur along the continental slope, re-suspended sediments can flow down-slope into deeper waters, covering organisms that would otherwise have been out of the way of the trawl (Pusceddu et al., 2014). In order to obtain 43 % higher catches of deep-sea fish, it is likely that trawling has covered larger areas (even when considering that trawl fisheries often cover the same ground repetitively), resulting in unknown amounts of additional bycatch of benthic species.

Many of the largest bottom-trawled fisheries, such as Orange roughy and Slender armourhead fisheries occur also on topographic highs, such as seamounts and ridges. Their irregular topography offers a mosaic of habitats while influencing local current velocities and often delivering food particles at a slightly higher rate to fauna. These habitats are often heavily populated by suspensions feeders, such as habitat forming deep-sea corals and sponges that have been shown to be hundreds of years old, along with a variety of other species (Duineveld et al., 2004; Koslow et al., 2000; O'Hara et al., 2008, Watling et al., 2011). The deep-sea fish also take advantage of seamounts, where they often aggregate to feed, spawn and live (Clark et al., 2007). These aggregations make ideal candidates for deep-sea fisheries, resulting in deep-sea trawl fisheries targeting the summits and occasionally the sides of seamounts at depths shallower than 2000 m (Clark et al., 2007).

All seamounts where bottom trawling occurred and that have been investigated with remotely operated vehicles (ROVs) or towed cameras show large cleared areas where communities of suspension feeders once lived (Clark et al., 2016; Koslow et al., 2001; Waller et al., 2007; Williams et al., 2010). Despite knowing that these species live for centuries, we do not know what their rate of reproduction and pattern of recruitment is, so we have no certain way of determining how long it will take for the community to recover.

Non-governmental organizations (NGOs) such as the Deep-Sea Conservation Coalition (www.savethehighseas.org/) and Bloom Association (www.bloomassociation.org/) have also argued against deep-sea bottom trawl fisheries because of the damage such fishing does to benthic communities. In Europe, these and other NGOs initiated a campaign to ban bottom trawling in deep water, culminating in legislation in 2016. The legislation is complex, but essentially bans bottom trawling in waters deeper than 800 m (European Parliament and the Council of the European Union, 2016) thus providing some protection to both bottom habitat and non-targeted deep-sea fish species..

Within this context, it is worth considering the economic importance of deep-sea fisheries. Our analysis reveals that deep-sea fisheries focusing on species caught primarily below 400 m contribute a mere ~ 0.5 % to the total global capture fisheries (Table 2). While locally, deep-sea fisheries can be of economic importance, as for example in New Zealand, where in 2009 the Orange roughy fishery was estimated to be worth $282 million, globally their economic importance is trivial.

The impact of management on deep-sea trawling fisheries

Much of the reductions in catches reported, especially after 2000, are due to management measures that have been taken to reduce the possibility of species being over-fished. In some cases, such as with Blue ling, the problem of fishing on spawning aggregations was recognized and protection areas were introduced (Large et al., 2010). However, some of the NE Atlantic spawning aggregations have yet to recover and remain closed to date (ICES, 2017). In other cases, landings have been restricted as catch numbers declined e.g., for the NE Atlantic, see ICES-WGDEEP (2017) (see also, Villasante et al., 2012). Sometimes these management measures might have come too late. In the NE Atlantic, for example, Roundnose grenadier landings were always much below the TAC set for them (ICES-WGDEEP, 2017, p. 374). Similarly, the allowable catch numbers for Orange roughy in the NE Atlantic have been set at zero for several years and the MSY at roughly 30% of virgin biomass in the SW Pacific (Francis and Clark, 2005). For most deep-sea fisheries, the lack of biological information combined with assumptions from shallow fisheries prevents them from being suitably regulated from the start. Combining this, with the much higher catches documented here and hence not officially accounted for, has led to regulations that might not have been strict enough to allow recovery, particularly in mixed-trawl fisheries. For fisheries, such as the Greenland halibut concerns of depletion led to a reduction of quota which in turn caused high discards between from 1992 onwards. Some nations have enforced discard bans, but Iceland among others has a record of discarding Beaked redfish, potentially because vessels are not able to acquire quota within the transferable quota system or the fish are undersized. The diversification of target species through time reveals that the indiscriminate nature of deep-sea trawling creates a market for new target species as the stocks of the previous species decline and/or become more tightly regulated. Finally, there is the problem, of managing trawling in the high seas, that is, in areas of the ocean beyond any national jurisdiction. In 2006 an estimated 285 vessels were involved in high seas trawling, with the fisheries often occurring on isolated topographic structures, such as seamounts and ridges (Bensch et al., 2009). Management of fisheries and habitats in these waters has been proposed through United Nations General Assembly (UNGA) Resolutions. These call for the formation of Regional Fisheries Management Organizations (RFMOs) who are responsible for setting allowable catches of species under their jurisdiction and for limiting damage to Vulnerable Marine Ecosystems (VME). The latter are defined on the basis of “indicator species” agreed to by all nations and listed in various FAO documents such as Thompson et al. (2016). As seamounts have extensive coverage of VME indicator species and are often trawled leading to high degree of environmental damage, Watling and Auster (2017) have proposed that seamounts as a whole should be considered as Vulnerable Marine Ecosystems. This would warrant seamounts a stronger set of protections as laid out by UNGA Resolutions (Bensch et al., 2009; Rogers and Gianni, 2010) and potentially also limit or eliminate catches of seamount-associated fish species, thus limiting the associated environmental damage.

Conclusion

This study describes historical patterns in catches of deep-sea trawling fisheries since 1950 to 2015 by comparing and complementing the FAO landings data with reconstructed unreported landings and discards. The catches were shown to be underestimated by 43% with both unreported landings and discarding contributing equally to the discrepancy between the data sets. The major fisheries for this period include the Greenland halibut fishery in the North Atlantic, the Longfin codling in the NW Pacific and the Orange roughy in the SW Pacific. The reconstructed catches also suggest high discarding of Greenland halibut, Beaked redfish, Roundnose grenadier and the grouping Grenadiers *nei*. The new catch estimates suggest that much more biomass, encompassing both fish and habitat-forming species, has been removed from the deep-sea, altering this ecosystem in ways that have yet to be understood. Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author Contributions

LW and CN conceived the study. LV, LW and MP analyzed and interpreted the data. LV prepared the figures. LV and LW prepared the animation. LV and LW drafted the text and all authors revised and approved the final version of the manuscript.

Acknowledgements

We would like acknowledge our many colleagues who have discussed this topic with us over the years, especially M. Gianni and D. Curry, and D. Pauly for establishing and maintaining the Sea Around Us Project. A. Orlov helped us understand details of the Russian fishery data for the NW Pacific. We would also like to acknowledge M. Clark and T. Morato for their help with the compilation of the deep-sea fish species list. All data used within this study is available within the supplementary material.

Funding

The participation in this project of LV was enabled by a grant from National Environmental Research Council in the form of a SPITFIRE Doctoral Training Partnership (grant number NE/L002531/1) with the University of Hawaii.

Supplementary Material

The Supplementary Material for this article can be found online at:
https://www.frontiersin.org/articles/10.3389/fmars.2018.00098/full

Tables

Table 1. List of species taken primarily by bottom trawls at depths greater than 400 m and for which there is data in the FAO FishStat J landings database (a). Also included are species whose trawl fisheries are primarily between 200-400 m (b). Not included are species taken largely or exclusively by long lines.

Common name	Scientific name
a) > 400 m depth	
Antarctic toothfish	*Dissostichus mawsoni*
Arctic skate	*Amblyraja hyperborea*
Baird's slickhead	*Alepocephalus bairdii*
Beaked redfish	*Sebastes mentella*
Bigeye grenadier	*Macrourus holotrachys*
Bigspined boarfish	*Pentaceros decacanthus*
Birdbeak dogfish	*Deania calcea*
Black cardinal fish	*Epigonus telescopus*
Black dogfish	*Centroscyllium fabricii*
Black oreo	*Allocyttus niger*
Black scabbardfish	*Aphanopus carbo*
Blackbelly rosefish	*Helicolenus dactylopterus*
Blackmouth catshark	*Galeus melastomus*
Blue antimora	*Antimora rostrata*
Blue ling	*Molva dypterigia*
Bluntnose sixgill shark	*Hexanchus griseus*
Chimaeras, etc. *nei*	Chimaeriformes
Common Atlantic grenadier	*Nezumia aequalis*
Common mora	*Mora moro*
Deep-sea smelt	*Glossanodon semifasciatus*
Dogtooth grenadier	*Cynomacrurus piriei*
Great lanternshark	*Etmopterus princeps*

Greater argentine	*Argentina silus*
Greenland halibut	*Rheinhardtius hippoglossoides*
Greenland shark	*Somniosus microcephalus*
Grenadier cod	*Tripterophycis gilchristi*
Grenadiers *nei*	Macrouridae
Gulper shark	*Centrophorus granulosus*
Kamchatka flounder	*Atheresthes evermanni*
King dory	*Cyttus traversi*
Kitefin shark	*Dalatias licha*
Knifetooth dogfish	*Scymnodon ringens*
Leafscale gulper shark	*Centrophorus squamosus*
Little sleeper shark	*Somniosus rostratus*
Longfin codling	*Laemonema longipes*
Longnose velvet dogfish	*Centroscymnus crepidater*
Lowfin gulper shark	*Centrophorus lusitanicus*
Mediterranean slimehead	*Hoplostethus mediterraneus*
Mouse catshark	*Galeus murinus*
Northern wolffish	*Anarhichas denticulatus*
Norway redfish	*Sebastes viviparus*
Norwegian skate	*Dipturus nidarosiensis*
Orange roughy	*Hoplostethus atlanticus*
Pacific sleeper shark	*Somniosus pacificus*
Patagonian toothfish	*Dissostichus eleginoides*
Pelagic armourhead	*Pseudopentaceros richardsoni*
Portuguese dogfish	*Centroscymnus coelolepis*
Rabbit fish	*Chimaera monstrosa*
Ridge scaled rattail	*Macrourus carinatus*
Roughhead grenadier	*Marcrourus berglax*
Roughsnout grenadier	*Trachyrincus scabrus*

Round ray	*Rajella fyllae*
Roundnose grenadier	*Coryphaenoides rupestris*
Sailfin roughshark	*Oxynotus paradoxus*
Shortspine African angler	*Lophius vaillanti*
Silvery John dory	*Zenopsis conchifer*
Slender armorhead	*Pseudopentaceros wheeleri*
Slickheads *nei*	Alepcephalidae
Slimeheads *nei*	Trachichthyidae
Smooth oreo dory	*Pseudocyttus maculatus*
Spiky oreo	*Neocyttus rhomboidalis*
Spiny scorpionfish	*Trachyscorpia cristulata*
Splendid alfonsino	*Beryx splendens*
Straightnose rabbitfish	*Rhinochimaera atlantica*
Thorntooth grenadier	*Lepidorhynchus denticulatus*
Velvet belly	*Etmopterus spinax*
Whitson's grenadier	*Macrourus whitsoni*

b) 200 - 400 m depth

Alfonsino	*Beryx decadactylus*
Alfonsinos	Berycidae
Angler	*Lophius piscatorius*
Anglerfishes *nei*	Lophiidae
Benguela hake	*Merluccius polli*
blackbellied angler	*Lophius budegassa*
Blackspot(=red) seabream	*Pagellus bogaraveo*
Blue grenadier	*Macruronus novaezelandiae*
Bluenose warehou	*Hyperoglyphe antarctica*
Boarfish	*Capros aper*
Boarfishes *nei*	Caproidae
Cape bonnetmouth	*Emmelichthys nitidus*
Capro dory	*Capromimus abbreviatus*
Catsharks, nursehounds *nei*	*Scyliorhinus spp.*

Chilean grenadier	*Coelorinchus chilensis*
Deep-water cape hake	*Merluccius paradoxus*
Dories *nei*	Zeidae
Eaton's skate	*Bathyraja eatonii*
Golden redfish	*Sebastes norvegicus*
Greater forkbeard	*Phycis blennoides*
Hapuku wreckfish	*Polyprion oxygeneios*
Ling	*Molva molva*
Longnose spurdog	*Squalus blainville*
Megrim	*Lepidorhombus whiffiagonis*
Monkfishes *nei*	Lophiidae
Offshore silver hake	*Merluccius albidus*
Patagonian grenadier	*Macruronus magellanicus*
Pink cusk-eel	*Genypterus blacodes*
Rubyfish	*Plagiogeneion rubiginosum*
Sandpaper fish	*Paratrachichthys trailli*
Shallow-water cape hake	*Merluccius capensis*
Shortspine thornyhead	*Sebastolobus alascanus*
Skilfish	*Erilepis zonifer*
Splitnose rockfish	*Sebastes diploproa*
Spotted wolffish	*Anarhichas minor*
Thorntooth grenadier	*Lepidorhynchus denticulatus*
Wreckfish	*Polyprion americanus*

Appendix C

Table 2. Total reported (FAO data) and total estimated (FAO + SAUP) catch (tonnes) for the period of 1950-2015 showing a) the contribution of deep-sea bottom trawl fisheries to global landings, b) a breakdown of total deep-sea (>400 m) fish landings by FAO fishing region.

a)	Reported	Total Estimated
Global fisheries catch	3,916,784,240	5,183,437,078
Deep-sea bottom trawl catch	14,397,146	24,905,883
Portion of global catch	< 0.4 %	< 0.5 %

b) Fishing Region	FAO	*Sea Around Us*
Atlantic, Northeast	5,714,858	8,862,807
Pacific, Northwest	1,810,983	5,639,395
Pacific, Southwest	1,575,128	4,281,410
Atlantic, Northwest	3,365,650	3,749,962
Atlantic, Southwest	558,596	586,350
Indian Ocean, Antarctic	261,666	359,503
Pacific, Northeast	263,759	308,787
Pacific, Southeast	264,929	287,715
Mediterranean and Black Sea	103,857	256,111
Atlantic, Southeast	138,663	140,928
Atlantic, Eastern Central	101,561	134,600
Indian Ocean, Eastern	54,740	99,149
Atlantic, Antarctic	96,483	95,223
Pacific, Antarctic	45,792	42,857
Indian Ocean, Western	25,563	36,109
Arctic Sea	12,617	12,617
Pacific, Western Central	0	7,817
Atlantic, Western Central	68	2,368
Pacific, Eastern Central	2,233	2,175

Table 3. A list of deep-sea bottom trawled species, including target and bycatch species caught primarily below 400 m depth, and their reported (from FAO database) and estimated total (FAO data with unreported estimates from the Sea Around Us Project (SAUP)) in tonnes for the period of 1950 – 2015.

Species	FAO	FAO + SAUP
Greenland halibut	4,887,801	7,639,088
Longfin codling	8,663	3,509,542
Grenadiers	571,055	2,993,797
Orange roughy	1,317,328	1,815,861
Beaked redfish	1,399,585	1,679,056
Roundnose grenadier	999,020	1,354,031
Patagonian toothfish	901,591	1,034,946
Kamchatka flounder	547,459	716,491
Slender armorhead	610,331	671,361
Blue ling	538,905	549,388
Black dogfish	444,243	492,497
Blackbelly rosefish	363,261	408,816
Longnose velvet dogfish	328,619	328,667
Black scabbardfish	223,544	224,984
Antarctic toothfish	158,671	163,280
Velvet belly	128,951	157,963
Chimaeras, etc. *nei*	1,876	132,195
Smooth oreo dory	123,130	123,130
Common mora	90,164	97,586
Northern wolffish	85,850	92,161
Ridge scaled rattail	79,750	84,724
Splendid alfonsino	2,052	83,866
Black cardinal fish	59,970	78,113
Portuguese dogfish	42,655	75,975
Thorntooth grenadier	71,523	71,523
Roughhead grenadier	63,673	64,136

Deep-sea smelt	1,339	56,271
Greater argentine	49,677	54,905
Black oreo	54,315	54,315
Blackmouth catshark	7,552	53,750
Slimeheads *nei*	22,466	47,131
Ghost shark	NA	44,363
Little sleeper shark	42,500	42,500.
Leafscale gulper shark	33,686	34,367
Baird's slickhead	29,160	29,773
Kitefin shark	15,534	20,992
Gulper shark	16,275	20,348
Rabbit fish	4,244	18,599
Mediterranean slimehead	158	17,672
Greenland shark	3,289	13,513
Bluntnose sixgill shark	452	10,867
King dory	7,591	9,362
Longnose spurdog	7,612	8,632
Norway redfish	6,113	7,226
Knifetooth dogfish	6,298	6,372
Pelagic armourhead	5,812	5,941
Silvery John dory	5,243	5,243
Spiny scorpionfish	5,143	5,143
Common Atlantic grenadier	38	4,937
Mouse catshark	4,700	4,700
Birdbeak dogfish	3,271	4,536
Blue antimora	2,163	4,498
Lowfin gulper shark	2,995	3,526
Spiky oreo	2,732	2,929
Blunt scalyhead	1,690	1,690
Roughsnout grenadier	1,487	1,517
Whitson’s grenadier	1,445	1,445

Round ray	463	463
Shortspine African angler	454	454
Giant boarfish	356	356
Slickheads *nei*	334	334
Arctic skate	223	223
Grenadier cod	143	168
Splitnose rockfish	149	149
Norwegian skate	57	143
Sailfin roughshark	139	139
Bigeye grenadier	73	73
Bigspined boarfish	45	52
Pacific sleeper shark	36	36
Great lanternshark	20	20
Straightnose rabbitfish	3	3
Dogtooth grenadier	1	1

Figures

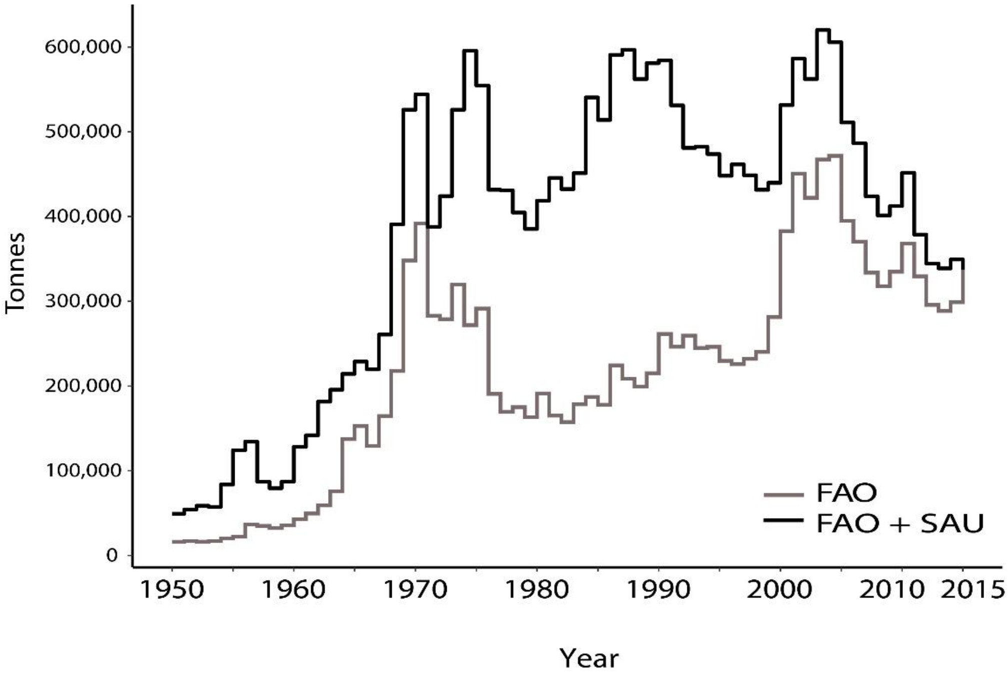

Figure 1. Total landings of deep-sea (>400 m) bottom trawled species by the FAO and *Sea Around Us* data series for the period of 1950 – 2015.

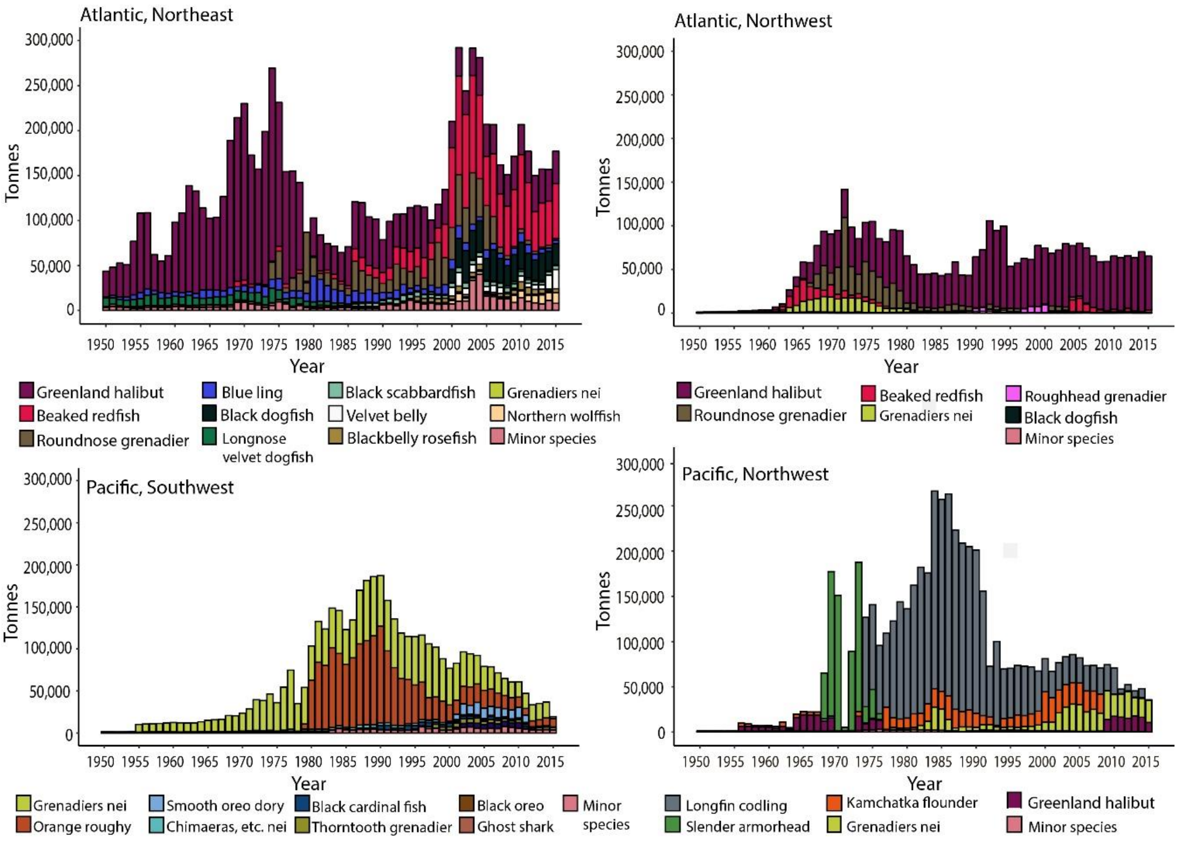

Figure 2. Estimated total landings (*Sea Around Us* data) of deep-sea fish caught primarily at depths >400 m for the major fishing regions showing species targeted. a) Northeast Atlantic, b) Northwest Atlantic, c) Southwest Pacific and d) Northwest Pacific. Species under the Minor species category include those contributing less than 1% to the total landings of a region.

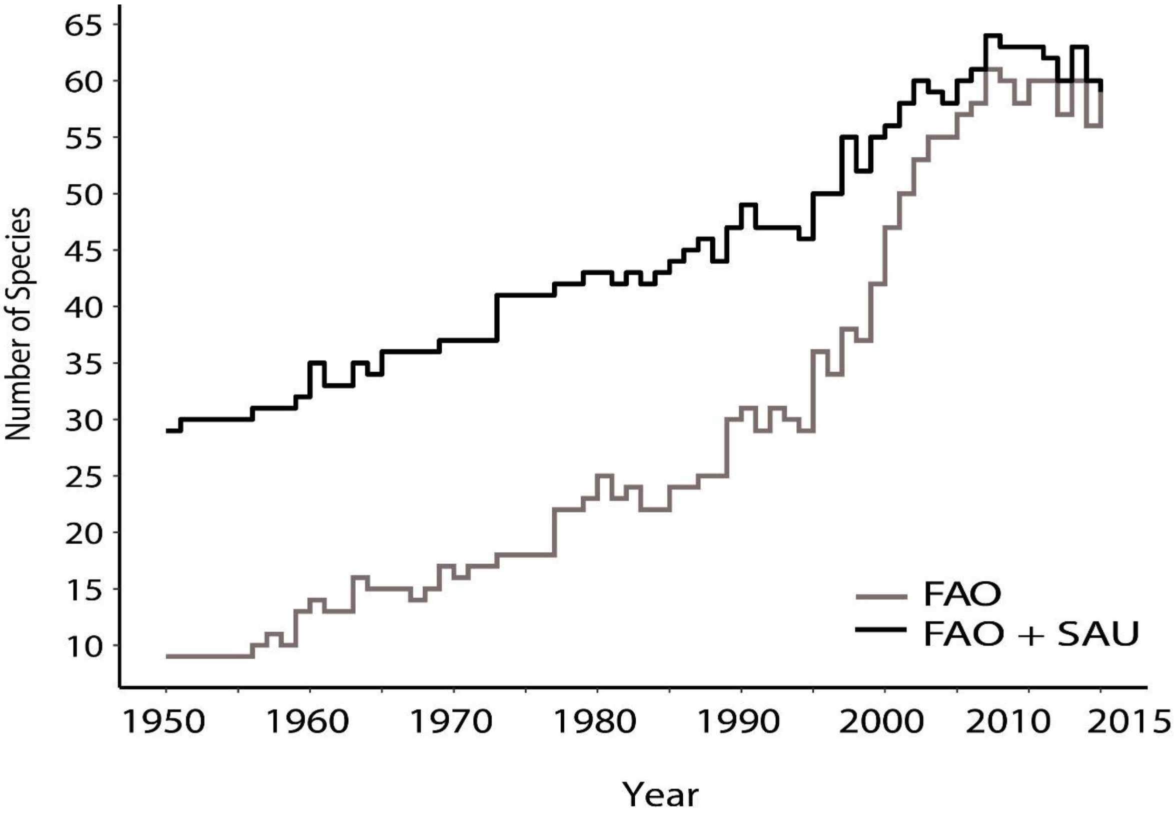

Figure 3. Number of deep-sea species primarily caught at depths > 400 m by bottom trawling each year in the FAO and *Sea Around Us* data series for the period 1950 – 2015.

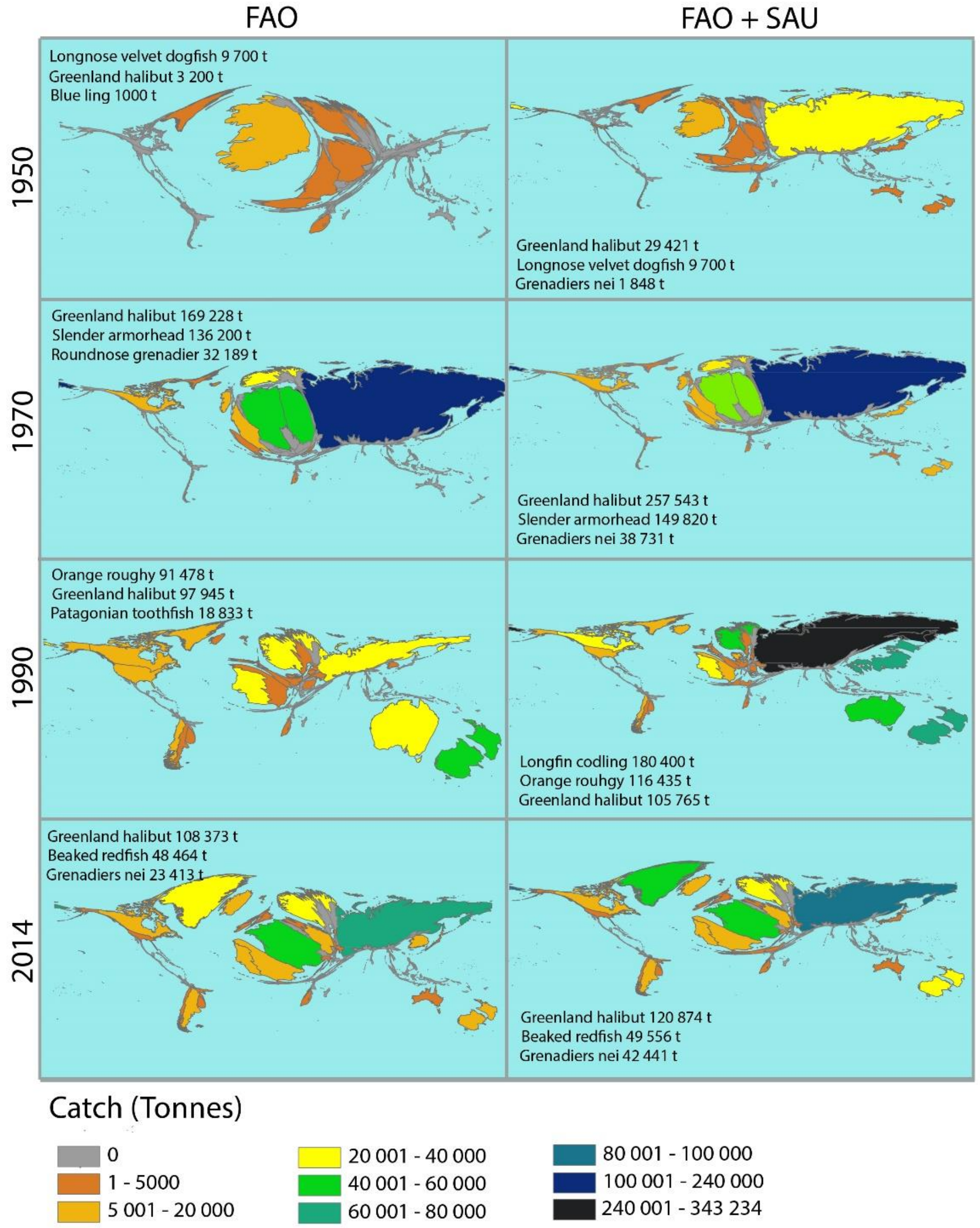

Figure 4. Selected cartograms illustrating the changing patterns of deep-sea (primarily >400 m) trawled fish catch by country for the years 1950, 1970, 1990, and 2014. Maps are based on FAO and FAO + SAUP (Sea Around Us) catch data. The size of the country reflects the reported catch (tonnes) of deep-sea bottom-trawled species. Each country is also color-coded according to range of catch data. The species within the figure represent the top three species with catches in tonnes. A full set of cartograms for the period 1950-2015 is included as an animation in the supplementary material.

Appendix C

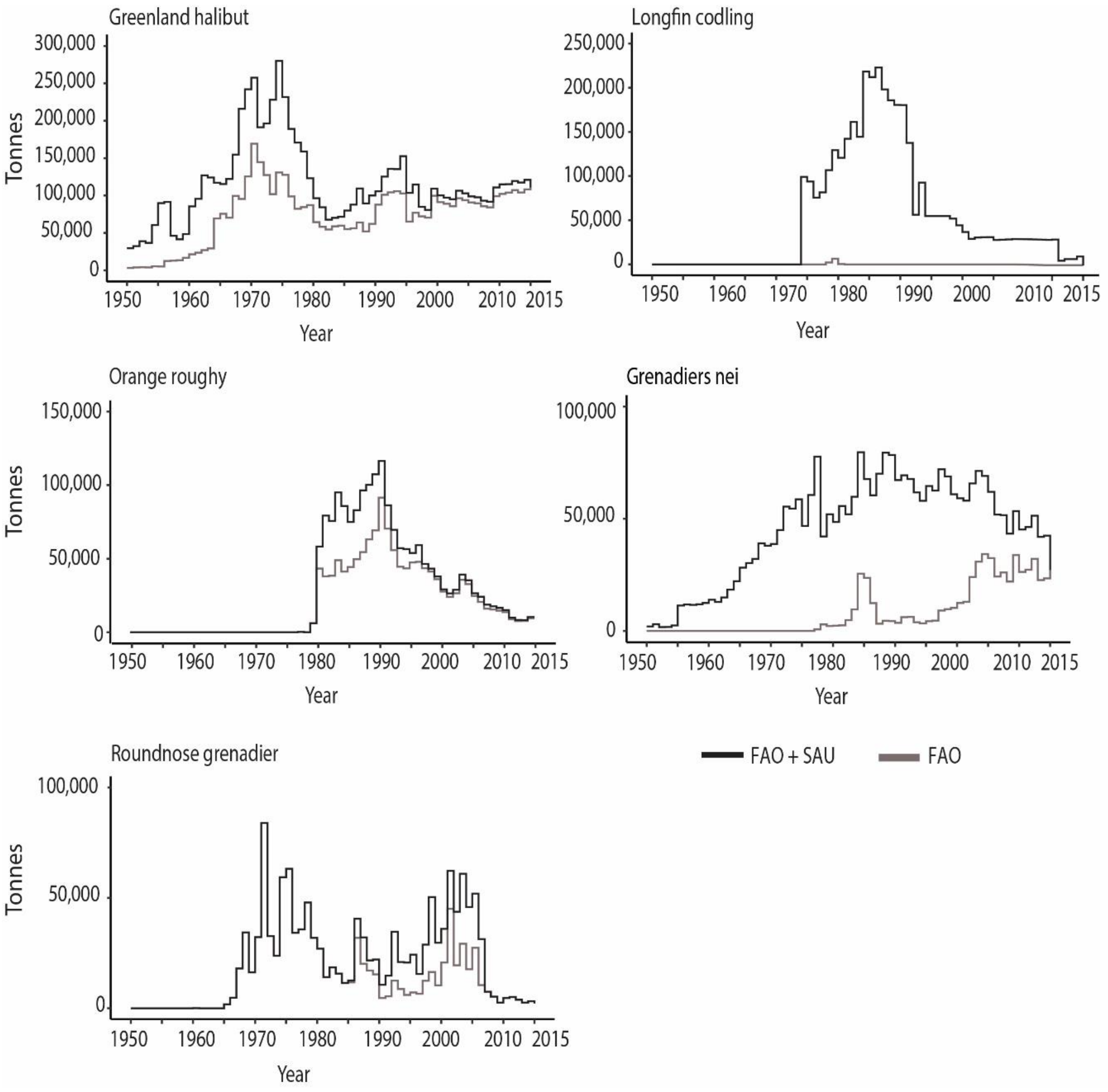

Figure 5. Landings from some of the most abundantly caught deep-sea (>400 m) bottom-trawled species between 1950 – 2015, which show strong discrepancies between reported (FAO) and estimated total (*Sea Around Us*) reconstructed catch data.

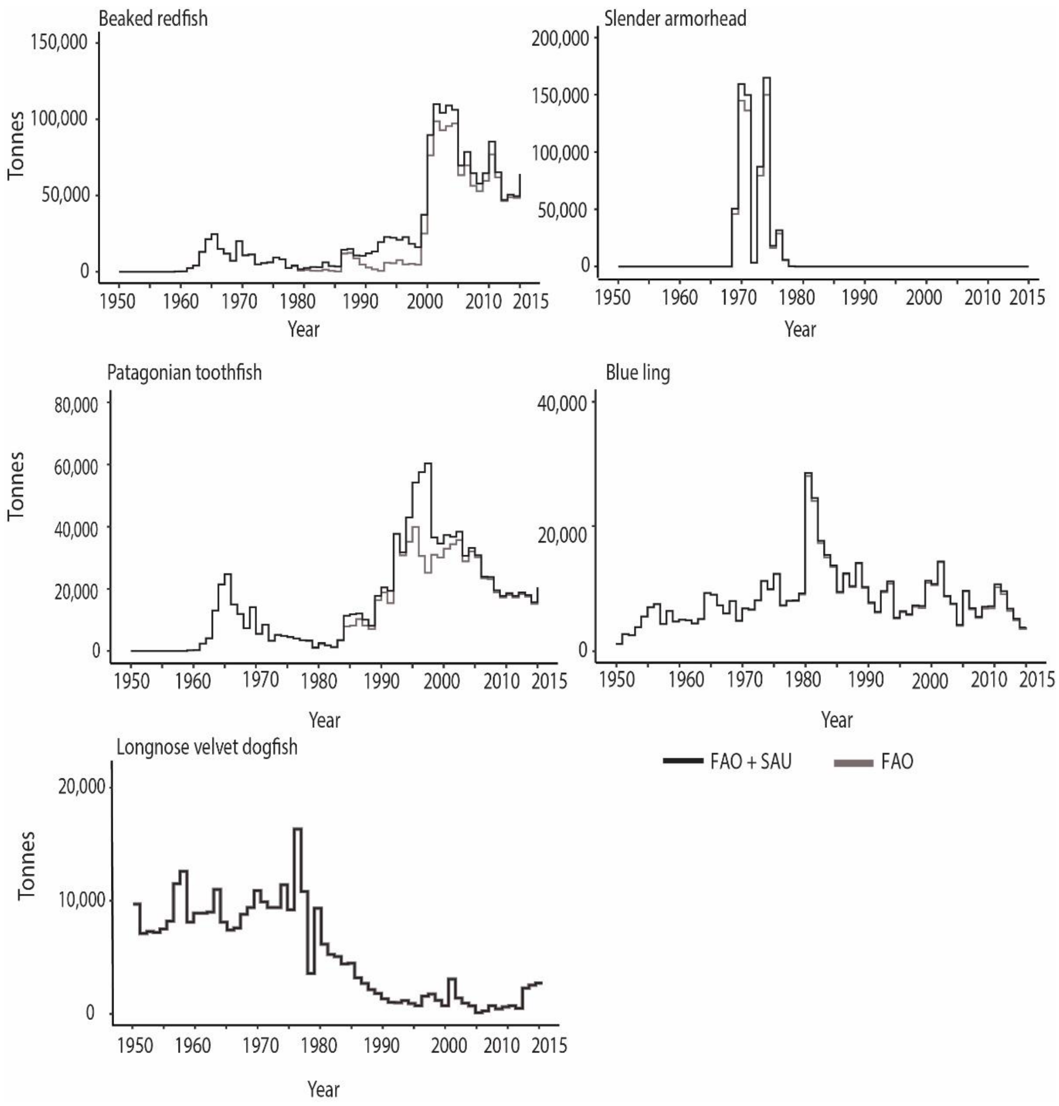

Figure 6. The landings for some of the most captured deep-sea (>400 m) bottom trawled species between 1950 – 2015, which have nearly similar reported landings (FAO) and estimated total (*Sea Around Us*) reconstructed catch data.

Glossary of Terms

Abbreviation	**Description**
AABW	Antarctic Bottom Water
AAIW	Antarctic Intermediate Water
ANOSIM	Analysis of Similarity
APEI	Areas of Particular Environmental Interest
CTD	Conductivity, temperature and depth
dbRDA	Distance-based redundancy analysis
EA	East Atlantic
EMP	Environmental Plans
FZ	Fracture Zone
GAM	Generalized Additive Models
ISA	International Seabed Authority
LCBD	Local Contribution to Beta Diversity
MAR	Mid-Atlantic Ridge
MOR	Mid-Ocean Ridge
NADW	North-Atlantic Deep Water
NE Pacific	North-East Pacific
NEC	North Equatorial Current
OFOP	Ocean Floor Observation Protocol
PCoA	Principal Coordinates Analysis
POC	Particulate Organic Carbon
ROV	Remotely Operated Vehicle
SACW	South–Atlantic Central Water
SCBD	Species Contribution to Beta Diversity
SIMPER	Similarity Percentage Analysis

Glossary of Terms

SMS	Seafloor Massive Sulphides
SW Pacific	South-West Pacific
TPI	Topographic Position Index
VIF	Variance Inflation Factors
VMEs	Vulnerable Marine Ecosystems

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