Exploring Hidden Reefs: A Study of Seamount Benthic Diversity Along the South-west Indian Ocean Ridge

by

Celia Hanna

Wolfson College



University of Oxford

Department of Biology

A thesis submitted for the degree of MSc by Research

April 2024

Declaration of authorship

I declare that the work presented in this thesis is my own, conducted under the supervision of Dr Gwilym Rowlands (University of Oxford) and co-supervision of Dr Michelle Taylor (University of Essex). I designed the studies, analysed the data, and wrote the chapters. Video data from which community data was extracted was collected during the RSS *James Cook* 066 NERC research cruise November 7th - December 21st, 2011 (Rogers & Taylor 2012).

This thesis is submitted in fulfilment of the requirements for the degree of Masters by Research at the University of Oxford. No part of this thesis has or is being submitted for any other qualification at this university or any other university.

Celia Hanna

Student no. 2355109
April 2024

Acknowledgements

First and foremost, I would like to acknowledge my supervisor, Dr Gwilym Rowlands, and my co-supervisor Dr Michelle Taylor for their help and guidance throughout this project. I thank them for their belief in me, especially throughout the early phases of the project when I didn't know where to start with this dataset. Without Dr Taylor’s expertise in deep sea taxonomy, making this dataset would not have been possible. I would also like to express sincere gratitude to The Fishmongers' Company who generously funded this work.

Thank you to the members of the Taylor Lab who, though remote, provided a source of community and support to me, providing valuable feedback on ideas and presentations. I thank Dr Amy Sing Wong for assisting me with ideas for community analyses in R. I thank Sumali Bajaj, Dr Chris Terry and Dr Talya Hackett in Oxford who all shared their expertise on statistical approaches.

I would like to acknowledge all those involved in organising and conducting the NERC funded *RRS James Cook* Cruise, 2011. The video footage collected during this expedition enabled me to build a community dataset to analyse. The challenges associated with running scientific expeditions to such remote deep-sea locations are immense, and I greatly appreciate these efforts.

On a personal note, I would like to express appreciation to my family for their love and support throughout the past 2 years. Thank you to my partner, Csabi, who has been a source of joy, comfort, and laughter to me even on the most stressful of days. I would also like to thank my dear friend, Shreya, who has offered incredible support to me throughout difficult times during my postgraduate experience. I am forever grateful for the friendship we have shared and the light and humour we have found in times that to me felt so dark.

Table of Contents

Abstract ***6***

An Introduction to Seamounts ***7***

What is a Seamount? **7**

Geological Origin and Global Coverage **8**

Life on Seamounts **9**

Seamount Benthic Communities 12

Seamount Pelagic Communities 14

Anthropogenic Threats to Seamounts **15**

Seamount Fisheries 15

Seamounts as Targets for Deep Sea Mining 19

Other Threats to Seamount Biodiversity 20

Seamount Conservation 21

Measuring Diversity in the Deep Sea **24**

Measuring Alpha Diversity 25

Measuring Beta Diversity 28

Diversity Gradients in the Deep Sea **29**

Bathymetric Diversity Gradients (BDGs) 29

Depth-Diversity Gradients of Seamount Benthic Communities 31

Latitudinal Diversity Gradients (LDGs) 32

LDGs of Seamount Benthic Communities 33

Indian Ocean Seamounts **34**

Study Site: The South-West Indian Ocean Ridge (SWIOR) **35**

Conservation Along the South-west Indian Ocean Ridge 36

Outline of Thesis Chapters ***39***

Chapter 1: Exploring Depth Diversity Gradients of Habitat Building Species on Melville Bank, a Seamount in the South-west Indian Ocean ***40***

Abstract 40

Introduction **40**

Methodology **45**

Study Site 45

Data Collection 46

Environmental Metadata Collation 49

Data Preparation 50

Results **54**

Richness of VME Morphospecies Increases While Their Abundance Decreases with Depth on Melville Bank 54

Community Composition of VME Morphospecies Varies Significantly Between Depth Zones on Melville Bank 57

Significant Adverse Impacts (SAI) from Bottom Contact Fisheries 61

Discussion **62**

Conclusion **68**

Chapter 2: Exploring Latitudinal Diversity Gradients of VME Indicator Species along the South-west Indian Ocean Ridge ***69***

Abstract **69**

Introduction **69**

Methodology **73**
Study Site: The South-west Indian Ocean Ridge 73
Video Collection 75
Benthic Community Data Collection 76
Environmental Metadata Collation 77
Data Processing 79
Statistical Analyses 80

Results **83**
Diversity of VME Morphospecies Varies Significantly between Seamounts 83
Water Mass Characteristics, Depth, and Substrate Drive VME Richness Gradients Along the SWIOR 87
Porifera Diversity Increases With Latitude Across SWIOR Seamounts 90

Discussion **93**

Conclusion **99**

Conclusion Chapter ***100***

Summary of Chapters **100**

Implications for Biodiversity Conservation and Management Along the SWIOR **103**
Addressing Shortfalls in Data Availability along the SWIOR 105
Assessing Impacts of Bottom-contact Fisheries Along SWIOR 106
Identifying Environmental Drivers of VME Diversity along the SWIOR 107

Strengths and Limitations of Work **109**
Data Collection 109
Study Design 110
Limitations of Biological Dataset 111
Lack of Ecological Baselines 111
Limitations of Environmental Dataset 112
Measuring Diversity 112

Future research **113**

Conclusion **114**

Supplementary Materials ***115***

Bibliography ***130***

Abstract

Seamounts are common topographic features in the deep sea which play an important role in supporting ocean life (Rowden et al., 2010). Whilst global estimates predict there could be as many as ~100,000 seamounts worldwide, less than 4% of these have been sampled by science due to the financial and technological challenges associated with deep sea surveys (Kitchingham et al., 2007). Seamount benthic communities constitute Vulnerable Marine Ecosystems (VMEs) in acknowledgement of their functional significance as habitats and their vulnerability to fishing impacts (FAO, 2009). Understanding how the diversity of organisms making up VMEs (VME indicator species) is distributed within individual seamounts and along seamount chains is essential to inform the sustainable management of seamount resources. Seamounts in the Southwest Indian Ocean have been particularly overlooked by science, with little information on their biodiversity available to guide management by fisheries in the region. Work presented in this thesis marks a significant step towards characterising the diversity of VME indicator taxa at different spatial scales within this poorly studied ocean region. Findings indicate that diversity of VME indicator taxa can vary significantly on both local and regional scales. Bottom-contact fisheries reduce seamount VME diversity on a local scale. On a regional scale, diversity is influenced by water mass characteristics and substrate type. Overall, findings highlight the considerable variability in benthic diversity that can exist within seamount chains, which should not be treated as homogenous units by management bodies. Findings also highlight the negative impact of bottom-contact fisheries on diversity gradients even in these remote ocean settings.

An Introduction to Seamounts

What is a Seamount?

Seamounts, also known as undersea mountains, are a common deep-sea habitat found in all ocean basins. They are defined as topographic elevations rising steeply from the seafloor (Fig.1) (Rowden et al., 2010). Whilst geologists originally restricted the term to structures whose summits rose > 1000 metres from the seabed, biologists have adopted a more relaxed size criteria after observations that smaller topographic elevations could also be of ecological significance (Staudigel et al., 2010). The broader 'ecological definition' (Pitcher et al., 2007) therefore encompasses features over or equal to 100 metres from the seabed to include underwater knolls, hills and guyots. Consequently, the term 'seamount' is now used to refer to underwater structures of varied morphologies and depths.

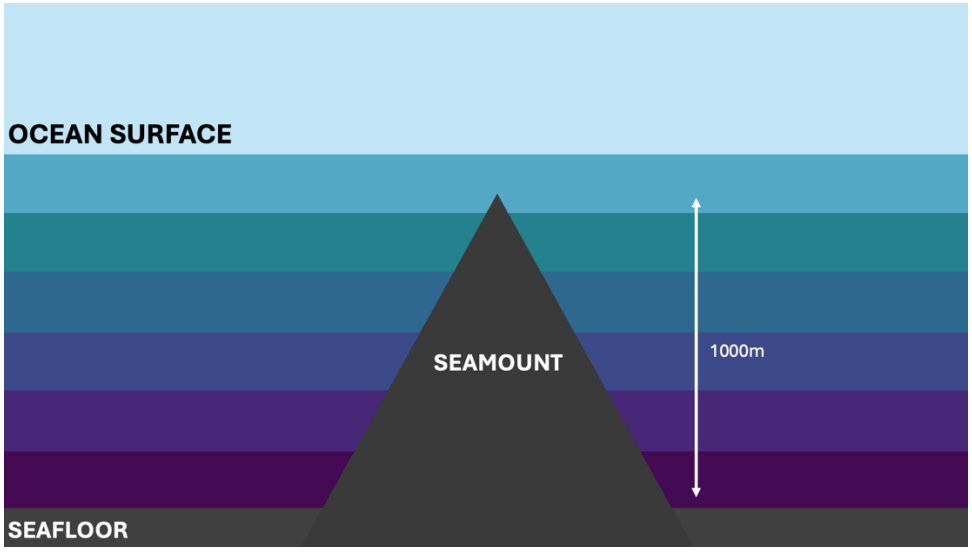


Figure 1. Cartoon illustration of a seamount.

Geological Origin and Global Coverage

Seamounts are most commonly volcanic in origin (Staudigel et al., 2010), formed via the intrusion of magma through oceanic crust. They may occur in isolation or in chains (Schmidt, 1999), and most are formed within a radius of a few hundred kilometres from mid-ocean ridges, intraplate hotspots or island arcs. Estimates of global seamount coverage vary, however advances in remote sensing capabilities are helping to uncover their true global distribution. Estimates from satellite altimeters, which detect small rises in sea surface to predict seamount location (Hillier and Watts, 2007; Yesson et al., 2011) report that there may be 100,000-200,000 seamounts worldwide with an elevation of ≥1000 metres, with a possible ≥25 million possessing an elevation of ≥100 metres (Wessel et al., 2010a). Seamounts thus occupy a significant area of global habitat space; approximately 3% of the globe (Harris et al., 2014). Worldwide, this represents an area of ~10 million km^2, rivalling the area occupied by tropical humid forests, temperate forest or all the world's wetlands (Etnoyer et al., 2010). Whilst seamounts are found in all ocean basins (Fig.2) (Clark et al., 2011; Yesson et al., 2011), the majority are located in the Pacific due to its high concentration of hotspots and volcanic activity that drive seamount formation (Huang et al., 2011).

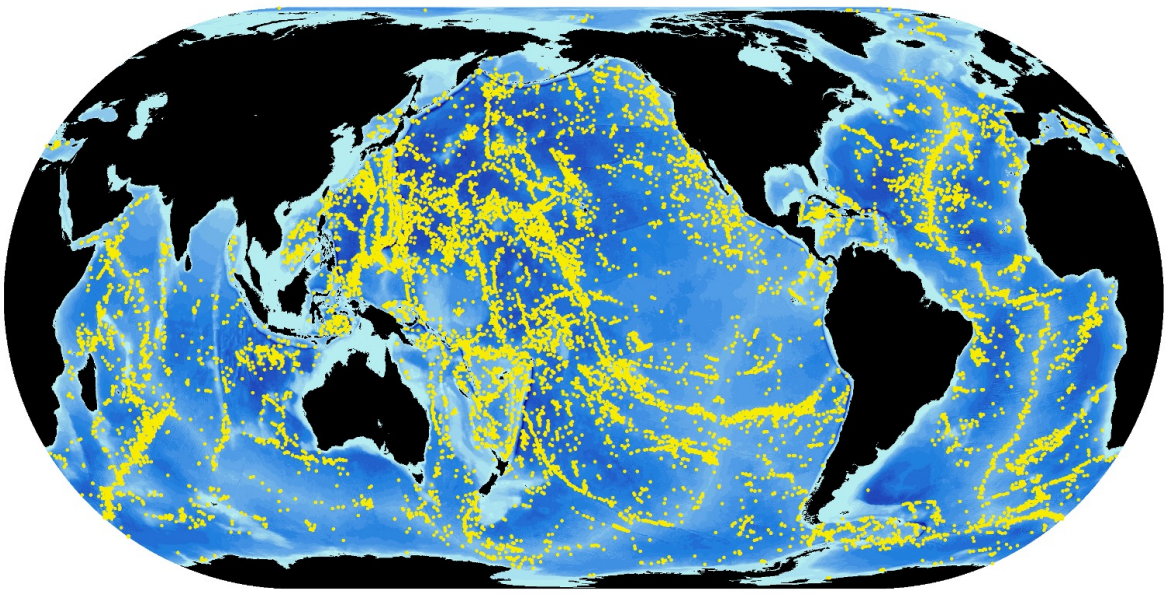


Figure 2. Visualisation of the global distribution of seamounts (Kitchingman and Lai, 2004).

Life on Seamounts

Whilst still only a minority of seamounts in the global ocean have been sampled by science (Clark et al., 2012), knowledge of the role seamounts play in supporting ocean life has made significant progress over the past 25 years (Rogers, 2018). Seamounts are now considered to be major ocean biomes, renowned for hosting diverse and abundant marine fauna compared to surrounding deep sea plains (Clark and Bowden, 2015; Moore et al., 2003; Morato et al., 2010; Richer de Forges et al., 2000; Rowden et al., 2010). Indeed, aggregations of zooplankton, micronekton, fish and large mesopelagic predators are commonly observed in close proximity to seamounts (Genin, 2004; Morato et al., 2010) supported by rich benthic communities beneath (Bridges et al., 2022; Davies et al., 2015). The explanations for observed seamount biodiversity have been attributed to i) the effect of seamount topography on

ocean circulation (Lavelle et al., 2010) and ii) topographic blockage of vertically migrating zooplankton (Genin, 2004).

Seamounts on Ocean Circulation

Seamounts impact ocean circulation at both regional and local scales (Rogers, 2018) (Fig. 3). On a regional scale, they induce current deflection, eddy formation, and energy dissipation. At a more localised level, they contribute to the formation of Taylor columns, tidal amplification, and wave generation. These combined mechanisms result in the upwelling of nutrient-rich deep water, stimulating the growth of phytoplankton and other primary producers within the water column thereby promoting elevated primary productivity (Rogers, 1994). Recent analysis using satellite data has provided evidence of enduring seamount-induced chlorophyll enhancements across seamounts in the western and central Pacific Ocean (Leitner et al., 2020). This finding supports the plausibility of nutrient upwelling effects above seamounts persisting long enough to support increased populations of zooplankton grazers, thus fuelling marine food chains. Notably, the same study revealed that seamounts exhibiting chlorophyll enhancements also demonstrated higher fisheries yields compared to those without such enhancements.

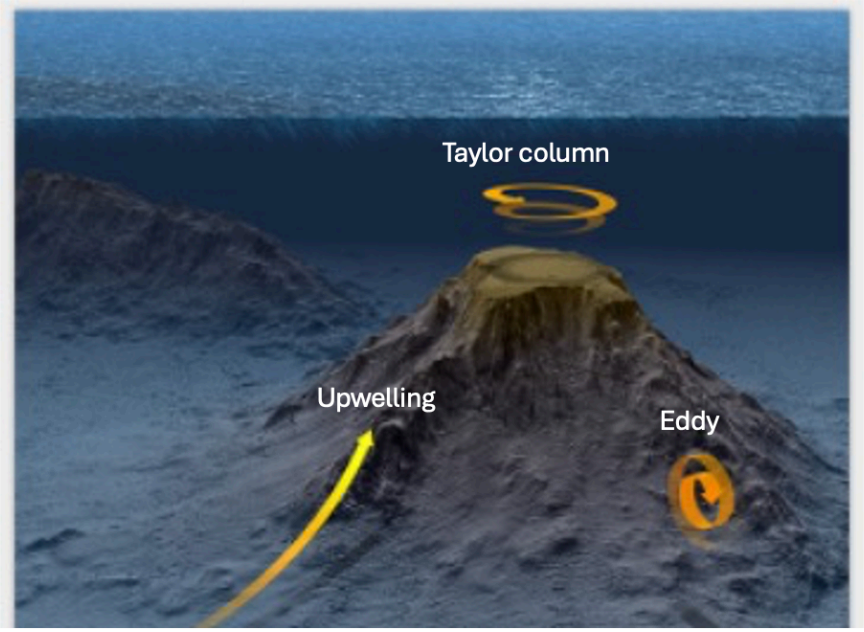


Figure 3. Illustration showing the effect of seamount topography on local currents. Published by National Geographic, artist Stefan Fichtel ixtract GmbH (“Mountains in the Sea,” 2012)

Topographic Blockage of Migrating Zooplankton

Another phenomenon thought to contribute to biodiversity on seamounts is the topographic blockage of zooplankton (Valle-Levinson et al., 2004). During their diurnal ascent and descent, the zooplankton encounter shallow seamount features, which hinder their downward movement (Genin, 2004). This leads to the accumulation of zooplankton on these features, providing abundant feeding opportunities for phytoplankton and thereby enhancing primary productivity. Additionally, the altered water flow around seamounts may change the migration paths of zooplankton, resulting in closed water circulations and their localised trapping. This phenomenon further contributes to the creation of rich feeding grounds for higher trophic levels.

Seamount Benthic Communities

The topographic diversity provided by seamounts, including rocky outcrops and slopes, generates current amplification and provides hard attachment surfaces that favour colonisation of diverse benthic communities (Mello-Rafter et al., 2021; Richer de Forges et al., 2000; Rogers et al., 2007) (Fig. 4). These consist of primarily sessile filter feeders such as cold-water corals (Cnidaria) and sponges (Porifera). Cnidarians often constitute the majority of seamount benthic biomass (Wessel et al., 2010b), with the exception of Arctic seamount benthos which have been found to be largely sponge dominated (Roberts et al., 2018; Stratmann et al., 2022) (Fig. 5d). Corals that occur on seamounts are primarily from the class Anthozoa, and consist of the Scleractinia (stony corals), Antipatharia (black corals) and Zoanthidea (zoanthids) and the Octocorals (sea fans).

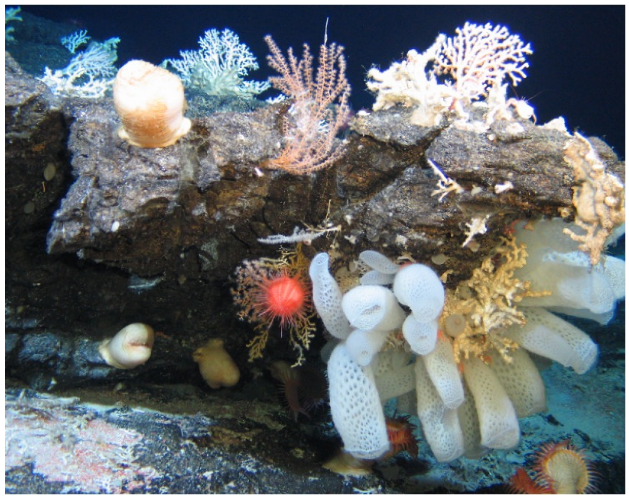


Figure 4. A community of sessile filter feeders attached to rocky outcrop on Atlantis seamount in the South-West Indian ocean (Rogers and Taylor, 2012).

Oftentimes, a single species of stony coral dominates large areas as thickets (Fig. 5a,b) forming complex structural habitat for smaller invertebrates (crinoids, ascidians,

molluscs and cirripeds) (Anderson et al., 2016), and serving as an anchor point for other sessile fauna in the absence of hard substrate (Rogers, 1994; Rowden et al., 2010; Rueda et al., 2019; Samadi et al., 2006). These reef frameworks have been observed to host a range of other suspension feeders within their calcium carbonate matrix, including crinoids, sponges, ophiuroids and antipatharians, making these benthic organisms an essential ecosystem component (Buhl-Mortensen and Mortensen, 2004). Octocoral gardens comprising various species of sea fans have also been observed on seamounts (Fig. 5c).

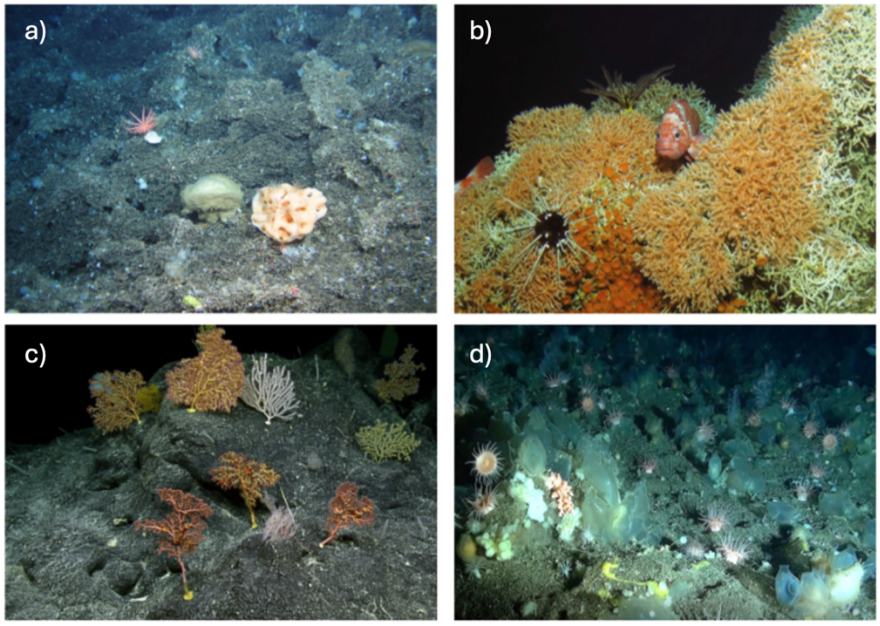


Figure 5. Examples of benthic communities found on seamounts. a) Scleractinian reef matrix on Coral seamount in the Southwest Indian Ocean (Rogers and Taylor, 2012) b) Scleractinian reef matrix on Colahan seamount, north Pacific (Baco et al., 2020) c) Octocoral garden on a north Pacific seamount (Kennedy, 2016) d) Sponge assemblage on Shultz seamount in the Arctic ocean basin (Roberts et al., 2018)

Seamount Pelagic Communities

Since the 1800s, seamounts have been associated with large aggregations of demersal and benthopelagic fish (Boehlert, 1988; Koslow, 1996; Richer de Forges et al., 2000), notably the orange roughy (*Hoplostethus atlanticus),* pelagic armourhead *(Pseudopentaceros wheeleri)* and alfonsinos *(Beryx spp)*. In fact, it was these congregations of commercially important fish stocks that first indicated the existence of seamounts to humans. A total of 800 seamount-associated fish species have been recorded (Watson and Morato, 2004), attracted by high plankton biomass above seamounts which provides increased feeding opportunities compared to other ocean areas (Genin and Dower, 2007). Planktivorous fish in turn attract higher order predators, such as sharks, rays, cephalopods, tuna and swordfish (Morato et al., 2010). Furthermore, several species appear to use seamounts as spawning (Sala et al., 2003; Tsukamoto et al., 2003) and nursery sites (Hunt et al., 2011; Patel, 2023) (Fig. 6) likely due to the protection provided by their varied topography.

Seamounts appear to attract abundant and diverse mesopelagic predators across large geographic scales, including seabirds (Haney et al., 1995), cetaceans (Dede et al., 2022; Garrigue et al., 2015), sharks (Barnett et al., 2012) and pinnipeds (Maxwell, 2011) underscoring their importance in the otherwise food-sparse environment of the deep ocean. Their distinct magnetic features may also act as navigational waypoints in migrations, which may be the case for some sharks (Klimley et al., 1988), tunas (Holland et al., 1999) and other large pelagic predators (Sedberry and Loefer, 2001).

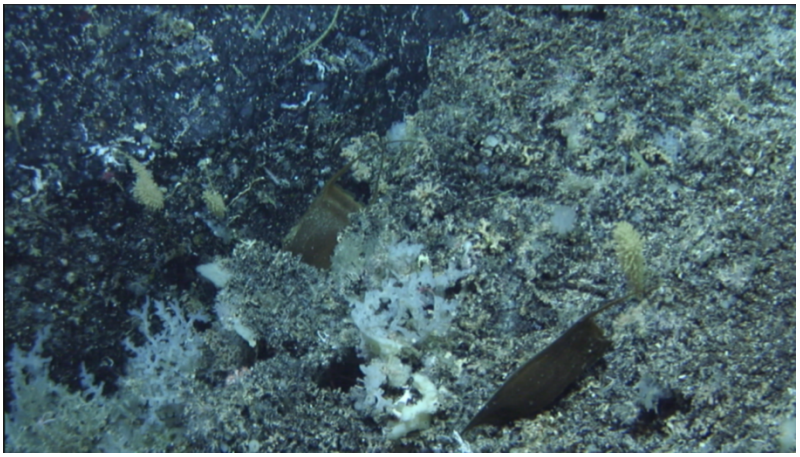


Figure 6. Shark eggs protected within Scleractinian reef matrix at ~1000m, observed on Coral Seamount, Southwest Indian Ocean Ridge (Rogers and Taylor, 2012).

Anthropogenic Threats to Seamounts

The United Nations has estimated that 60% of the world's major marine ecosystems are either in a degraded state or are unsustainably used (Steiner, 2011) and seamounts are no exception. Their capacity to attract large fish aggregations has led to their exploitation by commercial fisheries (Watson and Morato, 2004), and their rich mineral resources have rendered them future targets of deep-sea mining endeavours (Hein et al., 2010).

Seamount Fisheries

In the late 1960s, an intensive global search for seamount fishery resources was initiated by the former Soviet Union (Pitcher et al., 2007). Offshore trawler fleets systematically searched the Pacific, Atlantic and Indian Oceans for fish stocks. Upon locating large fish aggregations in several regions, commercial fisheries developed with many nations pursuing seamount fisheries. Improvements in deep water trawling

technologies in the 1980s meant that locations of deep-sea features could be accurately identified, and trawling nets strategically placed along the seafloor to maximise catch (Valdemarsen, 2001). Since then, seamount chains around the world (Fig.7) have generated large and highly profitable fish catches (Clark et al., 2007), conservatively estimated to total three million tonnes per year (Pitcher et al., 2010). Of this, a quarter of a million tonnes are caught by small-scale local fisheries, which seamounts also play an important role in supporting (Marques da Silva and Pinho, 2007).

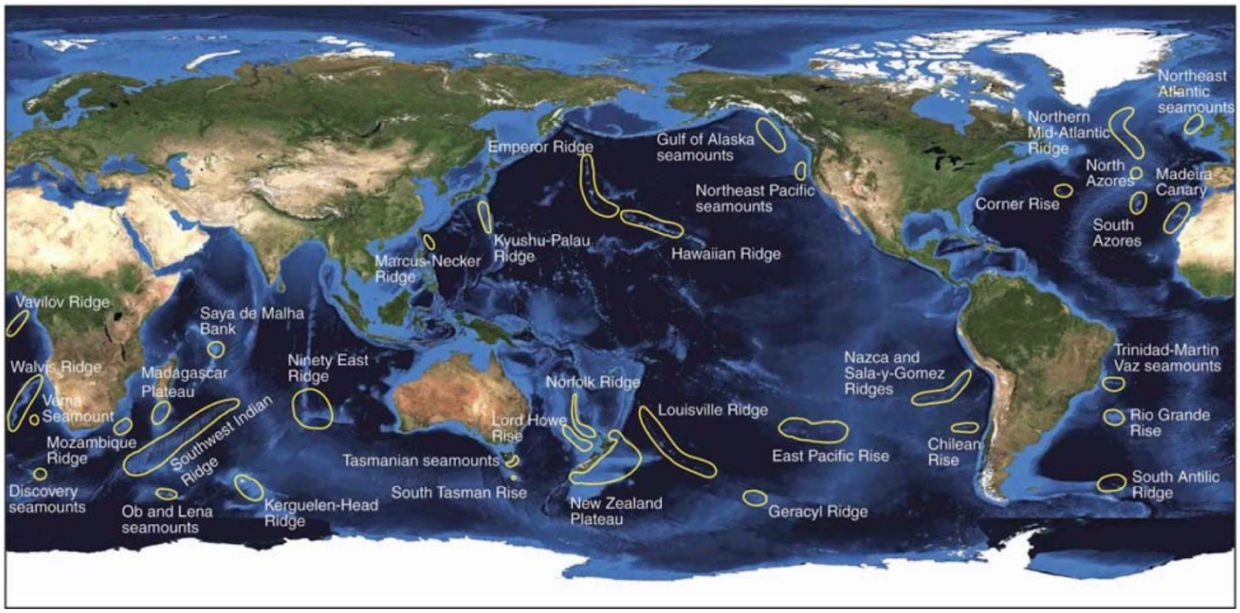


Figure 7. Global distribution of major seamount fishing grounds (Clark et al., 2007)

Seamount fisheries have been unsustainable overall, failing to maintain catch levels over time. Many have exhibited 'boom-and-bust dynamics' whereby catches rise and fall rapidly, sometimes within the space of just a few years (Clark, 2001; Pitcher et al., 2010). This is attributed to the life histories and ecological characteristics of deep sea species, which are long-lived, mature slowly and show low fecundity compared to

traditional commercial species from continental shelf areas (Morato et al., 2006; Pitcher et al., 2007). The orange roughy is commonly referred to as an example (Tracey and Horn, 1999) (Fig.8); it was heavily fished during the 1970s resulting in its populations becoming exhausted after just five to ten years across most fisheries (Clark, 2001).



Figure 8. Orange roughy, pictured on a seamount along the South-west Indian Ocean ridge (Rogers & Taylor 2012).

Seamount benthic fauna are also highly threatened by seamount fisheries (Clark & Koslow 2007, Consalvey et al. 2010, Clark et al. 2015) due to the use of highly destructive fishing gear. Bottom trawl nets used by commercial fishing fleets damage marine benthos through damage and removal of habitat forming species alongside the target catch (Clark & Koslow 2007, Mortensen et al. 2008). In some cases, weight of bycatch procured by trawling operations even exceeds the catch weight of target fish (Anderson & Clark 2003). This bycatch often contains high proportions of stony corals and associated invertebrates (Probert *et al.* 1997). In this way, trawling operations remove not just living fauna (Koslow *et al.* 2001, Hall-Spencer *et al.* 2002) but also accumulated biogenic substratum (Watling & Norse 1998), on which many seamount-dwelling species depend (O'Hara *et al.* 2008, Andrews *et al.* 2002). This

habitat loss is linked to declines in richness, density and diversity of seamount benthic fauna (Althaus *et al.* 2009).

Life history traits of seamount organisms such as slow growth rates, low larval output, limited spatial extent and low recolonisation rates restrict their ability to recover from disturbance caused by trawling events (Andrews et al., 2009; Huvenne et al., 2016; Williams et al., 2020). The seamounts off south Australia, which have been trawled intensively for orange roughy and oreo species, provide a striking example of the destructive consequences bottom trawling can have on seamount benthic diversity (Koslow et al., 2001). On the seamounts most heavily trawled, deep water coral reefs have been reduced to rubble. On New Zealand seamounts, a negative correlation has been shown between coral coverage and intensity of bottom trawling (Clark and O'Driscoll, 2003) with recovery not seen even a decade after trawling events (Williams et al., 2010). This is perhaps unsurprising given that seamount biogenic habitats have taken millennia to reach their current level of complexity (Andrews et al., 2005; Fallon et al., 2014). As such, there are no alternatives that provide the same habitat value and support associated species. That said, evidence from seamounts off Hawaii has shown recovery of some species on a 30 to 40-year time scale (Baco et al., 2019).

There is increasing evidence that marine species are being put under threat of extinction due to direct and indirect threats of fishing (Dulvy et al., 2004; Roberts et al., 1999). This is a particular concern for seamount species, pelagic and benthic,

many of which are believed to be endemic (Samadi et al., 2006). Given that the majority of seamount species are still to be discovered (Schlacher et al., 2010), the full impact of these threats on their populations is yet to be understood.

Seamounts as Targets for Deep Sea Mining

Offshore marine environments have thus far been largely excluded from metal mining due to challenges of accessibility. However, as demand for metal resources increases globally (Elshkaki et al., 2018), interest in seabed mineral resources has risen. As of November 2019, 30 mining exploration licences are active within international waters (Kung et al., 2021). Seamounts have been identified as areas of significant mining potential (Hein et al., 2010) due to their rich mineral sources including seafloor massive sulphides (SMS) and manganese nodules (Ramirez-Llodra et al., 2011). Whilst deep sea mining is yet to commence, its potential consequences on seamount biodiversity are concerning (Weaver et al., 2018). Physical damage to benthos will likely destroy sessile benthic fauna, and resuspended sediments could smother and interfere with their feeding and respiration (Aller, 1989). Noise and light pollution from mining equipment could disrupt the behaviour of deep sea species that rely on signalling through sound and bioluminescence (Drazen et al., 2020; Martini et al., 2019). Discharge of mining waste could introduce toxic chemicals onto the seabed (Miller et al., 2018). With the multitude of potential threats, deep sea mining efforts must proceed with caution to limit harm caused to fragile marine biodiversity that exist at these depths.

Other Threats to Seamount Biodiversity

Trawling and mining pose significant threats to life on seamounts through direct physical disturbance to seamount benthos (Schönke et al., 2022). However, seamount biodiversity is also threatened by the indirect effects of anthropogenic climate change (Ross et al., 2020; Turley et al., 2007). Global changes to ocean chemistry, including rapid deep ocean deoxygenation (Breitburg et al., 2018; Schmidtko et al., 2017), acidification (Gruber et al., 2019) and rising temperatures (Meyssignac et al., 2019; Wijffels et al., 2016) threaten the growth and available habitat ranges of deep sea species (Sweetman et al., 2017). Climate change is also expected to drive changes in ocean currents and upwelling patterns around seamounts, which could be disruptive to nutrient cycling and productivity that support seamount life (Mello-Rafter et al., 2021). Whilst mobile species can relocate in response to these changes (Robinson et al., 2009), this is not an option for the biogenic, sessile organisms that make up seamount benthic fauna, including cold water corals and sponges. Such organisms have adapted over millennia to survive in particular and constant conditions and will likely be unable to adapt to new ocean conditions, and will thus be faced with extinction (Danovaro et al., 2017) as has occurred for past deep-water corals (Remia and Taviani, 2005). For example, seamounts in the Northeast Pacific have lost 15% of their oxygen over the past 60 years (Ross et al., 2020), threatening the survival of their cold water corals.

Despite their remote nature, marine litter has also been found on seamounts (Woodall et al., 2015). Discarded fishing gear has been observed on seamount

habitats in the Indian and Atlantic Oceans, posing a risk to marine life through ghost fishing (Lively and Good, 2019). Internalisation of plastic microfibers by seamount organisms in the South-west Indian ocean has also been shown (Taylor et al., 2016) but their effect on biology of these organisms is yet to be investigated.

Seamount Conservation

To date, seamounts have received little environmental protection (Watling and Auster, 2020). Since most seamounts are located in areas beyond national jurisdiction (ABNJs), fishing activity often goes unregulated (Dunstan et al., 2012). In these areas, it is the Regional Fisheries Management Organizations (RFMOs) which define catch limits for commercial species and oversee fishing activities (Barnes, 2020). Even when regulations exist, their enforcement in such vast and remote locations used by multiple countries is logistically and politically challenging. The recent signing of the High Seas Treaty (Deasy, 2023) represents a pivotal step towards protecting deep sea habitats like seamounts. However, sustainable management of seamounts is hindered by the fact that they are chronically understudied (Clark et al., 2011). Historically, there has been little data gathered pertinent to the effective management of seamounts (Fulton et al., 2007). Inaccurate or false reports of fishing activities (Clark et al., 2007), the inability to relate catches to particular seamounts (Watson et al., 2007) and commercial confidentiality of fishery catch reports all complicate the development of seamount fishery models (Brewin et al., 2007) needed for sustainable management plans. For instance, impacts of fishing activities on seamount biodiversity is hard to establish in the absence of baseline data

describing community assemblages prior to trawling events (Clark and Koslow, 2007; Clarke et al., 2015).

In efforts to close the knowledge gap regarding seamount biodiversity, the Global Census of Marine Life on Seamounts ('CenSeam') 10-year initiative was launched in 2005 (Stocks et al., 2012). This initiative made substantial headway in mapping out seamount biogeography and biodiversity, identifying regions where more sampling was needed, and supporting research evaluating the effects of human activity on seamounts.

In 2006, the UN General Assembly adopted a series of resolutions aimed at protecting areas of high benthic diversity in the deep sea. Resolution 61/105 calls upon RFMOs to identify areas where 'Vulnerable Marine Ecosystems' occur and prevent Significant Adverse Impacts (SAIs) to these sites by fishing activities. Criteria for what constitutes a VME were established by the Food and Agricultural Organisation (FAO) in 2009, and follow 5 key rules relating to their rarity, functional significance and vulnerability (Fig. 9). VMEs include coral reefs, sponge grounds, hydrothermal vents and seamounts, all of which host endemic biodiversity with organisms specialised to live in these environments. VME indicator taxa have been referred to as 'ecosystem engineers' (Kenchington et al., 2013; Lockhart and Hocevar, 2021) and have great influence over macrofaunal assemblages through linking pelagic and benthic food webs (Ashford et al., 2019). Significant Adverse Impacts (SAIs) are defined as those which compromise ecosystem integrity in a way

that i) impairs the ability of populations to replace themselves, ii) degrades long-term productivity of habitats or iii) causes significant loss of species richness. Examples of SAIs on seamounts are shown in Figure 10.

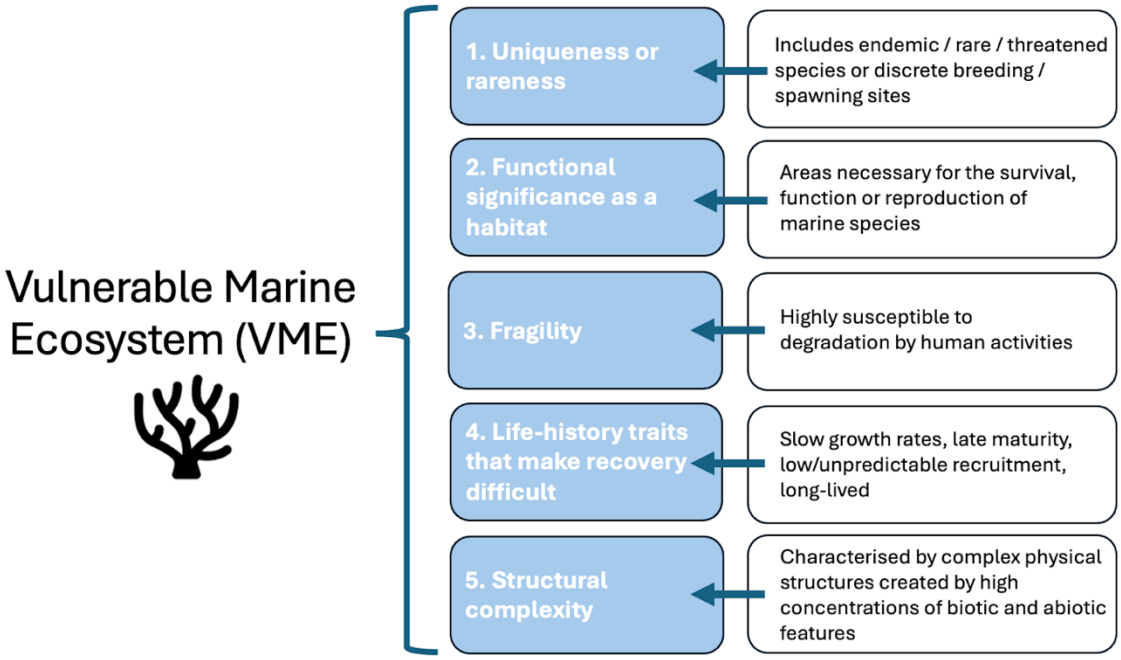


Figure 9. Criteria established by the FAO of what constitutes a Vulnerable Marine Ecosystem (VME) (FAO, 2009).

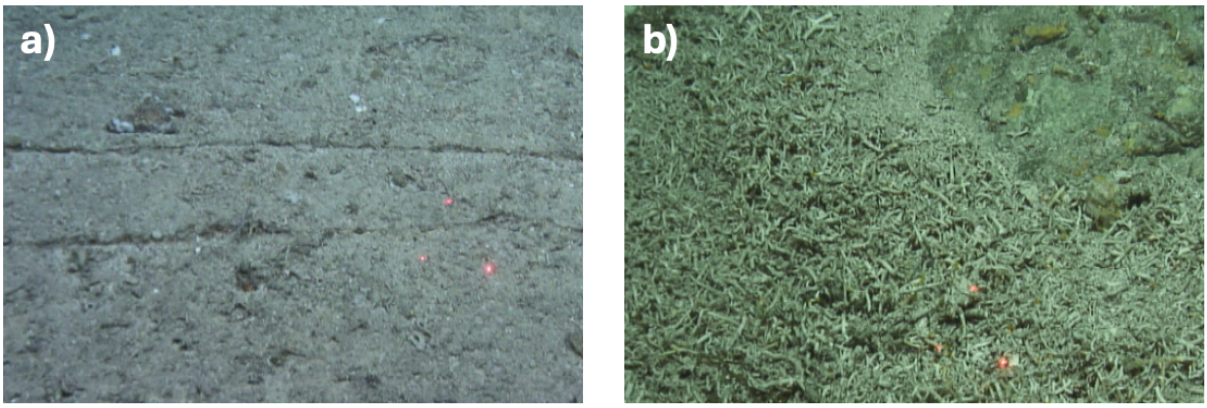


Figure 10. Examples of Significant Adverse Impacts (SAIs) from bottom contact fisheries on seamounts along the South-west Indian Ocean Ridge (Rogers and Taylor, 2012). a) Trawling scars b) Coral rubble.

Measuring Diversity in the Deep Sea

The sustainable management of deep-sea environments requires accurate measurements of their biodiversity its distribution (Powers, 2010). Such information is crucial for the allocation of conservation spaces by identifying and predicting areas of ecological significance (Ferrier, 2002). Observed spatial trends in diversity have led to the establishment of three primary metrics of diversity measurement in ecology; alpha, beta and gamma diversity (Whittaker, 1960), which measure diversity at different scales (Fig. 11). This thesis will focus on measurements of alpha and beta diversity. Alpha diversity refers to diversity found in a given area and is usually expressed as the number of species (species richness) in that area. Beta diversity measures changes in diversity between multiple fixed areas, and gamma refers to the overall diversity for multiple sites within a larger area.

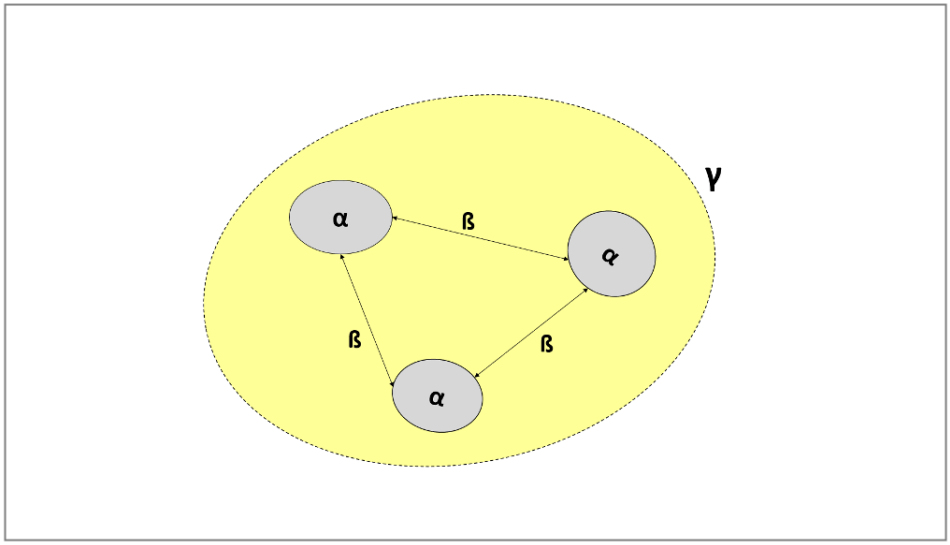


Figure 11: Schematic taken from (Andermann et al., 2022) illustrating established ecological diversity metrics and how they relate to one another.

Measuring Alpha Diversity

Among various metrics, species richness (the number of species) is the simplest and most popular way of measuring alpha diversity of an assemblage (Chao, 2006), and is the metric focused on in this thesis. It is often the most relevant diversity measure in many conservation analyses that use species range maps based on species presence-absence information (Fleishman et al., 2006; Grattarola et al., 2023; Palacio et al., 2021). However, accurate assessment of species richness requires a complete census of species in an area, which is nearly always unattainable due to sampling constraints. Thus, in almost every taxonomic inventory, there are undiscovered species (Bebber et al., 2007; Fisher et al., 2018), and simply counting species number will always underestimate true species richness.

Sampling constraints are particularly pronounced in deep sea settings, which require specialised equipment and substantial research budgets to survey (Howell et al., 2020). Species richness must therefore be inferred from available deep sea species inventories. There are two common approaches used to infer true species richness based on incomplete samples in order to make fair comparisons between multiple sites or assemblages. The first is an asymptotic approach via species richness estimation, and the second is a non-asymptotic approach based on rarefaction and extrapolation, which is used in this thesis.

Asymptotic Approaches

The asymptotic approach estimates richness based on the asymptote of a species accumulation curve, which visualises the relationship between sampling effort and diversity (Ugland et al., 2003). This approach assumes that as more individuals are sampled from a population, the rate of species discovery will decrease and eventually plateau. Eventually an asymptote will be reached which represents the true species richness of an area (Fig. 12). Various statistical models are employed to estimate the asymptote, both parametric and nonparametric, which extrapolate beyond observed data to predict total species richness.

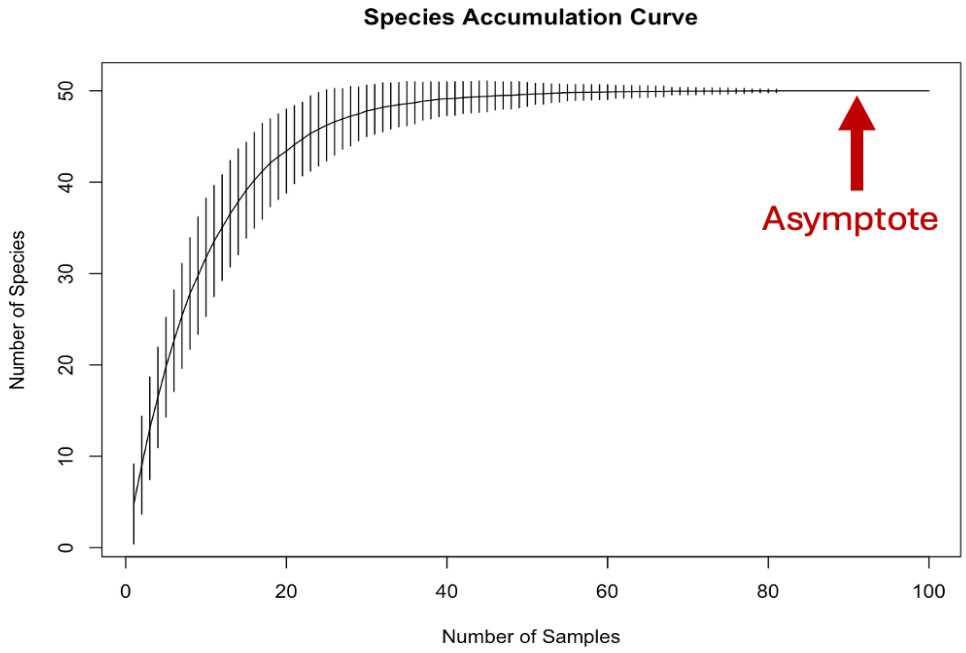


Figure 12. Example of a species accumulation curve showing that as sample number increases, the number of new species discovered decreases and eventually reaches a plateau (asymptote).

Non-asymptotic Approaches

Unlike asymptotic approaches, non-asymptotic approaches for richness estimation focus on using available data directly. They compare estimated richness of samples which have been standardised to a common size or level of completeness. Techniques such as rarefaction (estimating richness at smaller standardised sample sizes) (Hartwell et al., 2024; Salazar et al., 2016; Soetaert and Heip, 1990; Sogin et al., 2006) and extrapolation (extending richness estimates to larger sample sizes based on observed data) (Eguíluz et al., 2019; Grassle and Maciolek, 1992) are commonly used.

Ecologists typically use rarefaction to downsize larger samples until they are equal to the smallest sample, however this involves discarding data (Willis, 2019). To address this, Chao and Jost proposed standardising samples to a degree of sample completeness rather than size, developing a coverage based rarefaction methodology (Chao and Jost, 2012). Sample coverage refers to the proportion of the total individuals in a community that belong to a species that has already been sampled. A high coverage suggests that the samples contain most of the species in a community, and additional sampling would not substantially change richness estimates. A lower coverage estimate on the other hand suggests incomplete sampling and that additional sampling efforts would increase observed richness significantly.

This approach recognises the limitations of adjusting samples to equal sizes. That is, samples that have been standardised by size alone will usually have different levels of completeness, and so richness comparisons between equally sized samples may not give meaningful information on the actual degree of differences between communities (Fig. 13). This is particularly true for communities that consist of many rare species, as is the case in many deep sea communities (Carney, 1998; McClain, 2021), where sample richness may never stabilise as sample size increases.

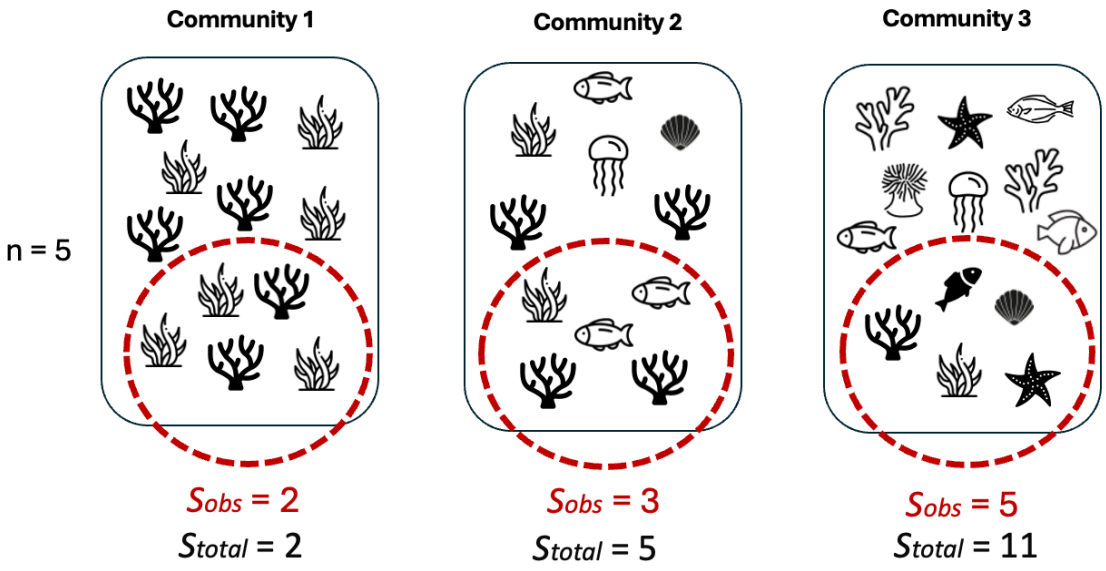


Figure 13. Graphical illustration of how standardising to a common sample size often does not give a meaningful indication of community richness for comparisons, particularly in scenarios where many species are rare (Community 3). S*obs* = observed species richness, S*total* = true species richness.

Measuring Beta Diversity

Beta diversity refers to the variation in species composition between ecological sites (Koleff et al., 2003). It is a critical concept in ecology for understanding biodiversity patterns across spatial scales, reflecting the influence of environmental gradients

(Bridges et al., 2022; McClain and Rex, 2015; Victorero et al., 2018), ecological processes (speciation, extinction, migration) and also potential human impacts. Characterising beta diversity is essential for conservation planning and ecosystem management in deep sea settings, as it helps to identify areas with unique species compositions. Measurement of beta diversity can occur through various methods including pairwise dissimilarity and multivariate techniques.

Diversity Gradients in the Deep Sea

Bathymetric Diversity Gradients (BDGs)

Bathymetric diversity gradients (BDGs) have been the focus of significant research efforts to understand community structuring in deep sea habitats (Bridges et al., 2022; McClain et al., 2010; McClain and Lundsten, 2015). Since the earliest stages of deep-sea exploration, it has been observed that species composition changes with depth (beta diversity) (Agassiz, 1888; Thomson, 1878). Early studies of bathymetric patterns of species change in the deep sea centred around placing boundaries at particular depths, known as 'zonation', with distinct zones defined by their dominant species (Le Danois, 1948), akin to methods used by early terrestrial ecologists for characterising biomes. However, more intensive deep sea sampling in the 1960s revealed that organising deep sea communities into 'zones' could be misleading, given that they appear to change in a more continuous manner (Gibson et al., 2005; Rowe, 1983; Sanders and Hessler, 1969) with varying rates of species replacement across depth. In reality, changes in deep sea community structures are less

delineated, with overlapping ranges of many species. Nonetheless, zonation is still used for convenience in methodology of deep-sea community studies (Gibson et al., 2005; Vedenin et al., 2021).

It has been traditionally established that species richness (alpha diversity) decreases with depth in ocean environments (Rex et al., 2006). However, primary literature from deep sea studies report variations on this pattern depending on the taxon, depth range, habitat type and ocean basin concerned (Etter & Mullineaux 2001; Maciolek & Smith 2009), with some reporting no pattern at all (Bodil *et al.,* 2011), and others reporting a peak diversity of certain taxa between 200-4000m (Brandt *et al*. 2004, Gage *et al.* 2000). One of the first studies documenting global depth trends in megafaunal species diversity comes from early twentieth century Russian and Scandinavian deep sea expeditions (Vinogradova, 1958), which found increasing diversity from upper bathyal depths to 2000 metres before declining toward the abyssal zone. The study also described diversity patterns for individual taxa including Porifera and Cnidaria, which displayed clear unimodal diversity-depth trends, with many exhibiting diversity peaks between 2000-3000 m. Whilst it is unclear how these results were influenced by sampling intensity at different depths, unimodal depth-diversity patterns were also upheld by later studies of macrofaunal invertebrates. For example, the observed richness of deep-sea megafaunal invertebrates off North Carolina was observed to peak at 1000 -1200 m before sharply decreasing towards the abyssal zone (Rowe and Menzies, 1969). This phenomenon has been attributed to this intermediate zone having higher energy availability than deeper waters and

increased environmental stability compared with shallower waters (Brandt *et al*. 2004; Rex *et al*. 2006; Gage *et al.* 2000). Such variations suggest local environmental regimes likely influence biodiversity patterns.

Depth-Diversity Gradients of Seamount Benthic Communities

Studies of BDGs in the deep sea so far have tended to focus sampling efforts on abyssal plains or continental slopes (Lambshead et al., 2002) with less attention paid to hard substrate topographies like seamounts. Existing studies of seamount benthic communities have reported mixed results with regard to richness gradient with depth (Bridges et al., 2022; Henry et al., 2014; Shen et al., 2021; Victorero et al., 2018). Several studies have reported no significant change in richness but rather in species turnover (beta diversity) with depth, as has been shown to be the case for benthic communities on seamounts in the Northeast Pacific (McClain et al., 2010; Preez et al., 2016), equatorial Atlantic (Victorero *et al*. 2018), South Atlantic (Bridges et al., 2021) and northwestern Pacific (Kaufmann et al., 1989; Shen et al., 2021).
Such findings could be due to i) the fact that many depth-related parameters (pressure, temperature, light availability, nutrient availability) impose bathymetric limits on certain taxa due to physiological constraints (Levin et al., 2003; Mestre et al., 2013) and ii) the considerable environmental heterogeneity (for example substrate, topography) that has been documented on individual seamounts with depth (Rowden et al., 2005) both of which dictate available habitat range of species, leading to different community assemblages at different depths.

Latitudinal Diversity Gradients (LDGs)

Differences in deep sea species diversity have been found to exist at oceanwide scales, opposing the long-held notion that the deep sea represents a uniform environment (Tyler, 2003). In terrestrial and coastal ecosystems, latitudinal diversity gradients tend to follow a parabolic relationship whereby species richness is highest in the tropics and decreases towards the poles, largely driven by solar-energy gradients (Clarke and Crame, 1997; Rohde, 1992; Roy et al., 1998). While some studies of deep sea species have also observed this pattern (Culver and Buzas, 2000; Hillebrand, 2004; Rex et al., 2000, 1993), others document a poleward increase (Lambshead et al., 2002; Tietjen, 1984) or unimodal relationship where diversity peaks at temperate latitudes (Rosa et al., 2008; Saeedi et al., 2019). Studies of deep sea LDGs to date have been fragmentary across taxa and ocean basins, largely biased towards macrofauna in the Atlantic (Lambshead et al., 2001; Quintanar-Retama et al., 2023; Rex et al., 2000). An understanding of global patterns thus remains incomplete.

Different water mass characteristics across ocean basins, including temperature gradients, food availability, and ocean currents all vary considerably across latitudes and depths to influence diversity in the deep sea (Puerta et al., 2020). Of these, temperature (Doi et al., 2021; Tittensor et al., 2010; Yasuhara et al., 2009) and productivity (Bridges et al., 2022; Corliss et al., 2009; Leduc et al., 2012; Macpherson, 2002; Woolley et al., 2016) have been cited as key drivers. Surface

primary productivity can influence richness of deep sea communities through falling organic matter as 'marine snow' which acts as a food source for benthic communities (Hopkinson and Vallino, 2005). Greater energy availability can support more complex and diverse biological communities through this enhanced food supply, as stated by the species-energy hypothesis (Wright, 1983). Temperature can influence distribution and diversity in deep sea communities through physiological thermal tolerance limits of different species. However, the interconnectedness of these two variables should be noted. It is likely that primary environmental richness drivers will vary with geographic scale, with a framework of interlinked environmental variables acting to collectively shape deep sea diversity, especially on more local scales (Saeedi et al., 2019).

Evolutionary processes unique to each taxon and ocean basin also influence diversity patterns measured today. For instance, it is now clear that the deep sea communities have not been consistent throughout geological time, but have undergone mass extinction events linked to surface climatic changes (Kennet and Scott, 1995), emphasising the interconnectedness between these seemingly isolated systems and the rest of the biosphere.

LDGs of Seamount Benthic Communities

Majority of seamounts exist within chains along ocean ridges spanning several hundreds of kilometres and broad latitudinal ranges. To date, few studies have been conducted to compare diversity between seamounts within chains (Baletaud et al.,

2023; Bridges et al., 2022; Goode et al., 2021, de forges). This is in part due to the lack of data available - it is estimated that of the estimated 100,000 seamounts that exist worldwide, less than 300 have been studied (Clark et al., 2010). Understanding how biodiversity differs with latitude along seamount chains, and primary drivers of this, is essential for tailoring effective regional management and aiding regional marine spatial planning within seamount fishing grounds (Fig.7). Building up regional datasets for seamount chains can then allow comparison with other regions, facilitating a better understanding of seamount ecology on a global scale.

Indian Ocean Seamounts

The Indian Ocean is the third largest ocean basin in the world, with a total area of ~70 million sq km (Wyrtki, 1973). It is a globally important region for fisheries, accounting for almost 15% of global catches as of 2019 (Boyd et al., 2022), and one of the few fishing areas worldwide where catches have been continuously increasing since the 1950s (Zeller et al., 2023). Despite its global significance, the Indian Ocean remains relatively unexplored compared with other ocean basins (Rogers, 2016). It was not until the 1960s that deep sea areas of the Indian Ocean were explored, and since then there has been a bias towards the Arabian Sea, leaving other areas chronically under sampled (Ramiro-Sánchez et al., 2023). Only 15 seamounts in the Indian Ocean have been explored from a biological standpoint (Sautya et al., 2011), with an even smaller number having been documented with regard to their benthic ecology. Consequently, benthic fauna of Indian Ocean seamounts is largely unknown (Kvile et al., 2014; Payne, 2015; Ramiro-Sánchez et al., 2023; Sautya et al., 2011).

Study Site: The South-West Indian Ocean Ridge (SWIOR)

The South-West Indian Ocean Ridge is a prominent geological feature extending from the central Indian Ocean to the Mid-Atlantic Ridge in the Southern Ocean. It represents a divergent plate boundary between African and Antarctic plates (Sauter and Cannat, 2010). Rising from depths of 6000m, it is one of the slowest spreading mid ocean ridges in the world (Sauter et al., 2013) and spans a complex hydrodynamic region where subtropical and subantarctic water masses converge (Froneman et al., 2007). Its high density of seamounts of varied morphologies attract abundant marine life, making the ridge target of many deep-water fisheries (Marsac et al., 2020) and licences for mining exploration of the ridge have been granted due to its rich mineral resources (Boschen et al. 2016). Whilst the physical oceanography and geology of the SWIOR has been relatively well documented (Read and Pollard, 2017; Rogers, 2016), large knowledge gaps remain regarding the biological diversity of its seamounts, particularly regarding their benthic ecology (Clark et al., 2011). Given current and predicted threats to seamounts along the SWIOR, characterising biological diversity of these seamounts is a conservation priority.

To address shortfalls in data from the SWIOR, the Global Seamounts Project (GSP) launched two exploratory research cruises along the ridge in 2009 - 2012 (AD Rogers et al., 2009; Rogers and Taylor, 2012). As a result, more studies have been conducted regarding marine life on these seamounts, but have largely focused on pelagic ecology (Djurhuus et al., 2017; Laptikhovsky et al., 2017; Swanborn et al.,

2023), with less attention paid to habitat-building VME taxa (Hestetun et al., 2017; Ramiro-Sánchez et al., 2023).

Conservation Along the South-west Indian Ocean Ridge

Whilst rich offshore fisheries exist in the South-west Indian Ocean, countries within the region have not been able to develop the infrastructure to access them (Obura, 2017). Consequently, they have allowed distant-water fishing fleets from more developed countries to access their fish resources through either multilateral or bilateral agreements. The SWIOR lies within the area of competence governed by the Southern Indian Ocean Fisheries Agreement (SIOFA), a legally binding treaty between ten nations established to guarantee the sustainable utilisation of fishery resources across the Southern Indian Ocean. Initiated in 2006 and coming into effect in 2012, SIOFA governs an area spanning millions of square kilometres. Its jurisdiction extends from south of 10° north to north of 60° south, encompassing a vast region between East Africa and Western Australia (Fig. 14). Prior to the formation of SIOFA, there was limited regulation of fishing in the Southern Indian Ocean - which had been subject to deep-sea fishing fleets for decades without governance structures in place. The establishment of SIOFA thus marked a pivotal step towards addressing governance challenges and ensuring sustainable management of fisheries within the region.

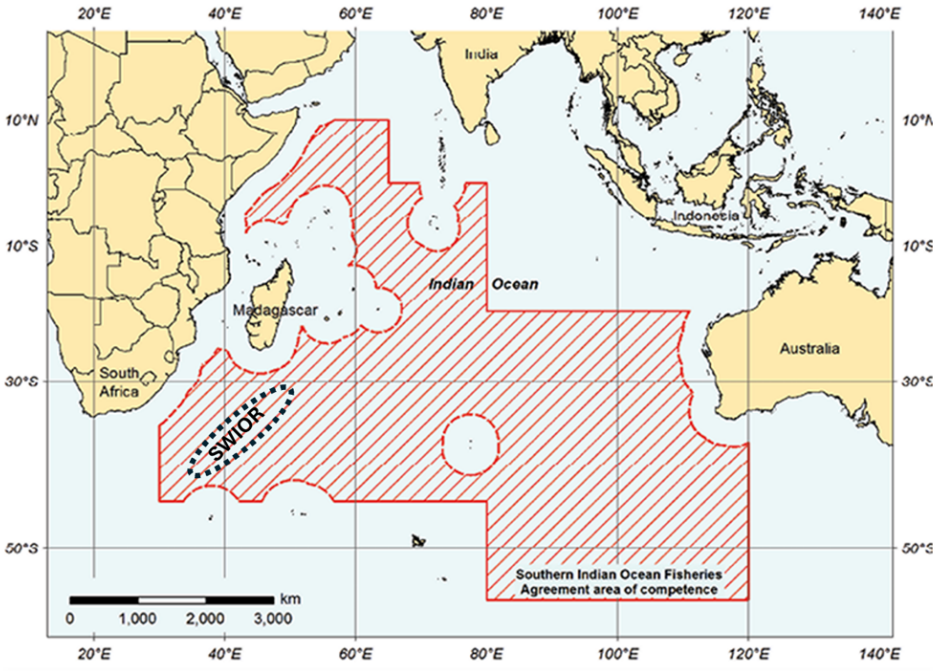


Figure 14: South Indian Ocean Fisheries Agreement Area of Competence, with the location of the SWIOR (South-west Indian Ocean Ridge) shown (Ramiro-Sánchez et al., 2023).

As other Regional Fisheries Management Organisations (RFMOs) in other ocean basins, SIOFA must comply with international obligations towards the conservation of VMEs against potential impacts from deep-sea bottom fishing. In this regard, since its relatively recent establishment in 2012, SIOFA has initiated management efforts to protect VMEs by identifying a list of VME indicator taxa for Indian Ocean waters (CMM 2018/01). SIODFA, (South Indian Ocean Deepwater Fishers Association), a group consisting of deep-water fishing companies operating in the South Indian Ocean, has designated 13 voluntary benthic protected areas (BPAs) where bottom trawling is not permitted by member vessels (CMM 2019/01) (Fig. 15). Three of these areas are seamounts along the SWIOR (Atlantis Bank, Coral, MOW) (SIODFA, 2015). However, such management decisions have been based on limited data

based on anecdotal evidence such as skipper reports, bycatch data, presence of fishing vessels in an area, and marine mammal sightings. Regional management would thus greatly benefit from a more systematic survey of biodiversity along this seamount chain to inform conservation decisions. This lack of scientific characterisation reflects a broader issue of data scarcity from deep-sea habitats within the Southwest Indian Ocean, described by Ramiro-Sánchez et al. (2023) as an 'epitome of data paucity'.

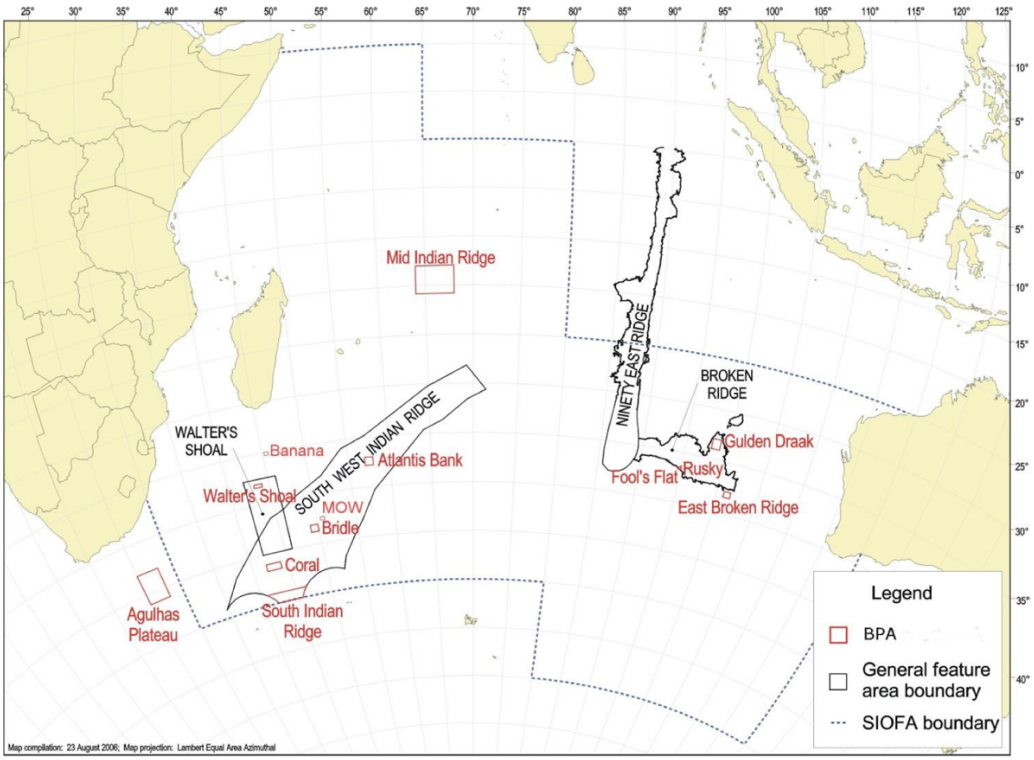


Figure 15. Locations of Benthic Protected Areas (BPAs) assigned by SIODFA in the Southern Indian Ocean (SIODFA, 2015)

Outline of Thesis Chapters

The two data chapters in this thesis explore the community ecology of Vulnerable Marine Ecosystem (VME) indicator taxa from seamounts along the South-west Indian Ocean Ridge (SWIOR). Video surveys of seamount benthos were used to generate community data from which key diversity patterns were identified over depth and latitudinal gradients. All data was collected during the R/V James Cook 066 NERC research cruise November 7th - December 21st 2011 in the southwest Indian Ocean (Rogers & Taylor 2012).

Chapter 1, entitled *'Exploring Depth Diversity Gradients of Habitat-building Species on Melville Bank, a seamount in the South-west Indian Ocean'* investigates how species richness and composition of VME indicator taxa change along a depth gradient of 100 - 1300 m on Melville Bank. The effect of bottom contact fisheries on VME richness is also explored.

Chapter 2, entitled '*Exploring Diversity of Vulnerable Marine Ecosystems (VME) On Four Seamounts Along the Southwest Indian Ocean Ridge'* explores seamount richness patterns along a latitudinal gradient and investigates the key environmental drivers of trends observed. Latitudinal diversity patterns of key VME groups Cnidaria and Porifera are investigated.

The final chapter discusses the broader scale implications of this work, as well as the potential limitations in methodology and future research directions.

Chapter 1: Exploring Depth Diversity Gradients of Habitat Building Species on Melville Bank, a Seamount in the South-west Indian Ocean

Abstract

The diversity of megabenthic assemblages on seamounts in the Indian Ocean is poorly documented, yet such knowledge is crucial for the conservation of Vulnerable Marine Ecosystems (VMEs) by regional fisheries management. This chapter resolves depth-diversity gradients of key VME indicator taxa on Melville Bank, a seamount along the South-west Indian Ocean Ridge that has been exploited by fisheries. A total of 4,272 individuals belonging to Cnidaria and Porifera were identified between 100 and 1300m, which were classified into 72 morphospecies. Communities in the first 900m were dominated by octocoral fans and massive sponge morphotypes, whilst deeper depths were dominated by branching glass sponges. Richness of VME indicator species increased with depth, but this pattern is confounded by impacts of bottom fishing which were shown to negatively impact richness. Overall, results highlight the considerable benthic diversity that can exist on an individual seamount and draw attention to the destructive impact of bottom trawling on richness of VME communities.

Introduction

Human pressures on ocean resources are increasing exponentially (Jouffray et al., 2020) threatening the health of marine ecosystems and their inhabitants. Deep sea environments - those below 200m - are becoming an increasingly viable target for many extractive industries given the depletion of coastal and land-based resources (Ramirez-Llodra et al., 2011) alongside advances in technology which facilitate easier

access to remote ocean areas (Petersen et al., 2017). Consequently, deep sea habitats now face a multitude of direct human pressures from commercial fishing, offshore oil and gas extraction, the imminent prospect of mineral mining (Sharma, 2015) as well as indirect threats from climate change (Sweetman et al., 2017). Simultaneously, our reliance on deep sea ecological services is being increasingly acknowledged (La Bianca et al., 2023), necessitating protection of these environments into the future.

The majority of deep-sea areas are located in Areas Beyond National Jurisdiction (ABNJ), for which no one nation has sole management responsibility. Implementing protection of deep-sea areas thus requires collaborative international frameworks based on sound understanding of deep-sea biodiversity and its distribution (Watling and Auster, 2017). Understanding depth-diversity gradients of habitat-forming marine organisms is a key component of this, especially given the expansion of fishing fleets to greater depths (Clarke et al., 2015).

Seamounts, topographic elevations rising 1000m from the seabed (Staudigel et al., 2010), are a common habitat in the deep sea. They represent unique environments due to their provision of rocky substrate (Serrano et al., 2017), topographic complexity (Swanborn et al., 2023), and manipulation of local hydrodynamic regimes (Rowden et al., 2010) which provide ecological niches not found in other deep-sea settings. In particular, their provisioning of hard attachment surfaces in the otherwise sediment-dominated deep ocean facilitates colonisation by rich benthic communities

of deep water coral and sponges (Rogers et al., 2007). These organisms serve as important biogenic habitat, spawning grounds and nursery sites for organisms at higher trophic levels (Hunt et al., 2011; Maguire et al., 2023) generating 'hotspots' of biodiversity in the deep sea (Morato et al., 2010). Large aggregations of pelagic species around seamounts has rendered them primary targets of commercial bottom-trawling (Clark, 2009), which leads to sharp declines in biodiversity through removal of benthic fauna as bycatch (Maynou and Cartes, 2012). Given that some deep sea coral and sponge species can be hundreds to thousands of years old (Roberts et al., 2006), their recovery is extremely slow (Williams et al., 2010), compromising the long-term ecological resilience of seamount ecosystems (Oliver et al., 2015).

In recognition of their susceptibility to fishing activity, seamount benthic communities now are protected as Vulnerable Marine Ecosystems (VMEs) under United Nations General Assembly (UNGA) rules. Species constituting VMEs, which will hereafter be referred to as VME indicator taxa, are defined as those that are easily disturbed and slow to recover (FAO, 2009). UNGA resolution 61/105 also calls for fisheries management to work to “prevent” significant adverse impacts (SAIs) to areas hosting VME indicator taxa. SAIs are defined as “those that compromise ecosystem integrity in a way that: (i) impairs the ability of affected populations to replace themselves; (ii) degrades the long-term natural productivity of habitats; or (iii) causes, on more than a temporary basis, significant loss of species richness, habitat or community types” (FAO, 2009). Understanding the depth-distribution of VME indicator taxa on seamounts will help to inform sustainable fisheries management and aid marine

spatial planning of these ocean habitats (van Denderen et al., 2022). For instance, fisheries management can use this information to implement measures such as setting depth restrictions on fishing activities (Clarke et al., 2015) and creating no-take zones (Sumaila et al., 2007).

Many abiotic and biotic parameters vary with depth (temperature, salinity, pressure, nutrient availability), thus imposing physiological constraints on species that dictate their distribution and available habitat space, leading to diversity differences in marine communities with depth (Gibson et al., 2005). Depth has also been shown to influence speciation in marine organisms (Ingram, 2011; Prada and Hellberg, 2021), known as the depth-differentiation hypothesis (Etter and Rex, 1990). While Bathymetric Diversity Gradients (BDGs) in deep-sea environments have garnered considerable research attention (Danovaro et al., 2008; Howell et al., 2003; Olabarria, 2005; Rex et al., 2005) most studies in this domain have concentrated on sampling continental slopes and abyssal plains (Culver and Buzas, 2000; Lambshead et al., 2001; Rex et al., 1993) with a focus on mobile benthic invertebrates (Aldea et al., 2008; Cartes and Sardà, 1992; Gage et al., 2000). Consequently, there remains a lack of understanding regarding the BDGs of sessile marine organisms on hard-bottom deep-sea habitats like seamounts (McClain et al., 2010; McClain and Lundsten, 2015; Victorero et al., 2018).

Studies to date documenting BDGs of seamount benthic communities have been largely biased towards Pacific and Atlantic ocean basins and reported mixed results,

with some documenting no relationship between depth and diversity at all between 250 and 950m (Bridges et al., 2022) or a unimodal relationship peaking at mid-bathyal depths (Brault et al., 2013). In this context, 'diversity' refers to alpha diversity - the variety and abundance of species within a specific depth zone. Several studies that have found no variation in alpha diversity between depths have however reported significant species turnover (beta diversity) in community composition at varying depths (McClain et al., 2010; Shen et al., 2021; Victorero et al., 2018). This may be due to the considerable environmental heterogeneity that has been reported to exist on individual seamounts with depth (Rowden et al., 2005), which provides habitat diversity for different species. Treating seamounts as single entities in conservation and management decisions could therefore overlook large variations in biodiversity, highlighting the value of individual seamount studies (Henry et al., 2014; McClain et al., 2010; Victorero et al., 2018).

This chapter aims to build on existing knowledge of BDGs on individual seamounts through analysis of VME indicator taxa on Melville Bank, a seamount located along the South-west Indian Ocean Ridge (SWIOR) in the Southern Indian Ocean. Deep sea biodiversity of the south-west Indian Ocean has been described as an 'epitome' of data paucity, hindering the development of effective conservation strategies in this region (Ramiro-Sánchez et al., 2023), which has been historically heavily targeted by bottom trawling primarily for orange roughy and alfonsino (Clark, 2009; Romanov, 2003) and is currently being explored for its mining potential (Marsac et al., 2020). Despite the multitude of threats to its marine life, little is known about the distribution

of benthic communities from seamounts along the SWIOR, with literature to date focused on species discovery and taxonomy (Hestetun et al., 2017; Serpetti et al., 2017; Taylor and Rogers, 2017) rather than systematic surveys of biodiversity distribution. To date, the impact of bottom contact fisheries on VME communities on SWIOR seamounts has also not been investigated.

This chapter will i) explore how alpha diversity (specifically richness and abundance) of VME indicator taxa varies along a depth gradient of 100 - 1300m on Melville Bank, ii) investigate changes in beta diversity by comparing differences in community composition between depths and iii) consider how SAIs from bottom contact fisheries influence the biodiversity patterns observed. Findings from this chapter will shed light onto bathymetric biodiversity gradients of VME communities on a fisheries-exploited seamount in the Indian Ocean and contribute to current understanding of benthic ecology gradients in this remote ocean setting.

Methodology

Study Site

Melville Bank is part of a seamount chain that makes up the South-West Indian Ocean Ridge (SWIOR), a prominent geological feature extending from the central Indian Ocean to the Mid-Atlantic Ridge in the Southern Ocean. It is located 38°28'S,42°49'E on the eastern side of the Fracture Zone of the SWIOR. The seamount is approximately 12 km along its longest axis, and is the shallowest

seamount on the SWIOR with a summit depth of under 100m (Gershanovich and Dubinets, 1991). It is elongated westwards, with its shallowest section on its eastern side and a deeper slope of 400 metres to the west. The shallower summit consists of ridges from north to south and east to west resulting from mass wasting events.

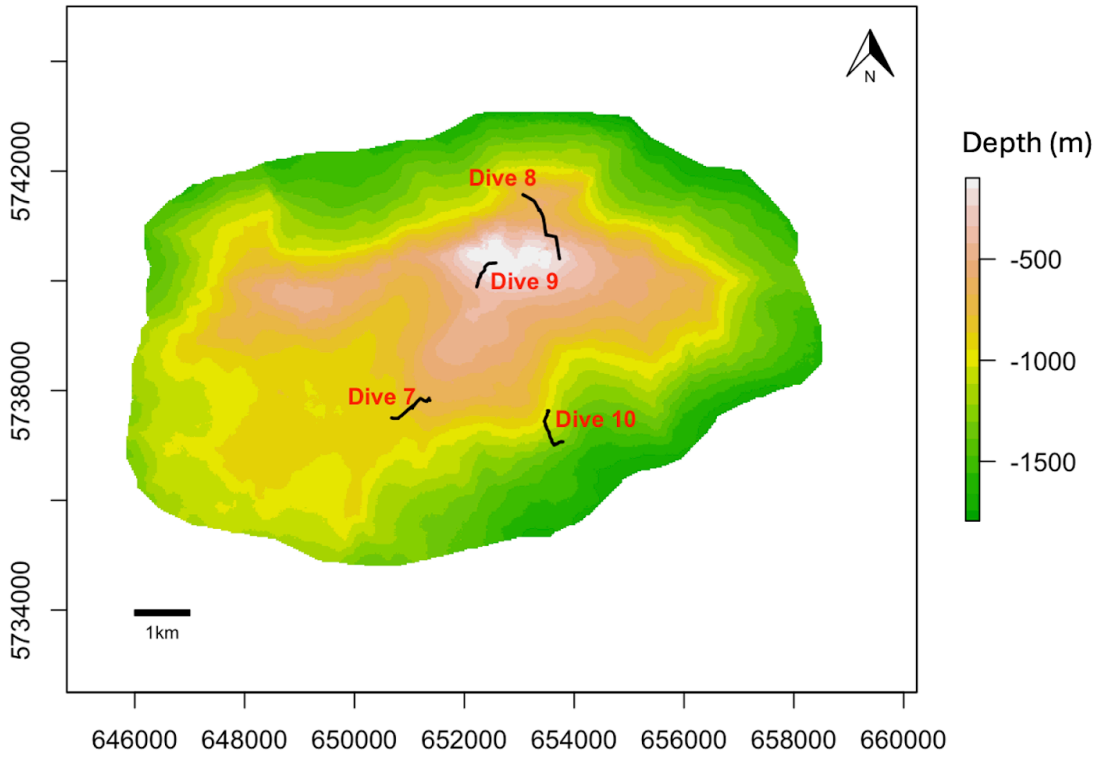


Figure 1.1: Bathymetric map of Melville Bank showing dive routes taken by ROV Kiel 6000.
Code: melville_routes.R

Data Collection

Video footage used for this project was recorded by ROV Kiel 6000 during the RRS *James Cook* 066 NERC research cruise November 7th - December 21st, 2011 in the southwest Indian Ocean (Rogers & Taylor 2012). A total of 16 dives were conducted

during the cruise. Dives 7, 8, 9 and 10 took place on Melville Bank seamount (Fig 1.1) on the 23rd, 24th, 25th and 26th November 2011 respectively.

All dive footage was first manually sorted to identify annotatable videos, which were subsequently converted into .mp4 format and imported into Biigle (Langenkämper et al., 2017), an annotation software specifically developed for processing of marine image databases. Annotations of benthic fauna were made, consisting of Porifera, Cnidaria, Echinodermata and Bryozoa. Organisms below a size threshold of ~3cm were not annotated. Given the small number of annotations made for Bryozoa and Echinoderms (Fig.1.2), these were discarded from further analyses. A total of 4272 individuals of Cnidaria and Porifera were used for analyses. Examples of organisms annotated are shown in Figure 1.3.

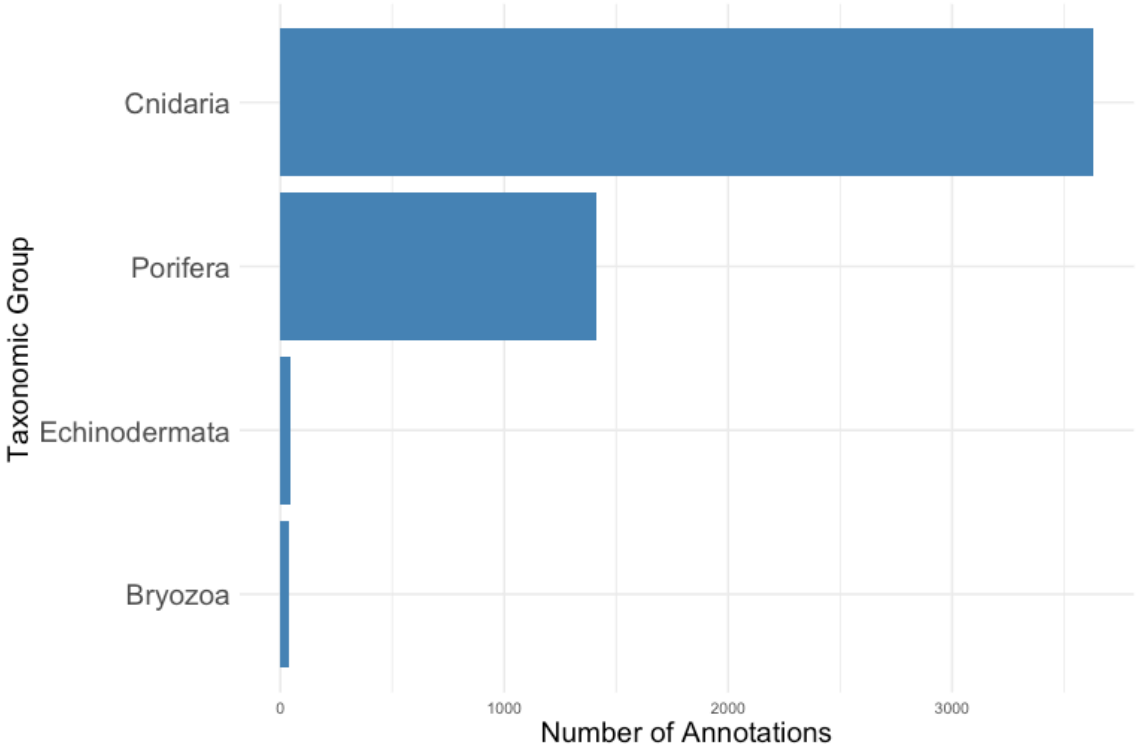


Figure 1.2. Number of annotations made on Melville Bank for Cnidaria, Porifera, Echinodermata and Bryozoa.

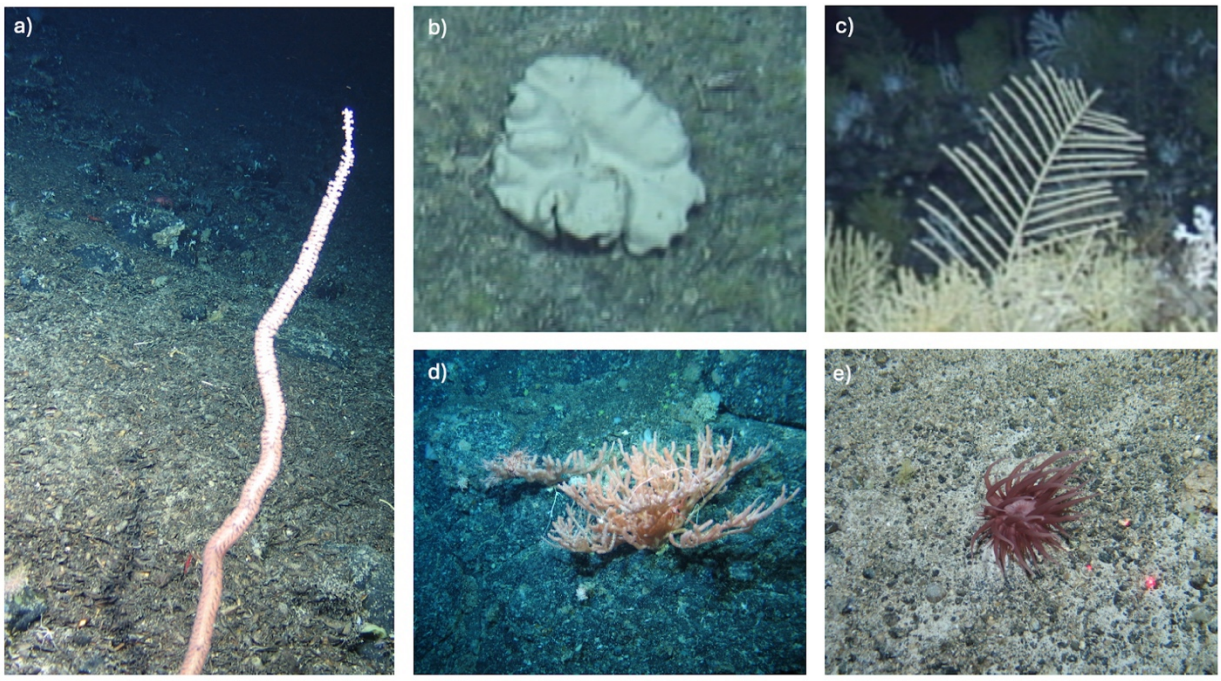


Figure 1.3. Example images of Cnidaria (1.3a, c, d e) and Porifera (1.3b) annotated on Melville Bank.

Organisms were identified first by assigning high level morphological classifications following the CATAMI scheme to annotations (Althaus et al., 2015). As standard approaches for determining taxonomy are not applicable to video data, the taxonomic resolution of labels was further resolved to distinct morphospecies, which may correspond to a species, genus, family or higher taxonomic level. Each organism was assigned the highest taxonomic resolution possible with assistance from deep sea taxonomy expert Dr Michelle Taylor and reference to the SMarTaR-ID online database (Howell et al., 2019). Overall, a total of 72 morphospecies from Cnidaria and Porifera annotations were identified. Due to the visual limitations of identifying taxa from ROV video footage, most identifications are provisional and are likely an underestimation of diversity present as they ignore cryptic species and fauna smaller than the chosen size cut off. Despite these limitations, the methodology adopted here represents a widely used approach in deep sea research (Durden et al., 2016).

Environmental Metadata Collation

A CTD (Conductivity-Temperature-Depth) real-time probe (IFM-GEOMAR) was mounted on ROV Kiel 6000 to measure *in situ* salinity, temperature, pressure, and depth while recording the video footage. This information, alongside decimal coordinates for each annotation from dive logs, was collated with Biigle output reports using R scripting (R Core Team., 2022) based on common capture times to obtain relevant environmental data for each annotation made. A boxplot of environmental variables collected per depth zone is shown in Fig.1.3.

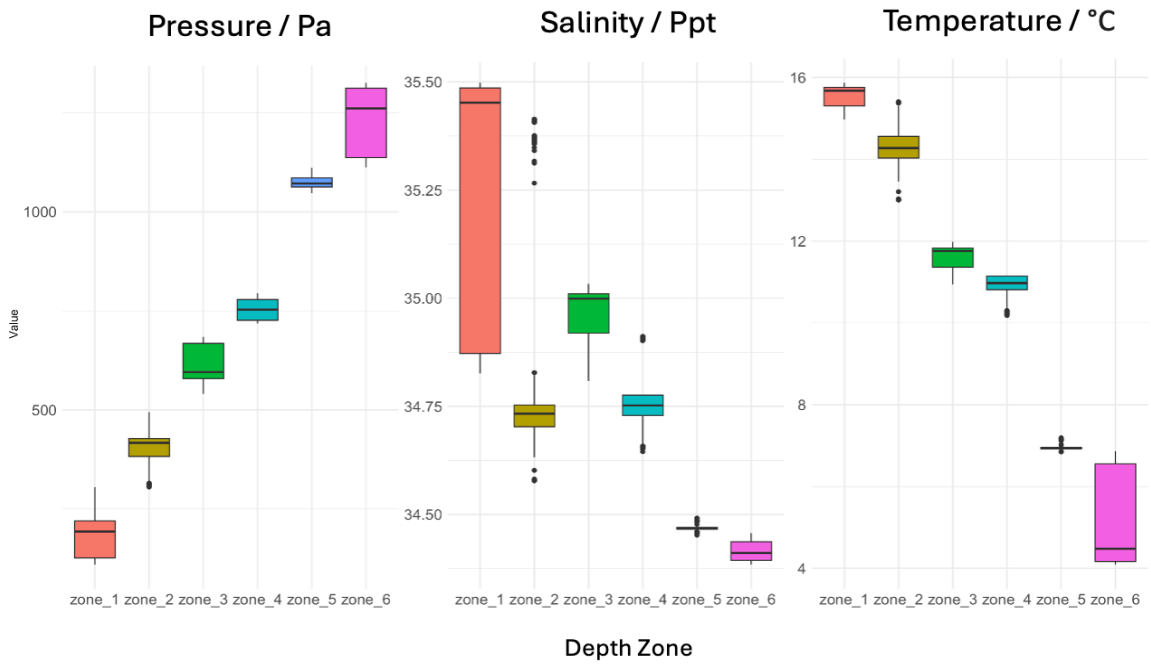


Figure 1.3. Boxplots of CTD collected environmental variables pressure, salinity and temperature per depth zone. Code: CTD.variables.R

Data Preparation

Biigle reports collated with relevant metadata from all dives were loaded into the statistical software R. Cumulative distances of dive routes were calculated, and dive routes were subsequently divided into 50 metre transects for analyses. A total of 66 transects were obtained, covering a total of 3.3 km (Table 1.1). Each transect was binned into a 200m depth zone starting from 100m which is equivalent to the summit depth on Melville Bank. It is acknowledged that this zonation is arbitrary, and that in reality changes in deep sea community structures are less delineated, with overlapping ranges of many species. Nonetheless, zonation is still used for convenience in deep sea community studies. To investigate alpha diversity with depth, a data frame was made which assigned a transect to each row with values for richness, abundance, and average environmental metrics. To investigate community composition, a morphospecies abundance matrix with rows as depth zone was created for community analyses using the vegan package (Oksanen J et al., 2022).

Table 1.1. Number of transects from each depth zone on Melville Bank and distance covered.

Depth range / metres	Number of 50 m transects	Total distance sampled / metres	Depth Zone
100-300	15	750	1
300-500	12	600	2
500-700	16	800	3
700-900	11	550	4
900-1100	3	150	5
1100-1300	9	450	6

Throughout video annotation, evidence of fishing impact on Melville Bank was observed. Discarded fishing gear (lobster pots, ropes, an anchor, trawling cables), coral rubble and trawling scars were seen in footage. To investigate the impact of bottom contact fisheries on VME morphospecies diversity, each transect was assigned a 'Y' or 'N' depending on whether evidence of significant adverse impacts (SAIs) had been observed in video footage. SAIs included trawling scars and coral rubble (Fig. 1.4), but not the presence of lost fishing gear alone.

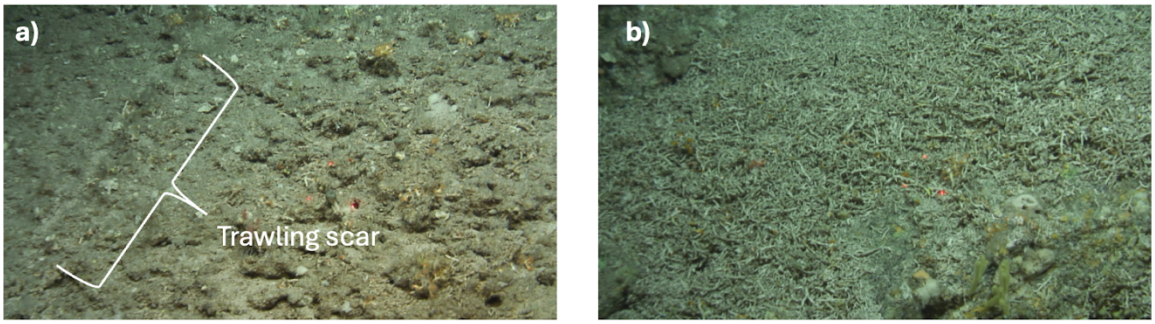


Figure 1.4. Examples of Significant Adverse Impacts (SAIs) from bottom contact fisheries on Melville Bank. a) Trawling scar at 319 metres, b) Stony coral rubble at 127 metres.

Statistical Analyses

All statistical analyses were conducted in R studio using *lme4* (Walker, S. and Machler, M, 2015), *glmmTMB* (Magnusson et al., 2017) and *vegan* (Oksanen J et al., 2022) packages. Environmental variables temperature, salinity and depth were standardised, and their correlation assessed. Given the strong correlation coefficients between temperature and salinity with depth, they were excluded from the model (Fig. S1.1). To assess the influence of depth on morphospecies richness while accounting for potential non-independence of observations from the same dive, a Generalised Linear Mixed Model (GLMM) was employed (Table S1.1). The response

variable in the model was morphospecies richness, a count variable representing the number of different morphospecies observed in each transect. Given the presence of overdispersion in the dataset, a negative binomial distribution was chosen as more appropriate than a Poisson distribution. Depth zone was set as a fixed effect. Dive number was included as a random effect to account for variation among dives, acknowledging that multiple transects come from the same dive and thus might not be completely independent.

A plot of sampling completeness for each depth zone was generated using the iNEXT package (Hsieh et al., 2016) and showed that sample coverage was > 0.8 for all depth zones (Fig. S1.2). Nonetheless, given that rarefaction curves did not level out for depth zones 4, 5 and 6 (Fig. S1.3), rarefaction to a given sample size was employed as a supplementary analysis to standardise morphospecies richness estimates from each depth zone to the same level of sampling effort (n = 80), allowing for direct comparisons. The sample size of 80 was chosen given that this was below the minimum number of individuals sampled in a depth zone. To obtain uncertainty estimates, we performed 100 bootstrap replicates of the rarefied datasets for each depth zone. Bootstrapping randomly draws individuals from the original dataset with replacement to create simulated samples or 'bootstraps' of a given size. Analysis of this rarefied dataset was used to investigate whether the richness trend established by the GLMM still held. It is acknowledged that random effect information of dive is lost during analyses of rarefied datasets, nonetheless rarefaction was still merited since sampling effort had not been exhaustive according to rarefaction

curves, which is often the case in deep sea datasets due to budgetary constraints that limit experimental design and sampling opportunity.

To investigate morphospecies abundance with depth, mean abundance per transect was calculated for each depth zone. An GLMM was then conducted to test for significant differences in morphospecies abundance with depth whilst again controlling for dive as a random effect (Table S1.2).

To investigate changes in beta diversity of VME morphospecies with depth, Bray-Curtis dissimilarities were calculated between depth zones. Bray-Curtis dissimilarity is a statistic that is used routinely in ecology to quantify the compositional dissimilarity between different sites based on presence absence as well as abundance data (Somerfield, 2008). The resulting dissimilarities were visualised using a dendrogram from a hierarchical clustering analysis (Fig. 1.8). A SIMPER (Similarity Percentage) analysis was used to identify which morphospecies were most responsible for observed richness differences between depth zones (Table S1.5).

To investigate the effect of bottom contact fisheries on VME richness, a negative binomial GLMM was used (Table S1.4). The model included SAI evidence as a fixed effect, with depth zone and dive number as random intercepts to account for variability across sampling locations and events.

Results

Richness of VME Morphospecies Increases While Their Abundance Decreases with Depth on Melville Bank

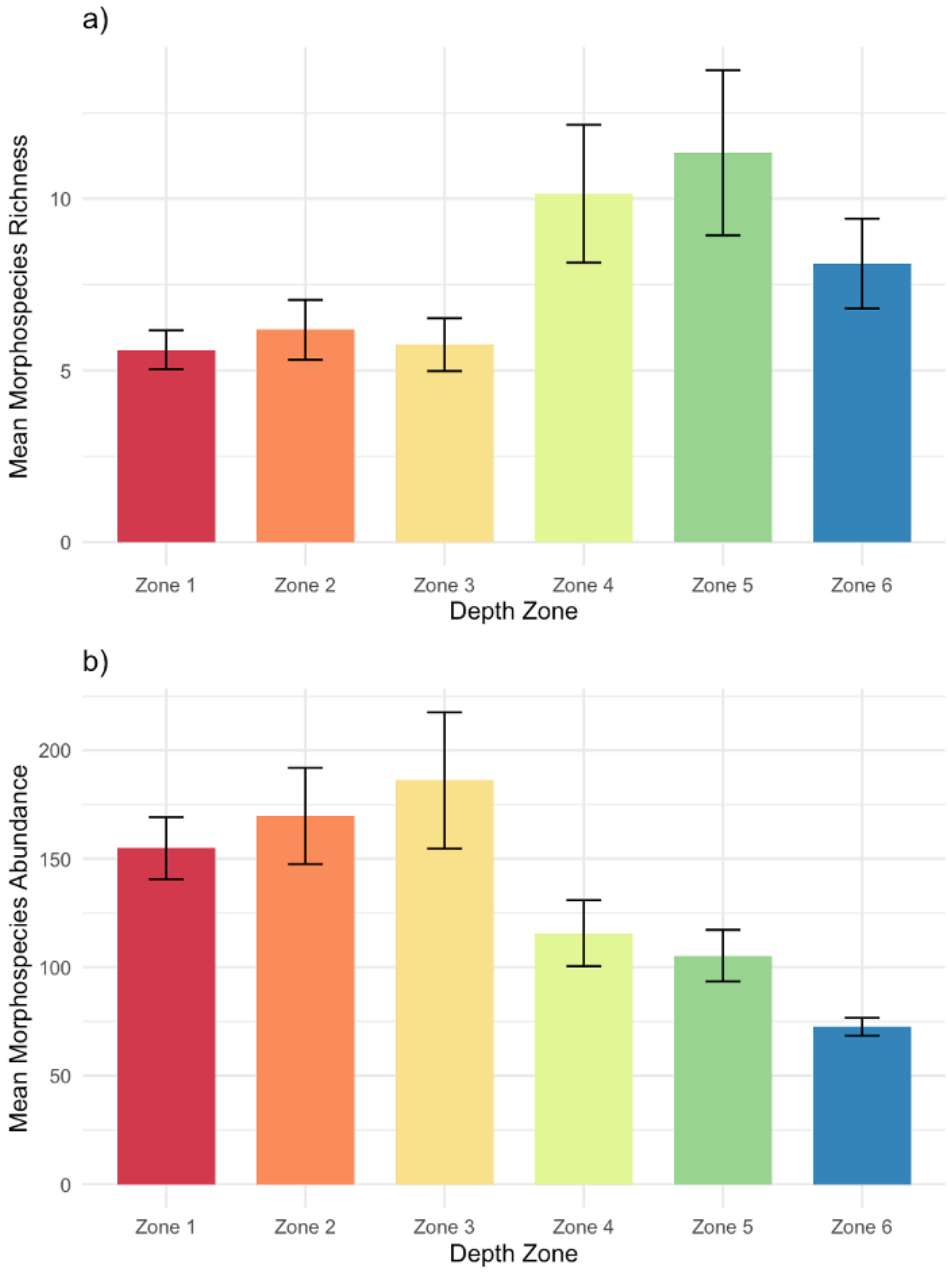


Figure 1.5 a) Barplot of mean VME morphospecies richness in each depth zone per transect and their standard errors. b) Barplot of mean VME morphospecies abundance per transect in each depth zone and their standard errors. Zone 1 = 100:300m, Zone 2 = 300:500m, Zone 3 = 500:700m, Zone 4 = 700:900m, Zone 5 = 900:1100m, Zone 6 = 1100:1300m. Code: chpt1.bargraphs.R

A plot of mean morphospecies richness per transect shows increasing richness with depth zone, peaking at depth zone 5 (Fig. 1.5a). A Generalised Linear Mixed Model (GLMM) revealed statistically significant increases in richness between the reference depth zone (zone 1) and zones 4, 5, and 6 ($p < 0.05$) (Table S1.1). The differences between zone 1 with 2 and 3, however, were less pronounced and were not statistically significant. There is a marked increase in richness from zone 3 (500-700m) onwards. These results suggest a clear variation in morphospecies richness, which is notably higher at depths below 700m. The trend of increasing morphospecies richness beyond 700m was also held after rarefaction of depth zone communities to account for unequal sampling efforts (Fig. 1.6).

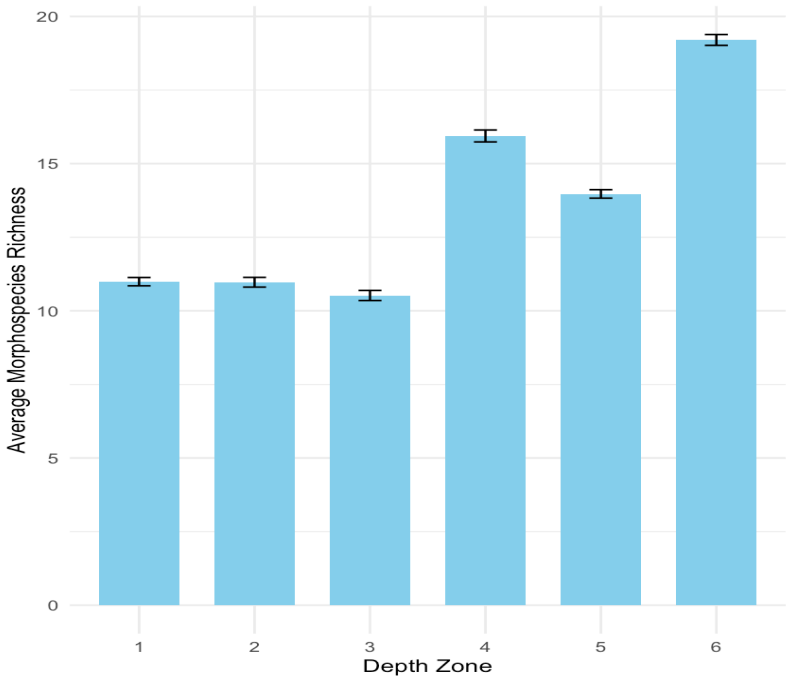


Figure 1.6. Barplot of mean morphospecies richness per transect at each depth zone from Melville Bank with their standard errors, based on average richness from 100 rarefied datasets (n = 80) per depth zone. Zone 1 = 100:300m, Zone 2 = 300:500m, Zone 3 = 500:700m, Zone 4 = 700:900m, Zone 5 = 900:1100m, Zone 6 = 1100:1300m. Code: chpt1_rarefaction.R

Contrasting general patterns seen for morphospecies richness, morphospecies abundance on Melville Bank was found to overall decrease with depth, peaking at 700-900m (depth zone 3) (Fig.1.5b). An ANOVA of log-transformed abundance data revealed that the difference in mean abundance between depth zones was statistically significant (P-value < 2e-08). This was further explored in a GLMM using a negative binomial distribution and controlling for the effect of dive (Table S1.2). No significant difference in abundance was found between the first 3 depth zones, however abundances at depth zones 5 and 6 significantly lower than depth zone 1 (P-value < 0.05). Figure 1.7 shows a cartoon illustration of these contrasting findings between VME morphospecies richness and abundance with depth.

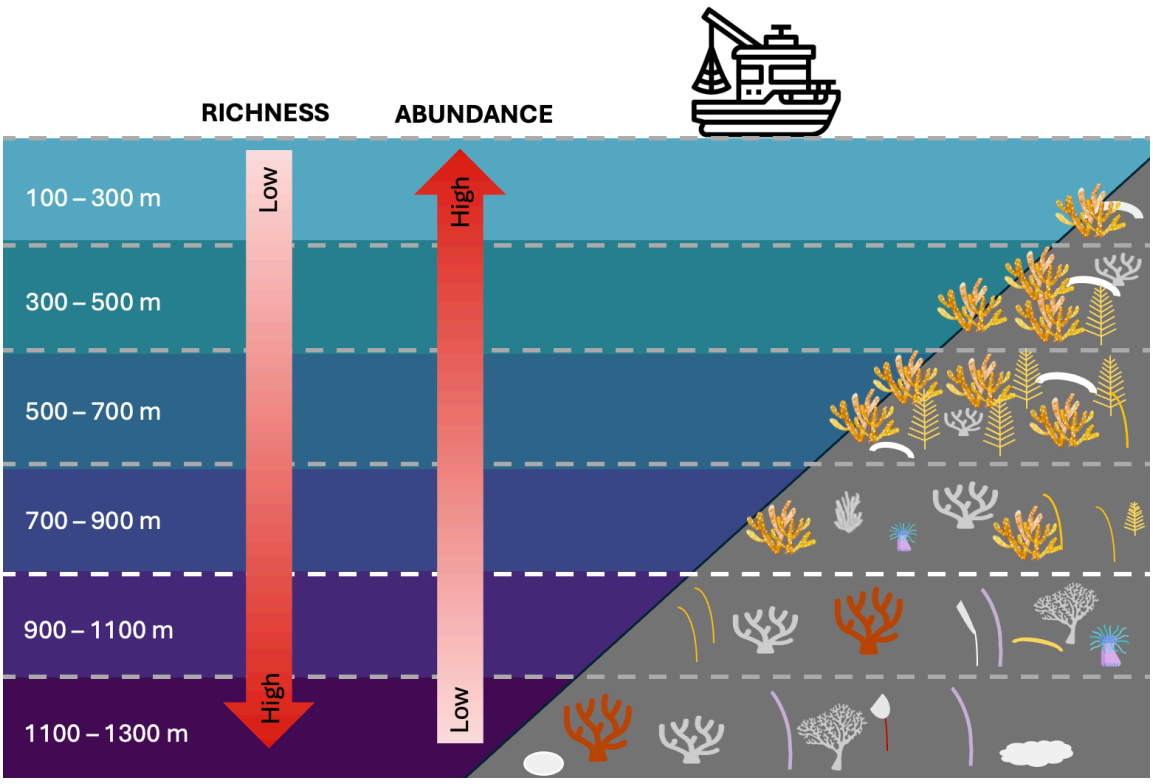


Figure 1.7. Cartoon depiction showing key patterns in VME morphospecies richness and abundance with depth on Melville Bank Seamount.

Community Composition of VME Morphospecies Varies Significantly Between Depth Zones on Melville Bank

An Analysis of Similarities (ANOSIM) based on Bray-Curtis dissimilarities indicated a statistically significant difference in community composition of VME morphospecies based on depth zone ($R = 0.4$, P-value < 0.0005) (Table S1.3). This indicates that depth has a substantial effect on community composition in the dataset. A dendrogram based on Bray-Curtis distances shows that clustering is observed between the two deepest depth zones (zones 5 and 6), and the 4 shallower zones (1-4) (Fig. 1.8).

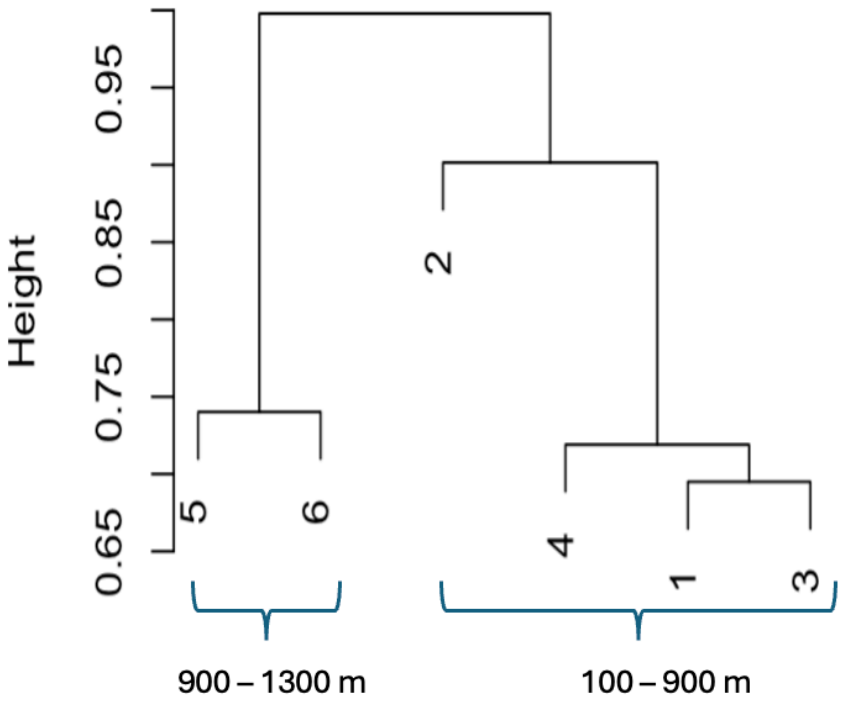
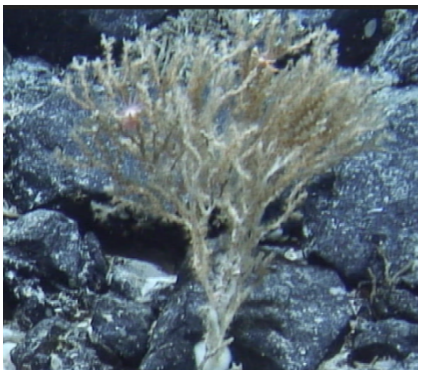


Figure 1.8. Dendrogram from hierarchical cluster analysis using Bray-Curtis dissimilarities between depth zones (1 = 100-300m, 2 = 300-500m, 3 = 500-700m, 4 = 700-900m, 5 = 900-1100m, 6 = 1100-1300m). Code: finalchp1_com_analysis.R

The morphospecies from each depth zone that appeared most frequently was recorded as the dominant morphospecies in that depth zone and are displayed in Table 2. The *Acanthagorgia* yellow fan dominates depths between 100-900, except for 300-500m where the dominant morphospecies is a 2D lamellate sponge. SIMPER analysis also identified *Acanthagorgia* yellow fans as driving Bray-Curtis differences between shallower and deeper depth zones (Table S3). Interestingly, only 1 morphospecies was present at all depth zones, a member of *Stylasteridae*. Moreover, almost half (32 of 72) morphospecies identified were only present at one depth zone.

Table 2. Dominant morphospecies identified for each depth zone on Melville Bank.

Depth Zone (m)	Dominant Morphospecies	Biigle Image
Zone 1 (100-300m) Zone 3 (500-700m) Zone 4 (700-900m)	*Acanthagorgia* yellow fan morphospecies	
Zone 2 (300-500m)	2D lamellate sponge morphospecies	
Zone 5 (900-1100m)	Primnoidae octocoral: *Primnoides flagellum*	
Zone 6 (1100-1300m)	Branching glass sponge: *Starostegia oculata*	

Among broad VME groups, the richness of Octocorallia stands out as being high in the first 900m (zones 1-4) (Fig. 1.9). Overall, 19 different morphotypes of Octocorallia were identified on Melville Bank, with a diverse octocoral garden found between 500 and 700m (Fig. 1.10).

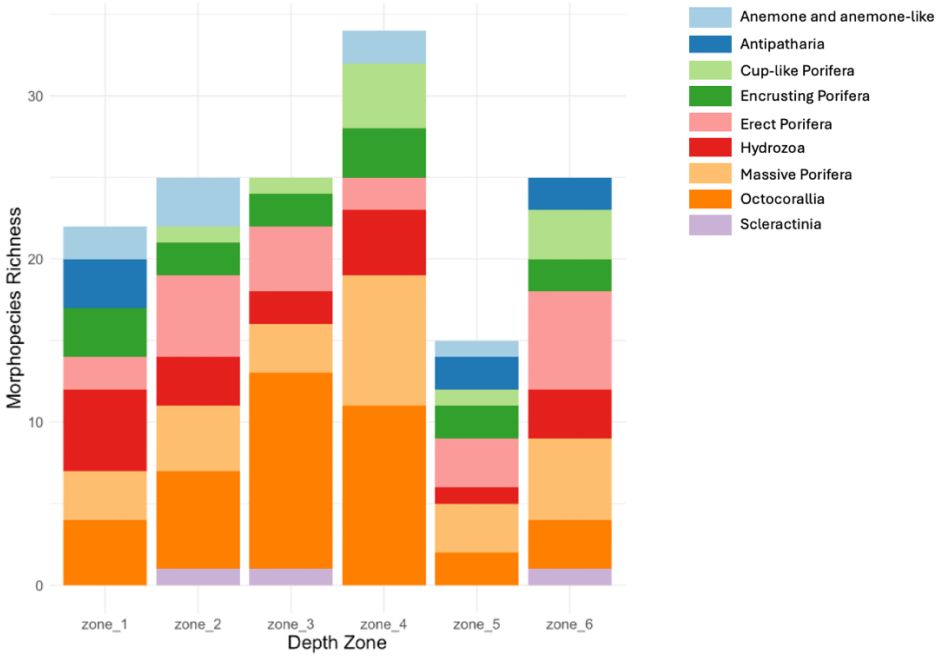


Figure 1.9. Stacked bar chart of overall morphospecies richness in each depth zone of high level VME groups. Zone 1 = 100:300m, Zone 2 = 300:500m, Zone 3 = 500:700m, Zone 4 = 700:900m, Zone 5 = 900:1100m, Zone 6 = 1100:1300m. Code: richness_VME_groups.R

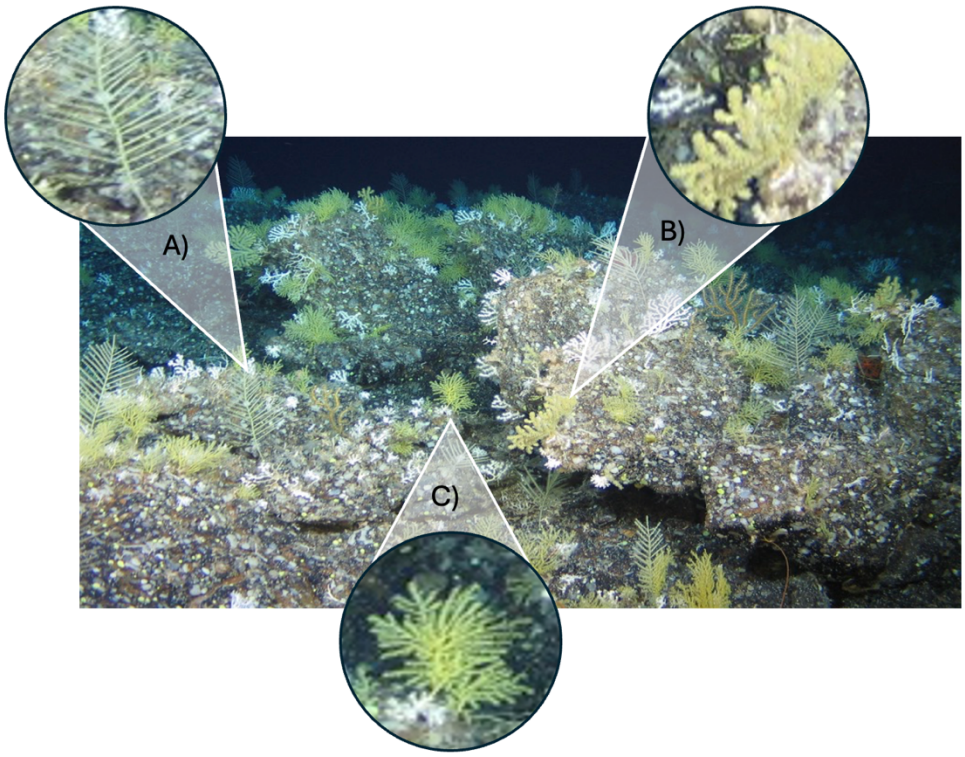


Figure 1.10. Image of an octocoral garden on Melville Bank at 500 - 700m (depth zone 3) with the most abundant octocoral morphospecies labelled. A) *Primnoeides sertularoides,* B) *Acanthogorgia* yellow fan C) Octocoral bush morphospecies.

Significant Adverse Impacts (SAI) from Bottom Contact Fisheries

The presence of trawling scars or stony coral rubble was recorded as evidence of Significant Adverse Impacts (SAIs) from bottom contact fisheries (Fig. 1.4). Majority of transects where SAIs were observed were in the first three depth zones (100 - 700m) (Fig. 1.11a), although SAIs were observed in every depth zone studied. Transects where SAIs were observed had a significantly lower richness of VME morphospecies than those which were not impacted (Fig. 1.11b). This was further explored using a negative binomial generalised linear mixed model (GLMM), setting depth zone and dive number as random effects (Table S6). The presence of SAI evidence was shown to have a direct negative impact ($p < 0.005$) on VME

morphospecies richness of transects. No significant effect was found when the same model was run using morphospecies abundance as a response variable.

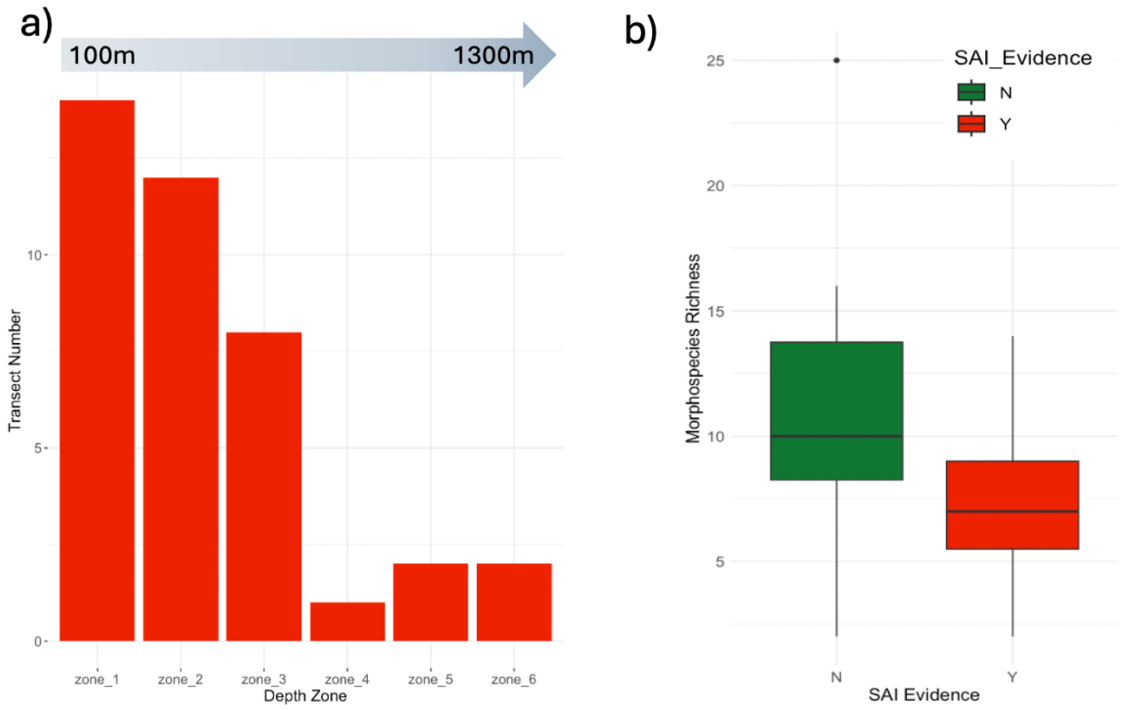


Figure 1.11. a) Bar plot showing the number of transects per depth zone in which evidence of SAIs was observed. b) Boxplot showing difference in VME morphospecies richness between transects where SAI evidence was present (Y) or absent (N). Code: finalchp1_ com_analysis.R

Discussion

This study found significant differences in richness, abundance, and community composition of VME morphospecies (Porifera and Cnidaria) along a depth gradient on Melville Bank seamount in the South-west Indian Ocean. A negative relationship between the presence of SAIs from bottom-contact fisheries and richness of VME morphospecies was also established.

Existing work on SWIOR seamounts to date has focused largely on their geomorphology (Swanborn et al., 2023), physical oceanography (Read and Pollard, 2017), and pelagic ecology (Laptikhovsky et al., 2017; Rogers, 2016; D. J. B. Swanborn et al., 2023), with less attention paid to their benthic inhabitants which play a foundational role in supporting life on seamounts (Bongiorni et al., 2010). The lack of overarching benthic ecological studies on seamounts is a concern in the face of the mounting anthropogenic pressures they face; pressures which have the potential to alter the ecological dynamics of benthic communities before baseline conditions are even established, complicating assessment of human impact (Clark and Koslow, 2007; Clarke et al., 2015; Williams et al., 2010) and any possible future restoration (Da Ros et al., 2019). This study, one of the few investigating seamount benthic ecology in the Indian Ocean (Hestetun et al., 2017; Marsac et al., 2020; Payne, 2015; Sautya et al., 2011; Taylor and Rogers, 2017), advances understanding of the ecology and vulnerability of VME communities in a globally significant yet chronically undersampled ocean region (Marsac et al., 2020).

Whilst global trends of marine biodiversity indicate an overall decrease of species richness with depth (Costello and Chaudhary, 2017), variation in this pattern has been shown to exist depending on the taxa, ocean basin and scale concerned. Previous studies investigating BDGs of seamount benthic communities have been historically concentrated in the Atlantic (Bridges et al., 2022; Eerkes-Medrano et al., 2020; Henry et al., 2014) and Pacific (McClain et al., 2010; Preez et al., 2016; Shen et al., 2021) where, because of their proximity to established American and European

oceanographic institutions and universities, a greater number of scientific research cruises have been undertaken than in the Indian Ocean (Ramiro-Sánchez et al., 2023). Such studies have shown mixed results, either finding no relationship between richness and depth over 250 and 950m depth range (Bridges et al., 2022), a unimodal relationship between 0 and 1600m (Henry et al., 2014) or a positive relationship, with increasing diversity with depth from 200 and 700m (Morgan et al., 2019). Our results show that on Melville Bank, richness of VME morphospecies significantly increases across the depth range studied (100 -1300 m), peaking at 900 - 1100m. The abundance of VME morphospecies on Melville Bank was found to significantly decrease with depth, a trend widely observed across deep sea environments (Costello and Chaudhary, 2017; Rex et al., 2006).

Depth is identified as a strong driver of benthic community composition on seamounts in the Atlantic (Bridges et al. 2022, Victorero *et al*. 2018) and Pacific (McClain et al. 2010; Du Preez 2016). Our results indicate that this trend holds true for a seamount in the Indian Ocean, with significant differences in beta diversity along a depth gradient of 100 - 1300m as shown by ANOSIM (Analysis of Similarity) and SIMPER (Similarity Percentage) analyses. A distinct community break is seen from 900m (Fig. 1.8), until which communities are dominated by assemblages of octocoral fans (Fig. 1.9) and lamellate sponges. Below 900m communities become richer, with dominating morphospecies being a branching glass sponge and whip coral. Deep sea octocorals are known to provide habitats and food for a variety of associated fauna, such as brittle stars, marine worms and crustaceans (Watling et al., 2011) thus

likely play an important biogenic role on Melville Bank (Taylor and Rogers, 2017). Interestingly, only one morphospecies, a Stylasterid, was found to be present in all depth zones investigated. Nearly half of all morphospecies identified were only found in one depth zone, potentially indicating niche specialisation of species with depth or limited dispersal (Melo-Merino et al., 2020). Such evidence supports the representation of multiple depths on seamounts in conservation strategies (Clark et al., 2012).

Bray-Curtis dissimilarity was highest between depth zones 1 and 6, and tended to be smaller between depth zones that were closer together (Table S1.5), indicating a gradual change in morphospecies composition with depth rather than sharp breaks between 200m depth zones, in agreement with globally established patterns for depth-diversity gradients (Gibson et al., 2005; Rowe, 1983; Sanders and Hessler, 1969). That said, there appears to be a large difference in composition between shallower (100 - 900) and deeper (900-1300) zones. This suggests that there may be a threshold or ecological boundary at around 900m, where conditions change and influence community structure. Such transition zones or 'ecotones' have been previously reported on seamounts at shallow depths related to the photic zone limit (Grinyó et al., 2018). In the case of this data, it is possible the community shift is linked to changes in temperature and salinities, which upon visual inspection appear to be distinct in zones 5 and 6 compared to other depth zones (Fig. 1.3), though in this study could not be statistically disentangled from depth (Fig. S1.1). Nutrient

availability, such as POC to depth, has also been shown to influence benthic megafaunal communities (Kuhnz et al., 2014) but was not investigated here.

As well as factors inherently linked to depth (temperature, salinity, pressure, light, nutrient availability) (Tyler, 2003), ecological factors (predation, competition, physical disturbance) can influence community composition (Dayton and Hessler, 1972). In this study, the effect of disturbance from bottom contact fisheries on VME diversity was measured based on the presence of SAIs (Fig. 1.4) in transects.

The destructive impact of bottom trawling on deep sea biodiversity has been well documented in soft-sediment environments (Maynou and Cartes, 2012; Pusceddu et al., 2014), with communities in trawled areas having reduced richness, abundance and an altered community composition (Tillin et al., 2006) compared to their undisturbed counterparts. Physical disturbance to seamount benthos from bottom contact fisheries has been documented in the north (Baco et al., 2020) and south Pacific ocean basins (Williams et al., 2010); 2020). In a study across 25 seamounts off Tasmania, bottom trawling was associated with dramatic decreases in habitat complexity and diversity (Williams et al., 2010), with recovery not seen even on a timescale of decades. The reduced diversity caused by trawling leaves an ecosystem functionally vulnerable, compromising its future ecological resilience (Pusceddu et al., 2014) and impacting deep sea services which are still being understood and quantified (La Bianca et al., 2023).

A previous study of deep sea litter along the SWIOR also using the video footage from the JC066 *RSS James Cook* Cruise established Melville Bank as having a high density of fishing gear compared to other nearby seamounts (Woodall et al., 2015), and is thus considered to be an exploited seamount. ROV footage used in this thesis showed evidence of SAIs from bottom contact fisheries on Melville Bank (trawling scars, coral rubble), which often coincided with depths at which discarded fishing gear was found. Despite the remote location of Melville Bank, we establish a significant negative relationship between evidence of SAIs from bottom contact fisheries and VME morphospecies richness (Fig. 1.11). Consequently, the ecological community on Melville bank cannot be considered pristine, it should be acknowledged that diversity trends established here may not be representative of Melville Bank's previous ecological status or 'baseline' prior to fishing activity. Currently, Melville Bank holds no protection status from the South Indian Ocean Fisheries Agreement (SIOFA). Results here highlight that despite its depth and remoteness, this seamount offers little refuge from industrial fishing.

Trawling activity influences not only benthic community richness but also community composition. For example, on seamounts along the Emperor Seamount Chain off Hawaii, trawled areas showed a shift in community composition away from stony scleractinian slow-growing corals and towards faster growing, structurally flexible communities of soft octocorals (Goode et al., 2020) that exhibited more resilience to trawling. It is thus a possibility that disturbed areas on seamounts undergo ecological ''phase shifts" akin to shallow-water coral reefs following bleaching disturbance

(McManus and Polsenberg, 2004), whereby those species with life histories more compatible to disturbance (faster growing, shorter generation times) begin to dominate. This could provide some explanation as to why most depth zones on Melville Bank were dominated by soft octocorals, which may have enough structural flexibility to avoid damage from trawl nets (Taylor, 2011). That said, with no data available of benthic communities prior to disturbance on Melville Bank, this remains speculation.

Conclusion

Work in this chapter represents the first attempt to resolve depth-diversity gradients of VME indicator taxa on Melville Bank, a seamount in the South-west Indian Ocean that has historically been heavily targeted by bottom-contact fisheries. VME communities provide important habitat frameworks for a range of deep-sea species; understanding their distribution with depth is thus key for informing effective management by regional fisheries management organisations such as SIOFA. Data presented here show that richness of VME morphospecies on Melville Bank increases with depth, with community turnover observed across the depth zones studied. This highlights the capacity for considerable community variation on individual seamounts, which should thus not be considered as single entities by scientific studies and management bodies. Evidence of fishing activity was found to directly contribute to reduced VME richness, highlighting the impact that human disturbance can have on diversity gradients in even these remote deep-sea habitats.

Chapter 2: Exploring Latitudinal Diversity Gradients of VME Indicator Species along the South-west Indian Ocean Ridge

Abstract

The Southwest Indian Ocean Ridge (SWIOR) is a region of global significance in terms of biodiversity and resource extraction, yet the benthic fauna of its seamounts remains poorly characterised. Understanding how the diversity of habitat-forming organisms constituting Vulnerable Marine Ecosystems (VMEs) is distributed spatially along this seamount chain is vital for informing management strategies by the South Indian Ocean Deep Sea Federation (SIODFA). This study investigates the richness of VME indicator species across four SWIOR seamounts, revealing a significant increase in richness along a latitudinal gradient that is influenced by water mass characteristics and substrate type. Among the seamounts studied, Coral seamount hosted the highest VME species richness, with diversity of Porifera morphotypes being particularly high. These findings illustrate the importance of deciphering patterns and drivers of deep-sea biodiversity on spatial scales relevant to the management efforts of Regional Fisheries Management Organizations (RFMOs) and caution against the treatment of seamount chains as homogenous units in global conservation efforts. Results also contribute towards characterising deep-sea diversity in this overlooked ocean basin.

Introduction

Increasing exploitation of deep sea resources (Armstrong et al., 2012) necessitates the implementation of sustainable management practices to safeguard marine biodiversity in offshore environments (O'Leary et al., 2020). The recent ratification of the High Seas Treaty (Deasy, 2023) aimed at conserving biodiversity in Areas

Beyond National Jurisdiction (ABNJ), marks a crucial advancement towards conserving deep sea habitats. Protecting ocean features that host Vulnerable Marine Ecosystems (VMEs), such as cold water corals and sponges, is particularly important given i) the foundational role these taxa play in supporting other deep sea species (Bourque and Demopoulos, 2018; Pham et al., 2015), and ii) their life history traits (slow growth rate, low fecundity) (Andrews et al., 2009, 2005) which render heightened vulnerability to the impacts of disturbance, for example, bottom contact fisheries (Bilan et al., 2023; Rogers, 2004; Williams et al., 2010).

Seamounts - defined as topographic elevations rising 1000m from the seabed (Staudigel et al., 2010) - are an example of a deep sea feature that host rich communities of VME indicator species (Bridges et al., 2021; Preez et al., 2016; Richer de Forges et al., 2000; Rogers et al., 2007; Watling and Auster, 2021). Seamount formation is closely tied to tectonic activity, particularly along mid-ocean ridges where the Earth's tectonic plates meet and diverge (Schmidt, 1999). Seamounts are thus often found in chains that can extend for hundreds of kilometres across the ocean floor, spanning broad latitudinal ranges and hosting unique and varied biological communities (Rogers, 2018). Understanding seamount VME distribution and its drivers on a latitudinal scale is therefore key for effective management of such vast areas by, for example, by Regional Fisheries Management Organizations (RFMOs) and the International Seabed Authority (ISA).

Latitudinal Diversity Gradients (LDGs) offer a lens through which to examine the broad biogeographical patterns of VME distribution (Gaston and Spicer, 2013). Well-documented in terrestrial and coastal marine taxa, LDGs often describe a parabolic relationship between species richness (number of species) and latitude, with richness peaking in the tropics and decreasing toward the poles (Whittaker et al., 2001), often linked to solar energy-temperature gradients (Clarke and Crame, 1997; Rohde, 1992; Roy et al., 1998). Yet, for deep sea environments like seamounts, our understanding of LDGs and their environmental drivers remains limited, largely due to the logistical challenges associated with deep-sea exploration (Llodra, 2006). Existing studies of LDGs in deep sea environments have reported mixed results, with the majority concentrated in the Atlantic, where both poleward decreases (Culver and Buzas, 2000; Hillebrand, 2004; Lambshead et al., 2001; Rex et al., 1993) and increases in richness have been demonstrated depending on the taxa concerned. Factors identified as driving patterns in latitudinal biodiversity in the deep sea include temperature, salinity, organic matter supply and oxygen (Puerta et al., 2020), and are inherently related to water mass characteristics. Given the lack of consensus on global patterns of deep sea LDGs, streamlining LDG research within the spatial boundaries of RFMO areas offers the greatest use for conservation efforts, ensuring that findings are, from a management perspective, directly relevant and actionable.

The Southwest Indian Ocean Ridge (SWIOR) is a seamount chain that extends 800 km from the central Indian Ocean to the Mid-Atlantic Ridge in the Southern Ocean. Rising from depths of 6000 metres, the ridge marks the separation between the

African and Antarctic plates and is one of the slowest spreading mid-ocean ridges in the world (Sauter et al., 2013). It contains a high density of seamounts of varied morphologies which has made it a target of many deep-water fisheries (Clark, 2009; Marsac et al., 2020; Rogers, 2018), yet is one of the least sampled deep-sea regions of the global ocean (Demopoulos et al., 2003).

The SWIOR traverses a subtropical convergence zone (Fig. 2.1), where the Agulhas Return Current, the Subtropical Front and the Sub-Antarctic Front create one of the most energetic hydrographic regions in the world (Pollard and Read, 2017). Seamounts along this ridge are thus exposed to a wide range of oceanographic conditions, including variations in temperature, salinity, and nutrient regimes (Djurhuus et al., 2017; Read et al., 2000). This complex hydrodynamic setup, as well as the ridge's varied topography and geomorphology (Swanborn et al., 2023), present a unique opportunity to assess how both oceanographic and physical features impact the diversity of Vulnerable Marine Ecosystems (VMEs). A better understanding of the latitudinal distribution of VME diversity and its environmental drivers along the SWIOR is crucial for the Southern Indian Ocean Fisheries Agreement (SIOFA) to implement informed spatial management strategies for these ecologically sensitive areas (Watling and Auster, 2017).

Through i) examining the latitudinal richness gradient of seamount VME communities across this unique hydrodynamic region, ii) exploring its environmental drivers and iii) investigating how richness of primary VME groups Cnidaria and Porifera change

along this gradient, this work provides a more detailed picture of how these taxa are distributed with latitude in this exploited ocean region.

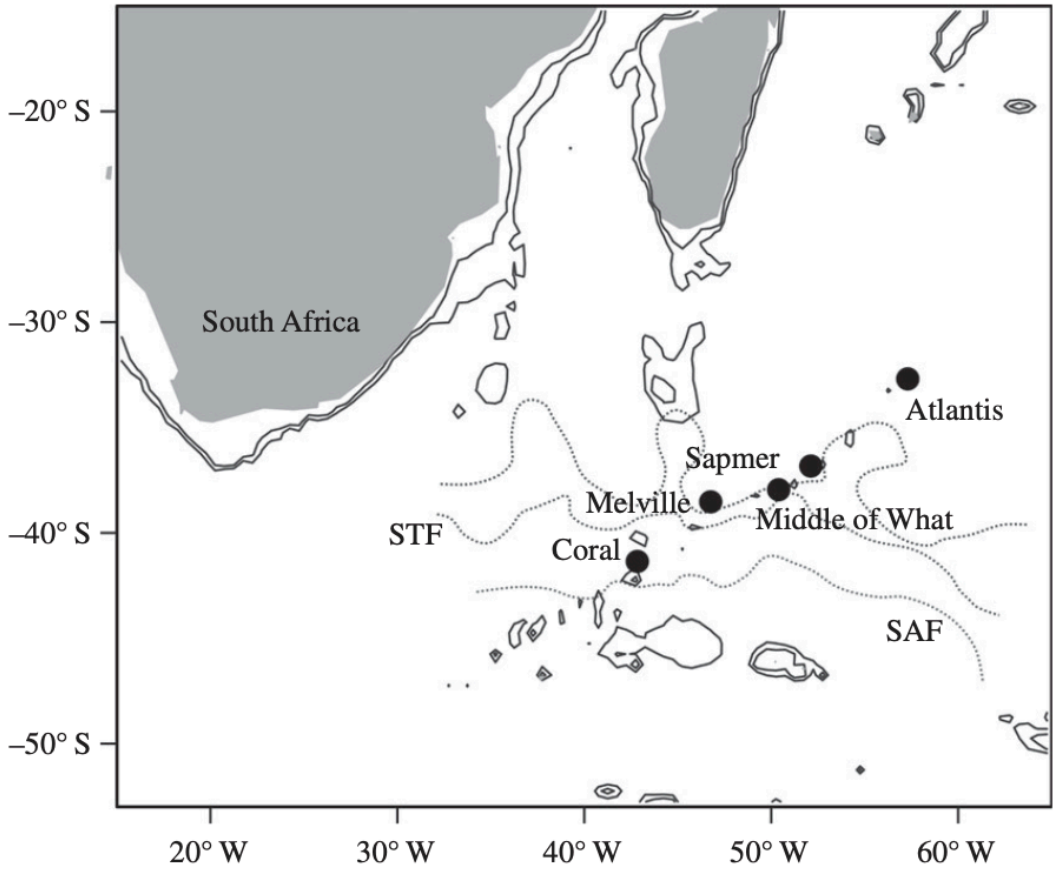


Figure 2.1. Locations of seamounts along the SWIOR in relation to regional water masses, taken from (Djurhuus et al., 2017). Solid lines represent the 1000m contour. Dashed lines represent the Agulhas Return Current, Sub-Tropical Front (STF) and Sub-Antarctic Front (SAF).

Methodology

Study Site: The South-west Indian Ocean Ridge

Atlantis

Atlantis seamount is located at 32°42'S, 57°16'E in sub-tropical waters (Fig. 2.2a). Its summit, which is dominated by areas of bare rock and sand, is at a depth of 700

metres with local topography extending 20 metres in height. It consists of cliff habitats characterised by anemones, sponges and octocorals. The seamount has been subject to fishing pressure, with gear damage visible in some areas. It has been assigned BPA (Benthic Protected Area) status by South Indian Ocean Deepsea Fishers Association (SIODFA).

Sapmer

Sapmer seamount is situated at 36°51'S, 52°9'E, along the central part of the SWIOR, west of the Galleini Fracture Zone at depths of 1600-2000m (Fig. 2.2b). The seamount is triangular shaped with three buttresses extending south-eastwards. The summit is at 250 metres depth and consists of irregular bathymetry.

Melville Bank

Melville Bank is located 38°28'S,42°49'E on the eastern side of the Indomed Fracture Zone of the SWIOR (Fig. 2.2c). It is elongated westwards over approximately 13.5km, with its shallowest section at about 100m on its eastern side and a deeper slope of 400m to the west. The shallower summit consists of extensive ridges from north to south and east to west resulting from mass wasting events (Pollard and Read, 2017). Melville Bank has been extensively targeted by bottom trawling as is evidenced by the prevalence of trawling scars and coral rubble (Fig. 1.4).

Coral

Coral seamount is located at 41° 25'S, 42° 51'E on a transverse ridge in sub-Antarctic waters (Fig. 2.2d), eastwards of the Discovery II fracture zone. It is located to the south of the Agulhas Return Current and Subtropical front and is thus bathed in cooler waters than the other seamounts surveyed. It has a depth range of 200m to

1200m and its shallowest point is 100m below the surface. Its summit area is located 200m below sea level and stretches southwards for approximately 18km. Flanks of the seamount are characterised by different slope gradients and morphologies. It has been assigned BPA status by SIODFA and is also recognised as an Ecologically and Biologically Significant Area (EBSA) under the Convention on Biological Diversity (CBD, 2015) due to its extensive framework of cold-water corals.

Video Collection

Data used in this project was collected during the JC066 cruise by the *RRS James Cook* (Rogers and Taylor 2012) from November 7th - December 21st in 2011 which set out to explore the benthic diversity of seamounts along the South-West Indian Ocean Ridge (SWIOR). Video footage during the research cruise was recorded by Remotely Operated Vehicle (ROV) Kiel 6000 which conducted survey dives over five seamounts. A high definition (HD) video camera attached to the ROV was run continuously during dives and the video data was saved onto a remote computer system on the *RRS James Cook*. Where possible, the ROV was surveying at 1m above the seabed at 0.2kts, however the rugged nature of the seabed made this difficult meaning the ROV was often between 1 and 2m above the seabed. A total of 16 dives were conducted during the cruise across four seamounts, spanning a latitudinal gradient from approximately 35 to 40 degrees south. Bathymetric maps of each seamount were generated using the *raster* package (Hijmans R, 2023) in R and the dive routes overlayed (Fig. 2.2). A CTD mounted on the ROV collected temperature, salinity and pressure information throughout dives. Three lasers, each

10 cm apart, were mounted on the ROV parallel to the camera to provide a triangle of points that provided a scale in images and videos.

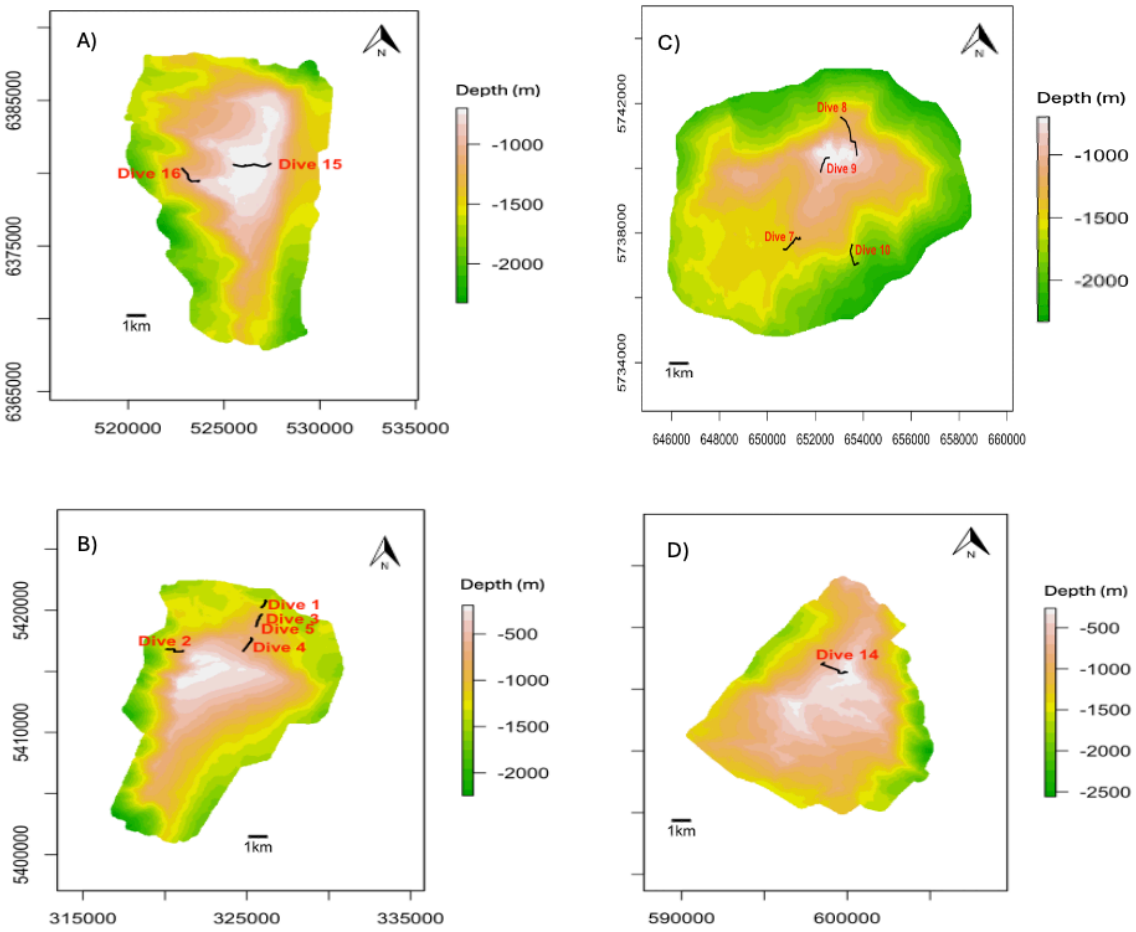


Figure 2.2. Bathymetric maps of a) Atlantis b) Sapmer c) Melville Bank and d) Coral seamounts with ROV dive routes used in this study overlayed. Code: atlantis_routes.R, sapmer_routes.R, melville_routes.R, coral_routes.R

Benthic Community Data Collection

All dive footage was first manually sorted to identify annotatable sections (those 1-2m from the seafloor and thus visible) and these videos were subsequently converted into .mp4 format and imported into Biigle (Langenkamper et al. 2017), an annotation software specifically developed for processing of marine image databases. Cnidaria,

Porifera, Echinodermata, Bryozoa and Crustacea were annotated. Individuals below a size threshold of ~ 3 cm were excluded from annotation. A total of 1,364 annotations were made on Atlantis, 1,219 on Sapmer, 5,228 on Melville Bank and 6,884 on Coral.

Organisms were identified first by assigning high level morphological classifications following the CATAMI scheme to annotations (Althaus et al. 2015). Using the 'largo' tool, any duplicate records were removed. Since standard genetic approaches for determining taxonomy are not applicable to video data, taxonomic resolution of labels was resolved to distinct morphospecies via grouping of organisms based on visual similarities. This grouping may correspond to a species, genus, family, or higher taxonomic level. Each organism was assigned the highest taxonomic resolution possible with assistance from deep sea taxonomy expert Dr Michelle Taylor and reference to the SMarTaR-ID online database (Howell et al. 2019).

Environmental Metadata Collation

Biigle output reports containing morphospecies observations were combined with geographic coordinates and CTD data (temperature, salinity, depth) from JC066 cruise reports based on common capture times using custom code in R (R Core Team., 2022). Gradient values for each coordinate of the dive route were extracted from seamount raster files in R using the raster() package and also added to the output report. Data on mean surface productivity was downloaded from Bio-ORACLE (Assis et al., 2018), resampled and reprojected to 50 metre resolution using a bilinear method in the raster R package and subsequently added to dive files. Substrate categories (Fig. 2.3) were manually added to transects based on referring to video

duration time. The output files were then run through an interpolation script (which considered depth and earth curvature using haversine formula) to obtain decimal coordinates for every metre of the dive route. These interpolated files were then divided into 50 metre transects (Table 2.1). Transects were filtered to contain VME morphospecies observations only. These included Cnidaria, Porifera, Bryozoa and stalked Crinoidea, in accordance with the VME indicator species list adopted by SIOFA (SIOFA, 2018). A total of 209 distinct VME morphospecies were identified across all four seamounts.

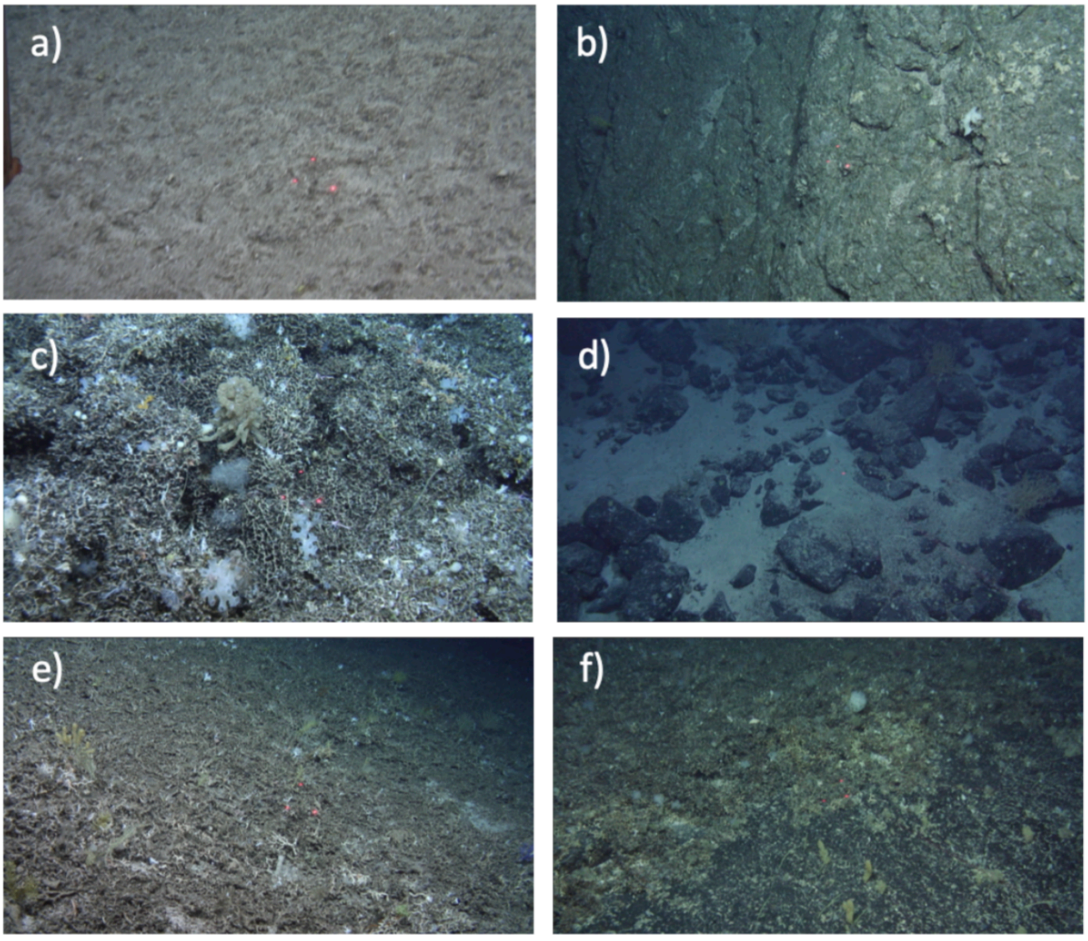


Figure 2.3. Example images of substrate classes seen in video footage, a) sediment, b) volcanic, c) biogenic matrix, d) volcanic and sediment, e) coral rubble f) volcanic and biogenic.

Data Processing

The relevant metadata for each 50 m transect was loaded as a .csv text file into R studio, where they were used to construct a data frame with each row representing a transect. Data describing the morphospecies richness, abundance, seamount name and dive number for each transect were added along with a binary code for presence of Significant Adverse Impact (SAI) evidence, taken to be either coral rubble or trawling scars (Fig. 1.4). Transect information for this dataset is shown in Table 2.1a. To compare diversity metrics while controlling for depth, a secondary analysis was restricted to only transects from within a 600 - 800 metre depth range from each seamount, thus standardising the depth of communities analysed (Table 2.1b). It should be noted that significant adverse impacts were seen within this depth range on Sapmer, with large trawling scars evident (S2.7), which may affect diversity measured at this site.

Table 2.1. Transects used in GLMMS a) all transects from all depths b) transects from 600-800m depth range only.

a)

Seamount	Number of 50m transects	Depth range (m)	Total distance / km
Atlantis	39	701-1100	1.95
Sapmer	27	381-701	1.35
Melville Bank	66	108-1304	3.30
Coral	89	517-1306	4.45

b)

Seamount	Number of 50m transects	Depth range (m)	Total distance / km
Atlantis	31	698 - 749	1.55
Sapmer	12	605 - 701	0.60
Melville Bank	18	600 - 785	0.90

Coral	**29**	**602 - 797**	**1.45**

Statistical Analyses

All statistical analyses were conducted in R studio. The completeness of sampling effort at each seamount was assessed based on sampling coverage curves generated using the iNEXT R package (Hsieh et al., 2016) (Fig. 2.4). Sampling coverage is a metric that gives information on what portion of the total number of individuals in a sample are accounted for by the species observed. It therefore offers a standardised level of sample completeness (Chiu, 2023). Based on observed data at each seamount, sample completeness was estimated at > 0.9 for each site and this was taken as adequate from which to calculate richness estimates and rarefaction was not conducted. Morphospecies richness for each site standardised by transect number was plotted with standard deviations (Fig. 2.5).

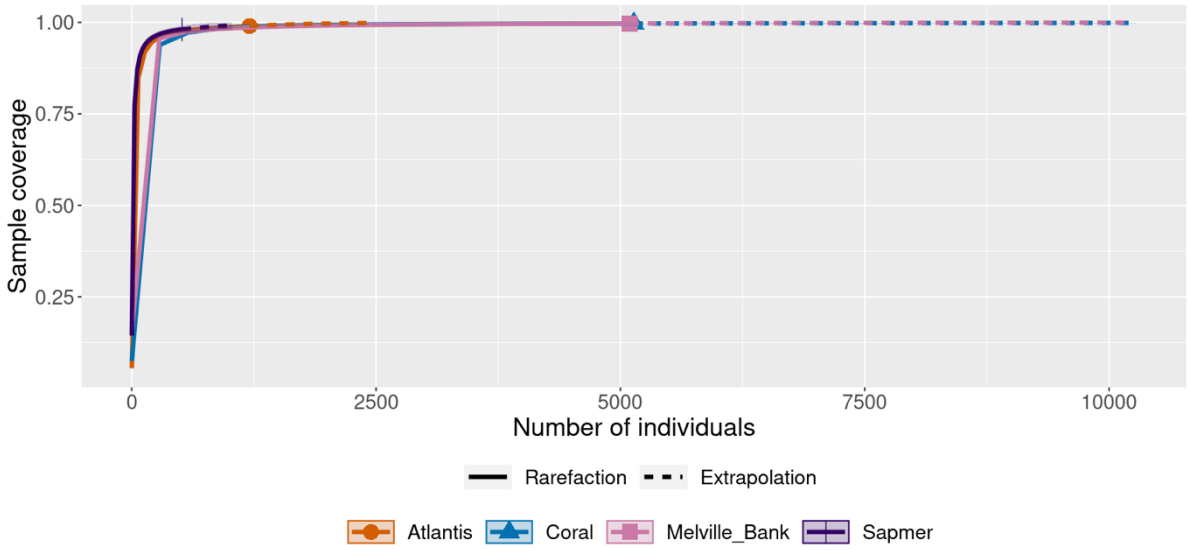


Figure 2.5. Sample completeness curve based on coverage using data from each seamount, generated using iNEXT.

Hill numbers (q = 0, q = 1, q = 2) were plotted out using all data for each seamount (Fig. 4). Given that our estimation of sample completeness was based on sample coverage, the metric (q=0) was used for further analyses. An Analysis of Variance (ANOVA) between seamounts showed significant differences in morphospecies richness, the direction and magnitude of which were further explored in a post hoc Tukey test (Table 2.2).

To explore environmental drivers of the biogeographic richness trends observed, a general linear mixed model (GLMM) was employed on data from all transects (Table 2.1a). A negative binomial distribution was selected based on the distribution of morphospecies richness variable and the presence of overdispersion in the dataset. Environmental variables salinity, temperature, gradient, and surface primary productivity were standardised to enable direct comparison using the scale() function in R, which gives variables a mean of 0 and a standard deviation of 1. Substrate categories (Fig. 2.3) were converted from character to numeric values and added as factors to the model. Prior to running the model, a Pearson's correlation analysis was performed on the scaled continuous environmental variables to assess the strength of linear relationships between them (S2.1). A cut-off was set for correlations of over 0.7. Temperature was strongly correlated with depth (p = -0.85). To account for this, depth was included as an interaction term in the model. Surface primary productivity is clustered strongly by seamount (S2.2), an expected consequence of the low-resolution Bio-ORACLE data, so this variable was not included in the model. Given the finding from Chapter 1 that SAI evidence can negatively impact morphospecies

richness, this factor was included in the model as a fixed effect. To account for sources of potential non-independence in the data, 'dive', was included as a random effect, which also accounted for the variation between seamounts. A sensitivity analysis was performed between four models (S2.3) to investigate their robustness using different distributions (negative binomial versus Poisson distributions) and either accounting for zero inflation or not. Using results from this analysis, a negative binomial distribution without zero-inflation was selected for the final model.

Given the observed correlations among temperature, depth and salinity across the dataset containing all transects, an analysis was conducted using a subset of the data that exclusively contains transects within a 600-800m depth range on seamounts (Table 2.1b). This approach aimed to mitigate confounding impacts associated with depth. Subsequent examination of pairwise correlations between variables with this reduced dataset showed all Pearson's coefficients to be < 0.7 (S2.5), and so all variables were included in the GLMM. A model sensitivity analysis again showed a negative binomial distribution without zero-inflation to be the best fit for this model (S2.8).

To investigate richness distribution among dominant VME groups, datasets were filtered for Porifera and Cnidaria morphospecies only (these are the main contributors to VME communities) and richness gradients for groups within these were plotted individually.

Results

Diversity of VME Morphospecies Varies Significantly between Seamounts

By plotting richness data standardised by transect number, richness of VME morphospecies was shown to increase from Atlantis to Coral seamount, with a dip at Melville Bank (Fig. 2.5). The pattern of increasing richness from north to south was confirmed using the reduced dataset from the 600-800m depth zone (S2.4).

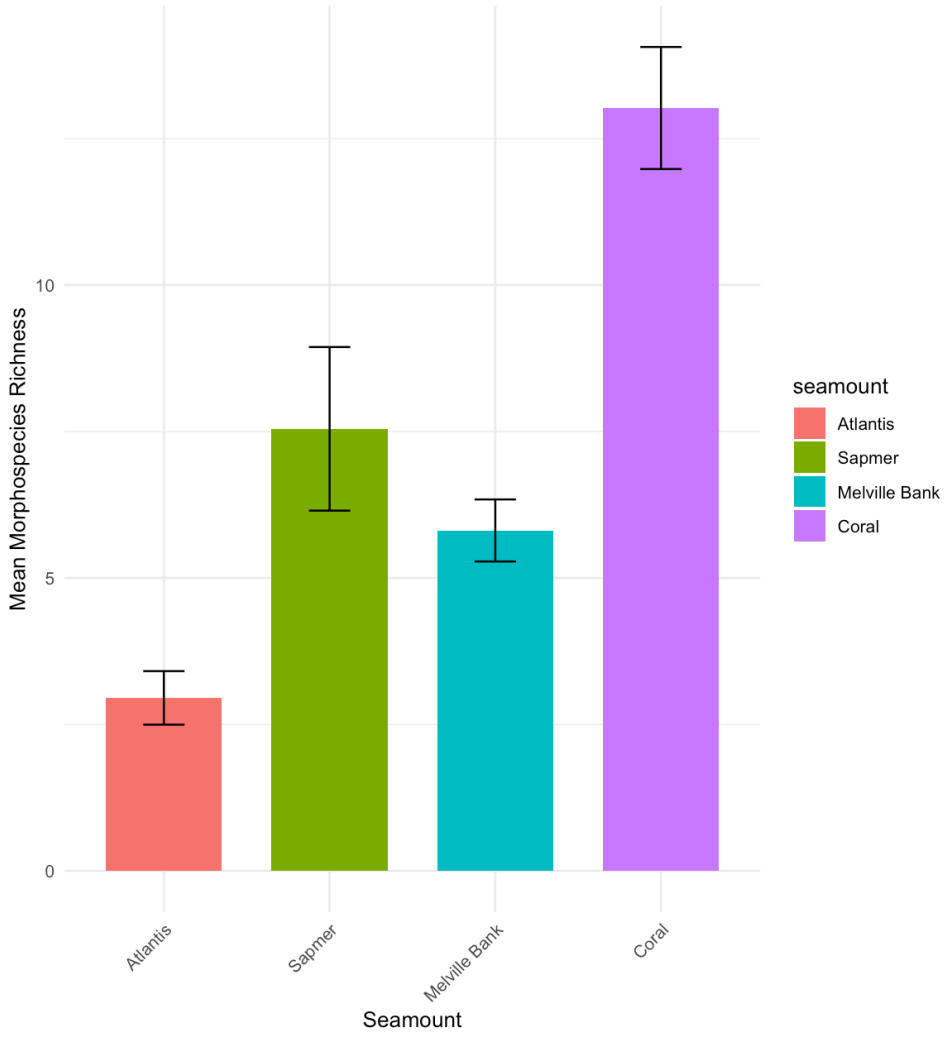
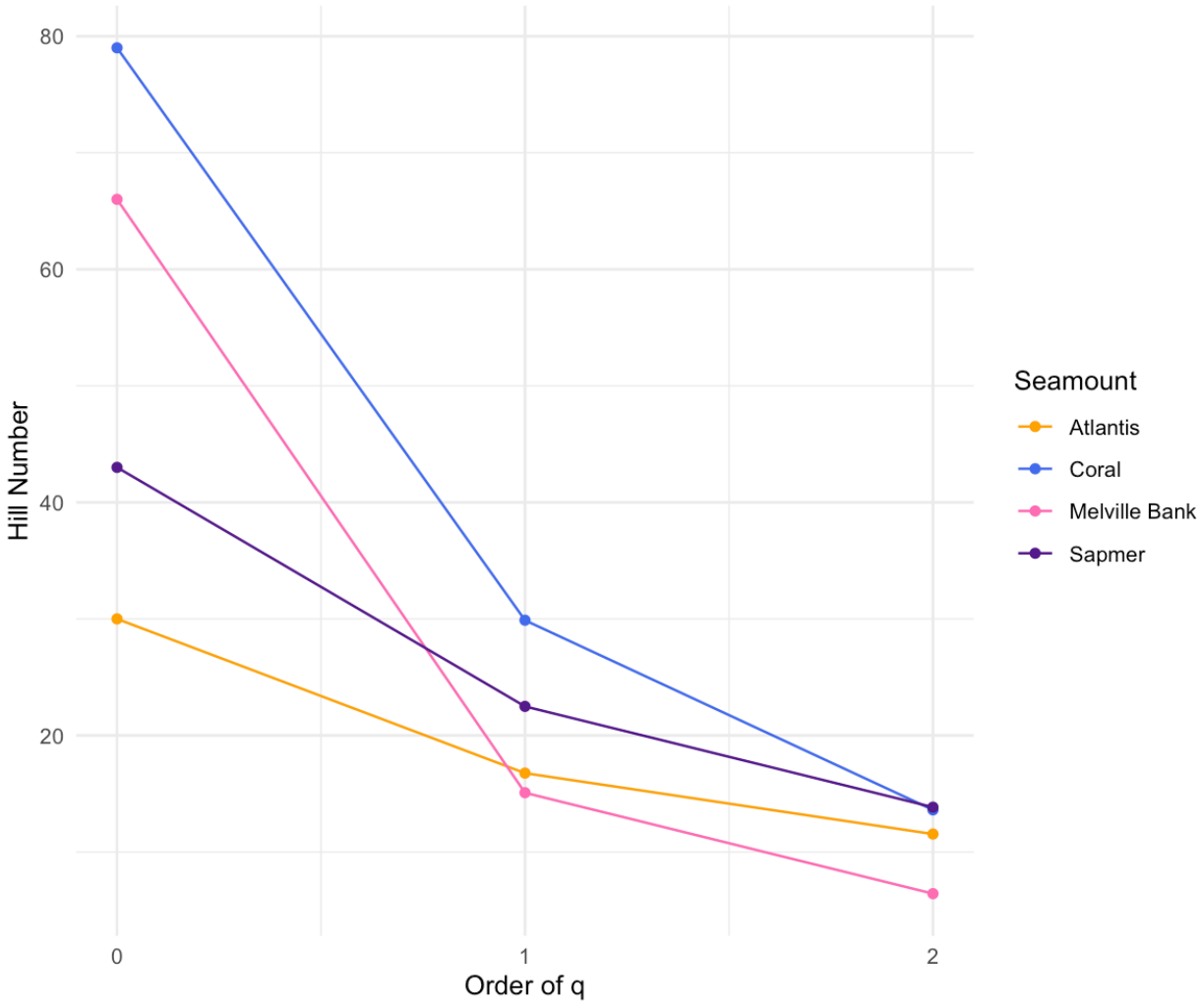


Figure 2.5. Bar plot of VME richness using data from all transects across all seamounts, standardised by transect number. Code: bargraphs2.R



igure 2.5. Hill numbers plotted for each seamount based on raw data. q = 0 is richness, q = 1 is Shannon index q = 2 is Simpson index. Code: hill_numbers_ANOVAS.R

A plot of Hill numbers calculated for each seamount (Fig. 2.5) shows that Coral had the highest diversity of all metrics tested except when q = 2, which considers morphospecies evenness. An ANOVA revealed that richness differences (q = 0) between seamounts were significant, and a post-hoc Tukey test showed that differences are significant between all seamounts apart from Sapmer and Melville Bank, with the largest richness difference being between Coral and Atlantis. Taken

together, this suggests increasing gradient of VME morphospecies richness from north to south along this seamount chain.

Table 2.2. Tukey test of differences in VME morphospecies richness between seamounts on raw data for q = 0

Seamount Comparison	diff	lwr	upr	p adj
Coral-Atlantis	5.57591472	3.6292073	7.5226221	**0.001** **
Melville Bank-Atlantis	3.0990676	1.0516173	5.1465179	**0.001** **
Sapmer-Atlantis	3.05698006	0.5190434	5.5949167	**0.01** *
Melville Bank-Coral	-2.47684712	-4.1235752	-0.8301191	**0.001** **
Sapmer-Coral	-2.51893467	-4.7462162	-0.2916532	**0.02** *
Sapmer-Melville Bank	-0.04208754	-2.3579386	2.2737635	0.9

Seamounts Are Bathed in Water with Significantly Different Properties

Boxplots of environmental variables temperature, salinity and density highlight the differences in water properties surrounding each seamount (Fig. 2.6). ANOVAs of temperature and salinity and post hoc Tukey test showed that waters bathing Coral have significantly lower temperatures than all other seamounts ($P < 0.0005$), due to its location in sub-Antarctic waters. Waters bathing coral this have an increased density compared to those surrounding other seamounts investigated in this study. Sapmer and Melville Bank were shown to have significantly higher salinity and temperatures than other seamounts, which is a likely by-product of their proximity to retroflection from the Agulhas current, a western boundary current of the south west Indian Ocean which transports warm, salty water along the east coast of South Africa

(Lutjeharms, 2007). Though productivity metrics were not collected during dives, this data was downloaded for each seamount from Bio-ORACLE and plotted (Fig. 2.7). This shows an overall trend of increasing surface productivity from Atlantis in the north to Coral in the south.

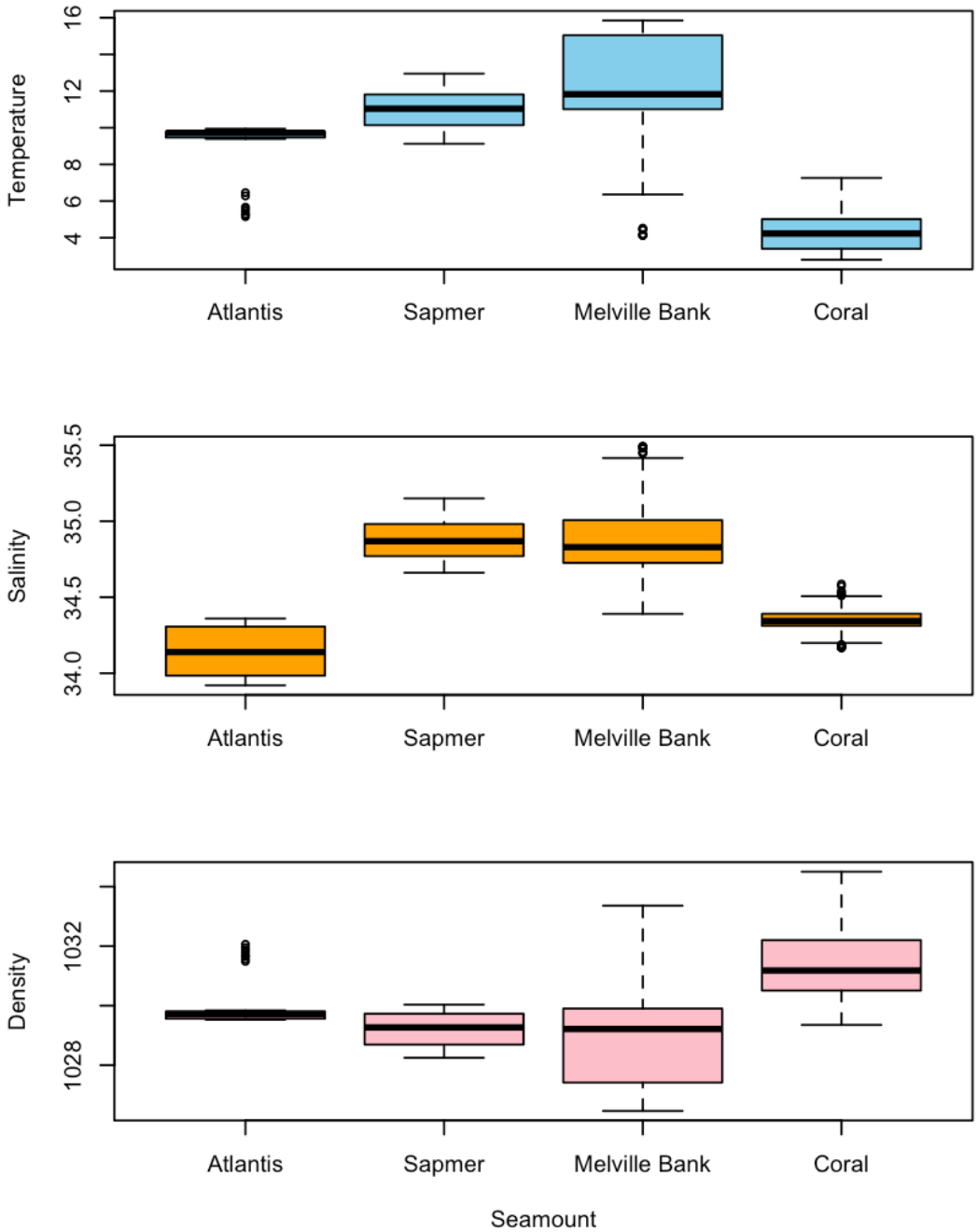


Figure 2.6. Boxplots of temperature, salinity and density values for each seamounts using data frmo all transects. Code: richness_models.R

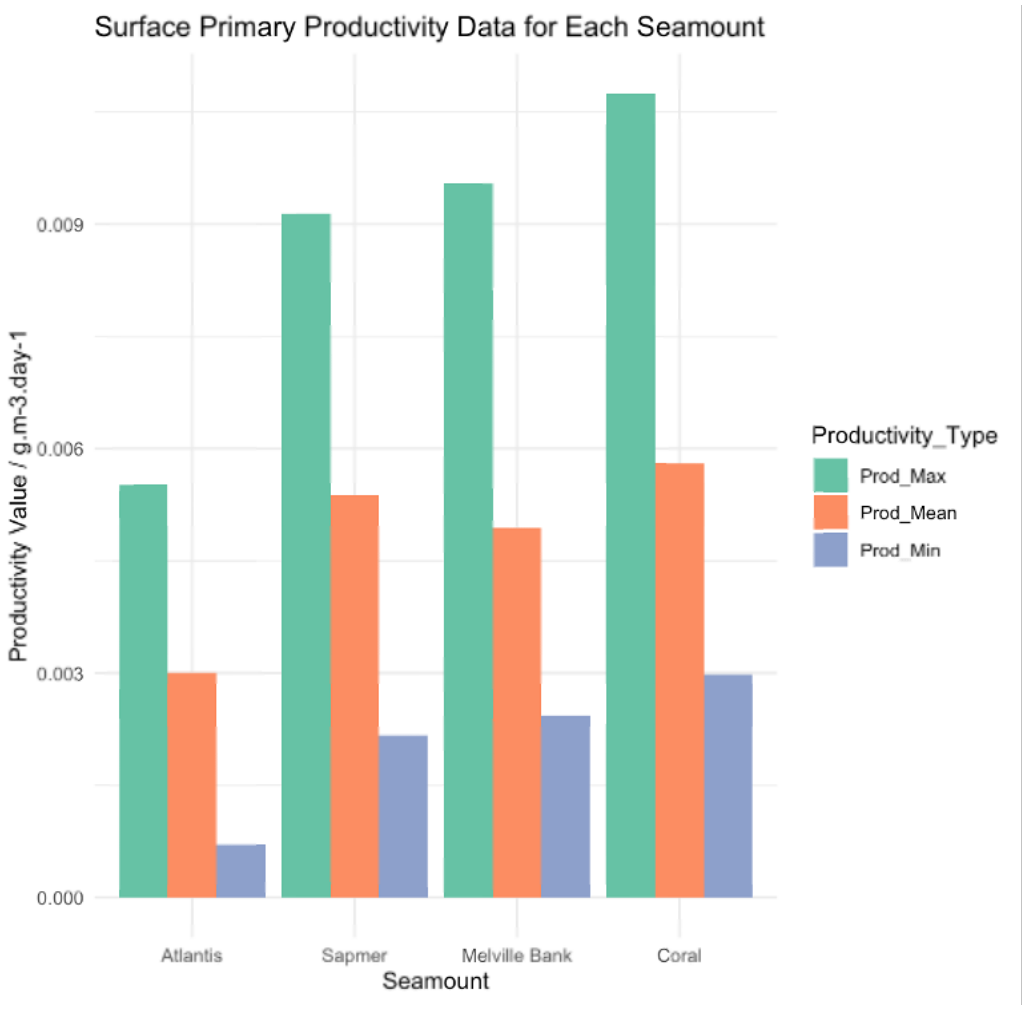


Figure 2.7. Surface primary productivity data for each seamount downloaded from Bio-ORACLE, showing minimum, maximum and mean productivity values from 2010 - 2020 (Assis et al., 2018).

Water Mass Characteristics, Depth, and Substrate Drive VME Richness Gradients Along the SWIOR

A GLMM following a negative binomial distribution showed several variables to be significant in driving VME morphospecies richness across seamounts (Table 2.3). Temperature and depth were shown to have a significant negative correlation with morphospecies richness, whilst salinity, gradient and biogenic matrix were positively associated with richness.

Table 2.3. Output of GLMM investigating drivers of VME richness across seamounts. Code: all_transects_GLMM.R

Variable	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	1.476165	0.18495	7.981	1.45E-15
Temperature	**-0.683017**	**0.134409**	**-5.082**	**0.0000004 *** **
Salinity	**0.399927**	**0.102253**	**3.911**	**0.00009 *** **
Gradient	0.118231	0.068678	1.722	0.09
SAI_Evidence	0.266876	0.149775	1.782	0.07
Volcanic and Sediment	0.132656	0.178328	0.744	0.5
Sediment	-0.338374	0.244236	-1.385	0.2
Biogenix matrix	**0.72117**	**0.251261**	**2.87**	**0.004 ** **
Depth	**-0.514539**	**0.152428**	**-3.376**	**0.0007 *** **
Temperature:Depth	*0.027281*	*0.108276*	*0.252*	*0.8*
Salinity:Depth	*0.033135*	*0.106012*	*0.313*	*0.7*
Gradient:Depth	*0.02279*	*0.060698*	*0.375*	*0.7*
SAI_Evidence:Depth	*0.063108*	*0.123708*	*0.51*	*0.6*
Volcanic and Sediment:Depth	*-0.009793*	*0.15194*	*-0.064*	*0.9*
Sediment:Depth	*0.108036*	*0.200647*	*0.538*	*0.6*
Biogenix matrix : Depth	*0.164182*	*0.251878*	*0.652*	*0.5*

The fact that there are no significant interaction terms between depth and any variables is reflective of the different hydrodynamic regimes that exist in the region.

Therefore, even though temperature is highly correlated to depth and salinity, as evidenced by its high Pearson's correlation coefficient (S2.1), their effects in the model appear to be separate when predicting richness.

A GLMM on the reduced dataset from a 600-800m depth zone showed temperature to be the most significant driver of VME morphospecies richness, followed by salinity. Lower temperatures and higher salinities were associated with a higher richness of VME morphospecies across the depth range studied (Table 2.4). Transects with volcanic and sediment or biogenic matrix substrates were also associated with higher richness.

Table 2.4. Output of GLMM investigating environmental drivers of VME morphospecies richness across seamount using reduced dataset from 600-800m. Code: richness_models.R

Variable	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.69006	0.24982	2.762	0.006
Temperature	**-0.82299**	**0.18457**	**-4.459**	**0.000008 ******
Salinity	**0.61757**	**0.1794**	**3.442**	**0.0006 ****
Depth	0.19728	0.63829	0.309	0.7
Gradient	-0.05112	0.13027	-0.392	0.7
SAI_EvidenceY	0.38947	0.32413	1.202	0.2
Biogenic_matrix	**0.64632**	**0.34449**	**1.876**	**0.06 .**
Coral_rubble	0.02089	0.27638	0.076	0.9
Volcanic_sediment	**0.8926**	**0.30308**	**2.945**	**0.003 ****

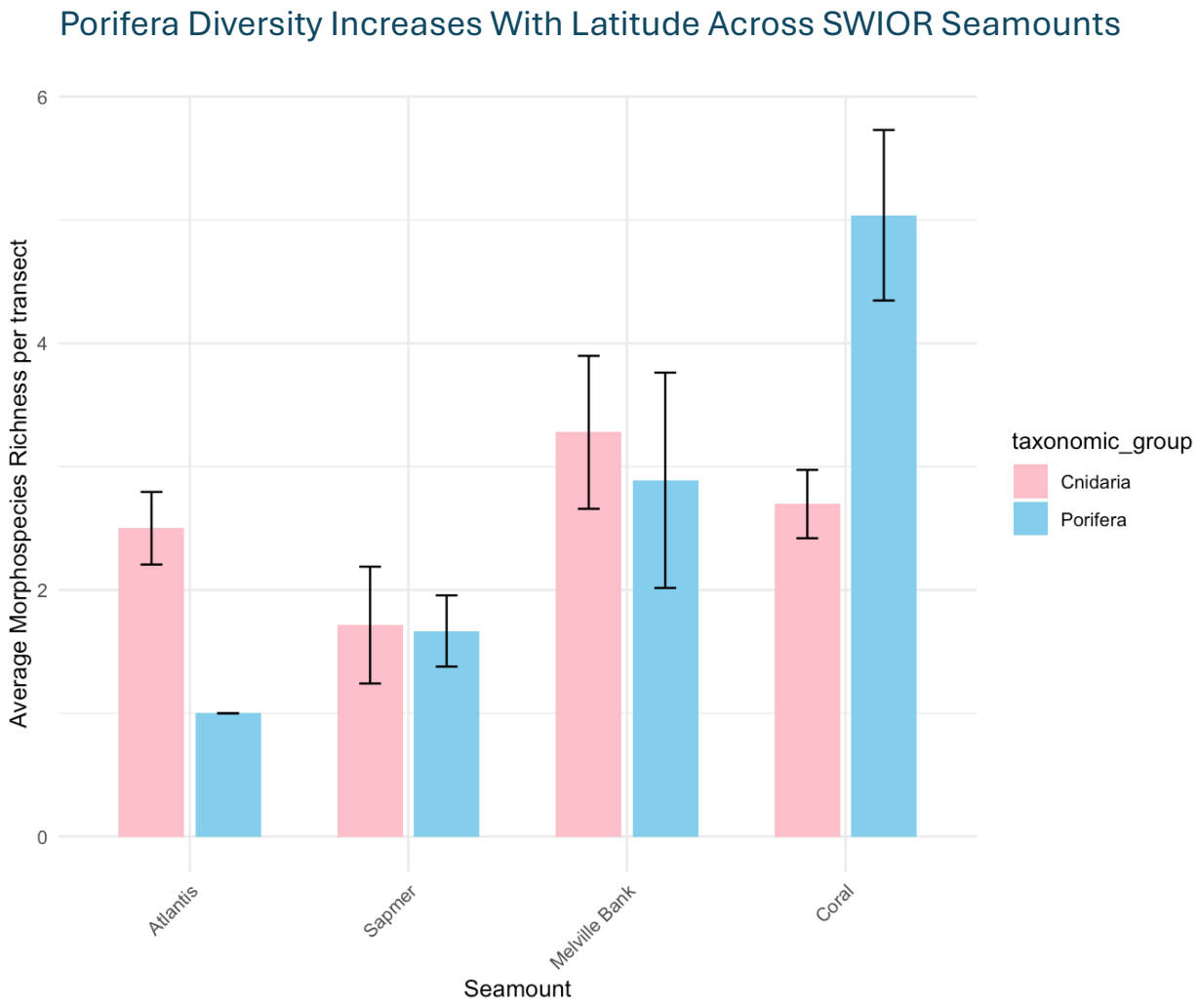


Figure 2.8. Bar chart showing average richness of Cnidaria and Porifera per transect per seamount, with error bars showing SEM. Code: comp_per_transect.R

A plot of average richness of Cnidaria and Porifera per transect on each of the seamounts revealed a significant increase in Porifera richness across seamounts from north to south, peaking at Coral seamount (Fig. 2.8). When the richness of Porifera morphotypes was plotted (Fig. 2.9), it was evident that this was driven

primarily by massive and cup-like sponge morphologies. Images of the most common sponge morphotypes on Coral seamount are shown in Figure 2.10.

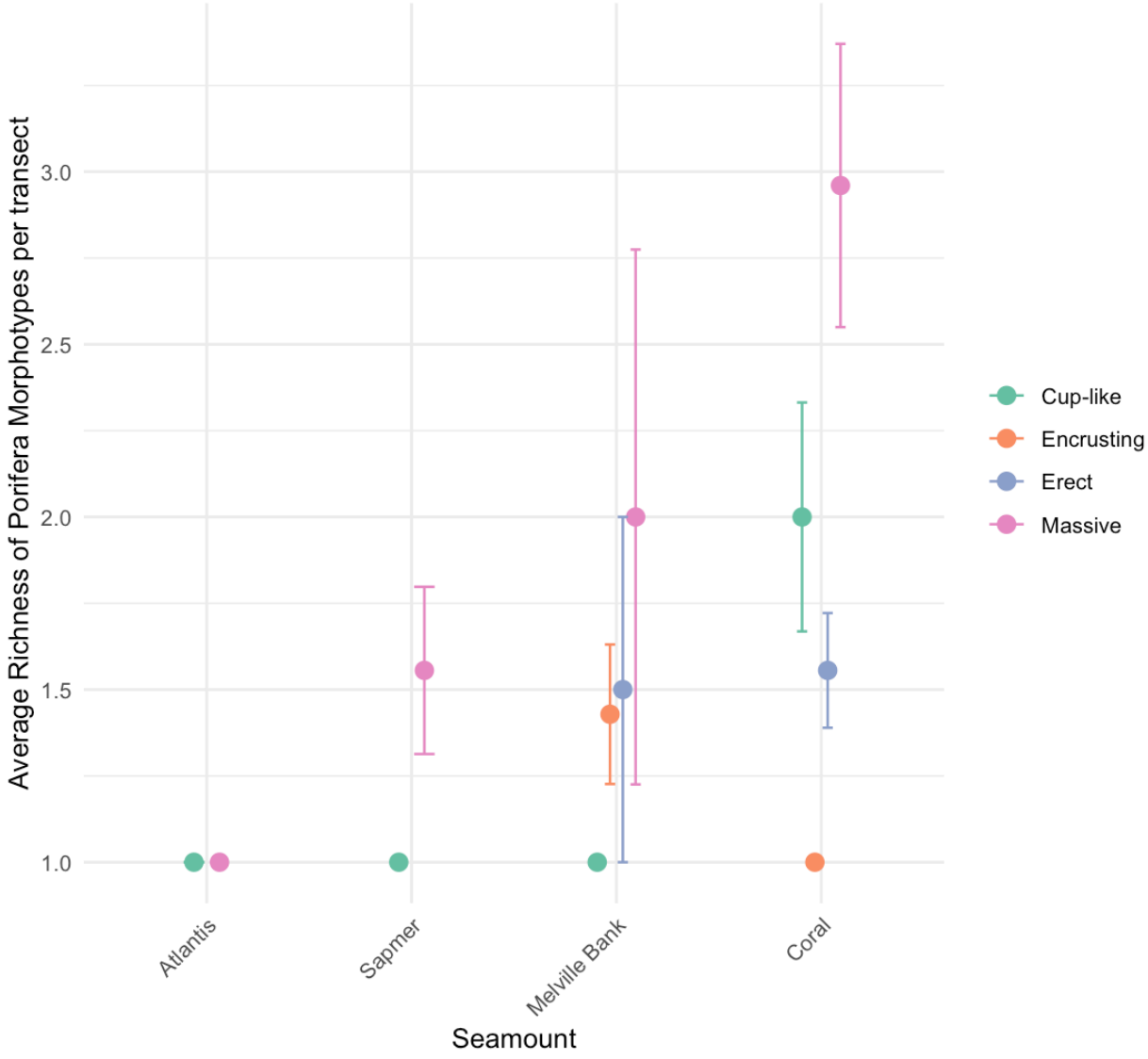


Figure 2.9. Variation in the average richness of Porifera morphotypes per transect across seamounts from reduced dataset. Error bars indicate standard error of the mean (SEM). R code: comp_finer_porifera.R

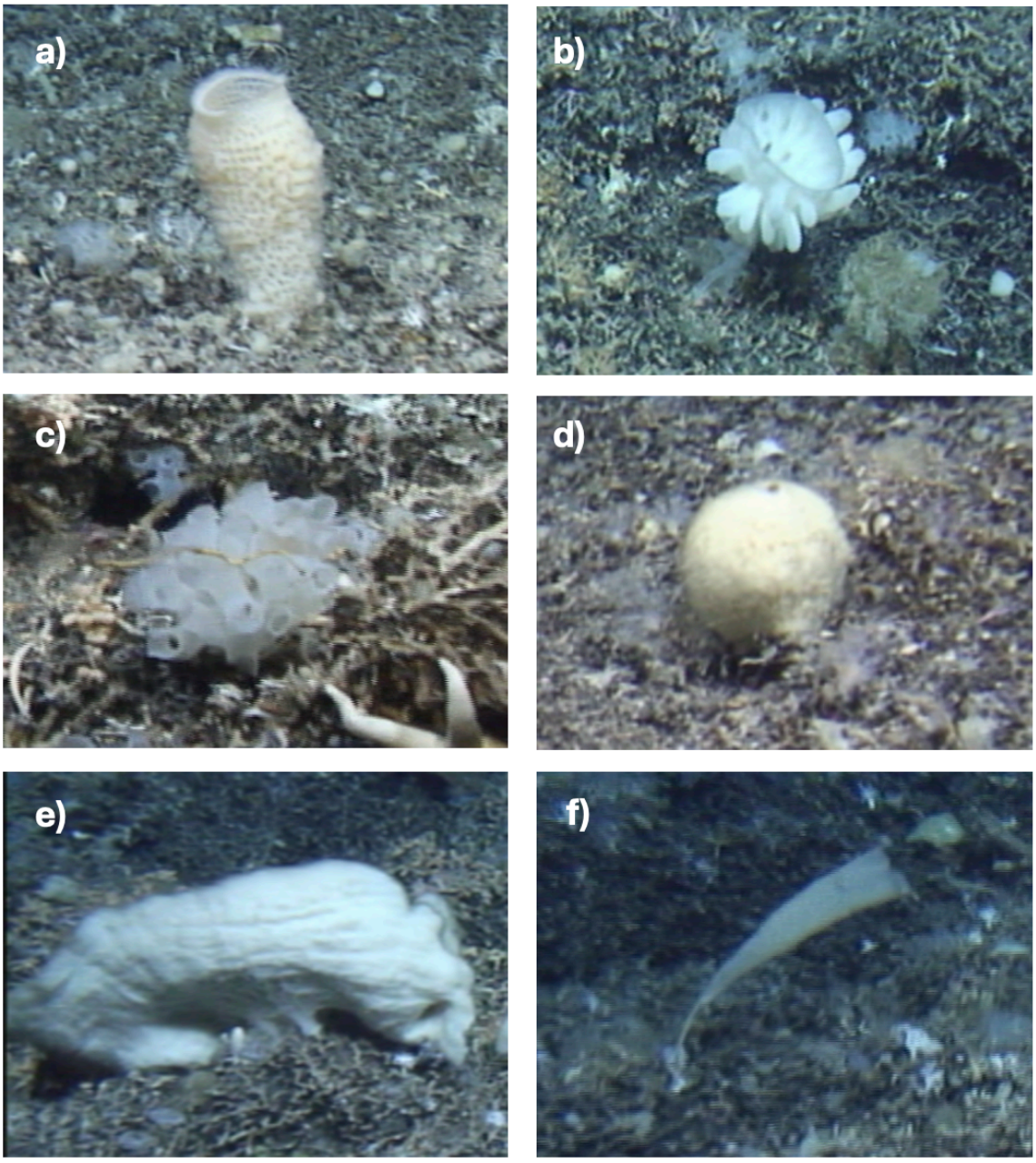


Figure 2.10. Images of common Porifera morphotypes found on Coral seamount from a 600-800m depth range. a) Euplectellidae msp. b) Aphrocallistes msp. c) Farreidae msp. d) Demospongiae ball msp. e) Demospongiae 2D lamellate msp. f) Hexactinellida stalked cone msp. (msp = morphospecies).

Discussion

Seamount biodiversity in the Indian Ocean is poorly understood compared to other ocean basins (Demopoulos et al., 2003). The SWIOR represents a globally significant region in terms of both marine ecology, hydrodynamics, geology and resource extraction (Marsac et al., 2020). To date, literature on benthic fauna along the SWIOR has focused on species discovery (Hestetun et al., 2017; Taylor and Rogers, 2017) and taxonomy (Serpetti et al., 2017) rather than systematic surveys of distribution and their drivers, which is required to inform spatial management of the biodiversity along this seamount system.

That water mass characteristics can drive biodiversity and biogeography in deep-sea fauna has been previously documented. Variables such as temperature (Yasuhara and Danovaro, 2016), flow regime (Mienis et al., 2014), oxygen concentration (Levin et al., 2003; Woulds et al., 2007), productivity (Cathalot et al., 2015), and circulation (Henry et al., 2014; Somoza et al., 2014) have all been shown to influence deep sea biodiversity distribution. Marine communities on seamounts along the SWIOR are exposed to a pronounced temperature gradient at the subtropical convergence zone, where the cooler sub-antarctic meets the warmer subtropical front (Fig. 2.1). Retroflections from the Agulhas current can also increase the temperature and salinity of water in this convergence zone. As a result, Coral seamount is situated in a temperature / salinity regime that is distinct from all other studied seamounts, being significantly cooler and less saline than the waters bathing Atlantis, Sapmer, and Melville Bank (Fig. 2.6). The seamounts also host diverse geomorphologies, characterised by sharp topographic gradients and a range of different substrate

types. Understanding how both these oceanographic and physical features impact richness of habitat-building species on a latitudinal scale was the primary aim of this chapter.

Our findings highlight the critical role of temperature in influencing VME richness across a latitudinal gradient on the SWIOR, with cooler conditions of the sub-Antarctic front fostering greatest morphospecies richness at Coral compared to other seamounts (Fig. 2.4). Salinity was positively associated with richness but had a smaller and less statistically significant effect than temperature. Temperature gradients have previously been shown to influence latitudinal diversity patterns among various coastal marine species (Harrison and Whitfield, 2006; Macpherson, 2002; Sharifian et al., 2021). Their effect on the richness patterns of deep sea species is less well understood, though there is evidence to suggest a significant relationship between temperature and diversity from studies of both modern and historical deep-sea communities in the Atlantic (Danovaro et al., 2004) and Pacific oceans (Doi et al., 2021). Less research attention has been paid to the role of temperature on latitudinal richness gradients of deep-sea biodiversity in the Indian Ocean. This study is therefore a useful contribution towards characterising deep sea species richness gradients in this overlooked ocean basin.

Temperature may be a significant factor shaping latitudinal diversity patterns due to the different physiological thermal tolerances of deep sea taxa (Tittensor et al., 2010; Yasuhara and Danovaro, 2016). It may also trigger effects on richness gradients in combination with other factors, such as productivity (Bodil et al., 2011; Bridges et al.,

2022; Corliss et al., 2009; Woolley et al., 2016) or oxygen content (Levin and Gage, 1998), which are inherently related to ocean temperature. The Southern Ocean is known for its highly productive, oxygen-rich waters due to continuous daylight hours throughout the Antarctic summer which enhances the photosynthetic activity of marine algae (Arrigo et al., 1998; Griffiths, 2010). The organic matter produced by algal blooms falls to the seafloor in dense, nutrient-rich, oxygenated water which descends from the euphotic zone to the ocean floor, supporting diverse benthic communities (Corliss et al., 2009). This may explain why Coral seamount, bathed in sub-Antarctic waters, was found to harbour richer VME communities compared to other seamounts studied here.

For this study, high-resolution surface primary productivity data were not available for inclusion in GLMMs to differentiate productivity effects from seamount characteristics, however plots using data from Bio-ORACLE(Assis et al., 2018) indicated the highest surface primary productivity at Coral and the lowest at Atlantis (S5), mirroring the trend observed in VME morphospecies richness. Previous work along the SWIOR has established increasing gradients of phytoplankton biomass from Atlantis to Coral seamount (Djurhuus et al., 2017). Concentrations of oxygen and nitrate have also been found to be highest at Coral seamount (Sonnekus et al., 2017), mirroring the trend found here in VME richness. Future studies which monitor these environmental variables at the same depth ranges as benthic video surveys are recommended to confirm links between nutrient and productivity regimes with benthic biodiversity patterns. The data from this study has been sampled from upper bathyal depths (< 2000m) and therefore may be influenced by surface primary productivity more than

deeper waters where organic matter is scarce due to bacterial remineralization (Goldthwait et al., 2005). It is therefore possible that trends observed here may not be observed in data sampled from deeper areas. Investigation of productivity on VME richness to test the energy-richness hypothesis for this region, which posits that species richness can be explained by the availability of energy in an environment (Evans et al., 2005) would be a valuable progression of this work.

Both GLMMs conducted in this study found that substrate type was a significant factor in driving VME morphospecies richness along the SWIOR. Biogenic matrix was shown to have a significant positive impact on VME richness. In the reduced dataset, the volcanic and sediment substrate class was also associated with higher richness of VME morphospecies. The influence of bottom substrate on benthic diversity in ocean environments has been well-documented, generally positing that increased substrate complexity and hardness is associated with increased species richness (Lacharité and Metaxas, 2017; Romoth et al., 2023). Our results support this notion, with rocky and biogenic matrix substrates consistently associated with higher VME richness than transects which were dominated by sediment or coral rubble. Benthic filter feeders such as corals and sponges preferentially attach to hard substrates (Goode et al., 2020) in order to gain the structural support needed for them to sustain their position in the water column for feeding and respiration. Softer substrates are also more susceptible to sedimentation, which can obstruct the feeding structures of benthic organisms and inhibit respiration. Substrate hardness has been shown to positively impact richness of benthic communities on Atlantic seamounts (Bridges et al., 2022). A study of the Andaman seamounts in the eastern Indian Ocean has

shown that richness of sessile fauna increases on cobble substrates compared to fine sediments, reinforcing the importance of substrate hardness in fostering benthic biodiversity (Sautya et al., 2011).

Deep sea Scleractinia often grow in thickets, forming complex 3D structures that themselves act as biogenic substrate and provide diverse microhabitats for a range of species (Anderson et al., 2016). The presence of rare species has also been found to increase with structural complexity of the substrate (Romoth et al., 2023). Our GLMM found a positive correlation between the presence of biogenic matrix substrate and VME richness. Extensive coral frameworks, primarily composed of *Solensomilia variabilis,* were found on Coral seamount. Whilst the framework was predominantly dead coral, live colonies of the species were also present; this low live to dead ratio for framework building coral is a common situation in the deep sea. As well as mobile fauna, the reef matrix hosted other VME species such as zoanthids and octocorals, with glass sponges appearing at notably high density and richness. This finding highlights the role that reef matrices play in supporting diversity, not just of mobile species (Auster et al., 2005) but of other habitat-building organisms, underscoring the importance of preserving these structures, which can be reduced to rubble by bottom trawling (Williams et al., 2010).

Coral seamount hosts a higher richness of Porifera than any other seamount, with cup-like and massive sponge morphologies being particularly numerous. Sponges have been reported to dominate Antarctic benthos in many cases (Barthel and Gutt, 1992; Cattaneo-Vietti et al., 1999; Dayton and Hessler, 1972; Teixidó et al., 2002)

and all sponge classes have been found in the Southern Ocean. The richness of sponges on the Antarctic Peninsula has been shown to be influenced by temperature, with cooler temperatures supporting increased richness (Kersken et al., 2016), complementing the findings from this study.

Sponge assemblages are a vital component of many deep sea environments, offering a range of ecosystem services including habitat provisioning and nutrient cycling; they also produce bioactive compounds used in medical research applications (Hogg et al., 2010). Their intricate three-dimensional structures not only offer shelter and serve as effective camouflage against predators (Freese and Wing, 2003) but can also play critical roles as spawning sites, nursery grounds, and feeding areas for various marine organisms (Beazley et al., 2013). Sponges play an important role in habitat provisioning for macrofauna, and have as such been described as 'living hotels' (Goren et al., 2021; Manjón-Cabeza et al., 2021). Members of the *Euplectellidae* family for example, which were found on all four SWIOR seamounts explored in this study, are notable for their symbiotic relationships with crustaceans (Saito et al., 2002). Sponges also play an important role in nutrient cycling, filtering organic matter and other nutrients from the water column thereby influencing energy exchange between depths (Pile and Young, 2006).

Finally, our GLMMs also showed depth to negatively impact VME richness along the SWIOR. This agrees with globally established patterns of depth-diversity relationships (Costello and Chaudhary, 2017). Whilst Chapter 1 found an increase in VME richness on Melville Bank seamount with depth, the GLMM used here shows a significant

decrease in VME morphospecies with depth when multiple seamounts are considered. That the depth-diversity trend on Melville Bank reports the opposite effect is testament to the localised impact that bottom trawling can have on diversity of VME species along this seamount chain.

Conclusion

Resolving biogeographic patterns of diversity on the spatial scale required for management by RFMOs is a key challenge in deep sea conservation. This study reveals that seamount VME communities along the SWIOR exhibit a latitudinal richness gradient, influenced by water mass characteristics and the presence of reef matrix. Our findings highlight the variation in species richness that can exist along a single seamount chain, driven by a variety of metrics, cautioning against interpreting diversity patterns as the product of a singular mechanism. Results also underscore the importance of not treating seamount chains as homogeneous units in conservation decisions. Whilst further understanding patterns of benthic diversity along the SWIOR would benefit from increased sampling efforts, this work already indicates a latitudinal richness gradient in seamount VME communities that should be considered in future conservation and management efforts.

Conclusion Chapter

Summary of Chapters

Seamounts are a major biome in the global ocean, hosting high levels of pelagic and benthic biodiversity (Morato et al., 2010). Though scientific understanding of seamount ecosystems has progressed greatly over the past 30 years (Rogers, 2018), the study of communities that inhabit these deep sea features remains in its infancy, especially when compared with that of coastal marine environments (Bell et al., 2023). In general, seamount biodiversity in the Indian Ocean is poorly understood compared to other ocean basins (Demopoulos et al., 2003), largely as a result of limited funding and technological capabilities in its surrounding countries (Wafar et al., 2011). Data used in this thesis were collected during the *RRS "James Cook"* expedition in 2011 (Rogers and Taylor, 2012) which was the first research cruise undertaken to systematically survey benthic biodiversity inhabiting the Southwest Indian Ocean Ridge (SWIOR), a seamount chain of particular scientific interest due to its position crossing major ocean currents, productivity gradients and due to the presence of cold-water corals. The data presented in this thesis mark a key contribution towards characterising benthic communities on seamounts in this understudied ocean region (Ramiro-Sánchez et al., 2023). By investigating how diversity of habitat-building species varies with depth and latitude, findings presented here not only improve ecological understanding of factors underpinning life on seamounts but form a more detailed picture of spatial distribution of key habitat-building organisms to aid management decisions by Regional Fisheries Management Organisations (RFMOs).

Chapter 1 investigates the depth-diversity gradient of VME indicator taxa on a single seamount, Melville Bank. Whilst variation exists depending on the taxa and ocean basin concerned, there is a consensus in the literature that both the overall richness and abundance of marine species decrease with depth (Costello and Chaudhary, 2017). Findings from this chapter indicate a significant decline in the abundance of VME morphospecies with depth in Melville Bank, complementing globally established patterns. VME morphospecies richness however showed an increase with depth. This finding might be attributed to the confounding effects of bottom-contact fisheries, evidence of which was found on Melville Bank in the form of trawling scars and coral rubble (Fig. 1.4). Being the shallowest seamount along the ridge, Melville Bank is likely the most accessible target for trawling efforts along the ridge. A previous study using video data from the same cruise found a high density of fishing litter on Melville Bank (Woodall et al., 2015) evidencing fishing activity. This work found that the presence of Significant Adverse Impacts (SAIs) on Melville Bank has a negative impact on VME morphospecies richness, even when controlling for depth zones. This highlights the negative impact of bottom-contact fisheries on seamount benthic biodiversity in the South-west Indian Ocean, where trawling impacts have so far not been investigated. However, with no baseline inventories of benthic biodiversity on Melville Bank prior to human impact to compare with, this result should be taken with caution.

Chapter 1 also shows depth to be a significant factor structuring communities on Melville Bank. Data collected from 200m depth zones showed that communities in zones closer together were less dissimilar to each other to those further apart. This finding complements that of other studies reporting species turnover over depth gradients on seamounts in the Pacific and Atlantic ocean basins (McClain et al., 2010; Victorero et al., 2018). It also emphasises the variation in VME indicator taxa that can exist on a single seamount, which host varied morphologies and occur at different depths that consequently lead to different local environments (Rowden et al., 2005). A nuanced approach to seamount management which ensures that protective measures are tailored to preserve the unique biodiversity and ecological functions at different depths is therefore recommended.

Chapter 2 explores latitudinal richness gradients of VME indicator taxa across four SWIOR seamounts: Atlantis, Sapmer, Melville Bank and Coral. The factors driving latitudinal gradients of habitat-building species in the deep sea are still poorly studied, but current evidence suggests a role of water mass characteristics (Puerta et al., 2020) as well as physical topography (Bridges et al., 2022) in influencing these gradients.

This chapter identified a gradient of increasing VME richness with latitude across SWIOR seamounts, driven by both substrate type and temperature-salinity regimes. Temperature was found to be significantly negatively correlated with VME richness. Coral, bathed in subantarctic waters significantly cooler than the other seamounts,

hosted the highest VME richness. Density calculated from temperature, salinity and pressure collected on the cruise showed waters bathing coral to be significantly denser than those surrounding other seamounts (Fig. 2.6). The richness of *Porifera* morphotypes was notably high at this seamount, with glass sponges particularly speciose, complementing existing reports of Antarctic benthos being sponge-dominated (Barthel and Gutt, 1992; Dayton et al., 1974). The presence of biogenic reef matrix was associated with significantly higher richness of VME morphospecies, highlighting the role that cold water coral frameworks play in supporting deep sea biodiversity. The finding of an increasing richness gradient should however be interpreted with caution due to the significant adverse impacts from fisheries observed at Sapmer and Melville Bank, which may have skewed results.

Implications for Biodiversity Conservation and Management Along the SWIOR

Seamounts along the SWIOR are situated outside of Exclusive Economic Zones (EEZs) over which countries have jurisdiction, and their resources are thus considered to be the 'common heritage of mankind' (Bourrel et al., 2018). There has historically been very little regulation over seamount fisheries in the South-west Indian Ocean, which supports industrial scale bottom trawl fisheries targeting Crustacea (van der Elst and Everett, 2015) and several pelagic fish species, notably the orange roughy and black cardinal fish (Rogers et al., 2017). Like most seamount fisheries, those along the SWIOR have exhibited unsustainable boom and bust

dynamics (Clark, 2009) and use highly destructive bottom trawling techniques to obtain catch (Kimball, 2004). Existing threats to seamount ecosystems from industrial fishing are now being compounded by future plans to commence deep sea mining (Sharma, 2015), with the International Seabed Authority (ISA) having granted licenses for a large area of the ridge to be explored for mining potential due to the presence of massive sulphides (Boschen et al., 2016). This current and future physical destruction to the benthos, against the backdrop of climate change, which has already altered ocean chemistry impacting the formation of habitat-building organisms such as corals (Sweetman et al., 2017) and their available habitat ranges in the deep sea (Morato et al., 2020).

Moving forwards, there is thus an urgent need to better understand the spatial distribution of key habitat-building species on seamounts along the SWIOR to inform policies by SIOFA which promote more sustainable resource extraction from seamounts, to preserve biodiversity in this region. Such policies may involve designation of areas for marine protection, implementation of depth restrictions on fishing, or banning the use of certain fishing gears. Ultimately, these measures will help meet the goals set out by the UN Ocean Decade (Ryabinin et al., 2019), a major initiative striving to protect life on the High Seas (Deasy, 2023). This thesis contributes to enhancing understanding of biodiversity along the SWIOR in three ways, i) addressing existing shortfalls in taxonomic inventories for the region ii) assessing impact of bottom contact fisheries on VME richness and iii) identifying key environmental drivers of VME diversity with latitude.

Addressing Shortfalls in Data Availability along the SWIOR

Currently, there are severe shortfalls in both distributional and taxonomic descriptions of VME indicator taxa within the area governed by the SIOFA, with the vast majority of biological sampling of the Indian Ocean being in coastal areas (Ramiro-Sánchez et al., 2023). There is thus an urgent need for increased biodiversity inventories of offshore locations to fill out these knowledge gaps. Until then, conservation decisions will have to be based on predictive approaches, which whilst useful and indeed the only option in data poor situations, are sub-optimal due to their associated uncertainty (Reiss et al., 2015; Ross and Howell, 2013). This thesis contributes towards closing this data shortfall for VME indicator taxa along the SWIOR. Morphospecies identified throughout this work were added to a dataset that will be made publicly available on SMARTar-ID, a standardised marine taxon reference image database developed for study of deep sea species (Howell et al., 2019). This database structure aims to address the lack of standardisation in image reference catalogues of deep-sea biodiversity, which complicates the ability to combine datasets across studies. Currently, the SMARTar-ID database lacks representation from deep sea environments in the Indian Ocean, and so the data contribution from this thesis marks a significant step towards increasing documentation of deep-sea life in this ocean basin, facilitating broader research collaborations and comparative studies. The inclusion of this data in the SMARTar-ID database also contributes to ongoing efforts to apply machine learning technologies for the rapid, accurate identification of deep-sea species, which could significantly improve the efficiency of ecological monitoring

and biodiversity assessments using underwater imagery and video (Beijbom et al., 2015; MacLeod et al., 2010; Schoening et al., 2012).

Assessing Impacts of Bottom-contact Fisheries Along SWIOR

The harmful impacts of bottom contact fisheries on marine benthic communities has been well-documented in many ocean regions (Collie et al., 2000; Hiddink et al., 2017; Sciberras et al., 2018). However, studies specifically investigating the effects of trawling on the diversity of VME taxa along the SWIOR have not been conducted. This thesis identifies trawling scars and stony coral rubble as indicators of Significant Adverse Impacts (SAIs) of bottom contact fisheries and investigates their influence on VME taxa richness.

Contact of trawl gear with the benthos leads to crushing, damaging and in many cases complete removal of benthic biota, which reduces species abundance and diversity. Deep sea benthic fauna are less resilient to the physical impacts of trawling than their shallow-water counterparts (Kaiser et al., 2002; Mortensen and Buhl-Mortensen, 2005), due to slow growth rates and high longevity that lead to prolonged recovery following disturbance (Clark et al., 2016a).

Whilst data used here showed that fishing impact was not a significant driver of seamount VME richness on a latitudinal scale along the SWIOR (Table 2.3), findings from Chapter 1 suggest a negative impact of bottom contact fisheries on the richness of Melville Bank VME communities. This finding aligns with SIODFA's stance, which

acknowledges that while bottom trawling in the South West Indian Ocean Region is not believed to have 'broadly harmed the aquatic environment', it may cause 'localised damage to epifauna on hard substrates in certain areas' (SIODFA, 2015). This study indicates Melville Bank is one such area, which is perhaps unsurprising given that it is the shallowest seamount along the ridge and thus more easily accessible by trawlers (O'Driscoll and Clark, 2005). Given the high level of disturbance witnessed at Melville Bank, it may be prudent to direct protection efforts towards other areas that have experienced less disturbance, where the ecological integrity and biodiversity of VMEs remain more intact (Dover et al., 2014).

Whilst no relationship between VME abundance and fishing impact was found, it is possible that the measure of abundance used here - spanning a wide range of VME indicator taxa - might not effectively reflect fishing impacts. This is because post-disturbance abundance could be maintained by faster-growing species, obscuring the decline of slower-growing organisms such as stony corals.

Identifying Environmental Drivers of VME Diversity along the SWIOR

Understanding environmental drivers of VME richness with latitude along the SWIOR is key both for identifying areas of high biodiversity for current MPAs and developing models that predict how species distributions might shift under different climate change scenarios (Hu et al., 2020). Findings from chapter 2 indicate that VME diversity is driven by both water mass and substrate along the SWIOR. Using data

from all depth levels, the presence of biogenix matrix was found to have the largest effect on VME richness. This underscores the vital importance of prioritising areas for conservation where deep water coral frameworks are known to exist (Roberts and Cairns, 2014). Whilst habitat suitability modelling of cold water corals is a key part of this endeavour (Davies and Guinotte, 2011; Georgian et al., 2020; Rengstorf et al., 2013), this thesis shows that such frameworks can support high diversity of VME taxa even after they have died. Few of the framework building colonies witnessed on Coral seamount were alive, yet there was high diversity of other VME species such as bryozoans, octocorals and sponges supported by the dead coral matrix. Focusing protection efforts on areas where these cold-water coral species can survive may therefore ignore regions where considerable biodiversity is still supported.

The GLMM (Table 2.3) also showed temperature played a significant role in influencing VME richness, with cooler temperatures driving increased richness. As a result, Coral seamount, which is bathed in sub-antarctic waters of the subtropical front, hosts higher richness than other seamounts. This temperature-species richness relationship suggests that the effect of climate change on subtropical circulation could impact benthic diversity in the SWIOR. Predictions indicate that atmospheric warming will weaken the subtropical circulation (Zhou et al., 2024), potentially affecting the temperature distribution across SWIOR seamounts and, consequently, their species richness. Findings from this thesis therefore merit further studies of how ocean circulation features impact seamount biodiversity in this region, ideally using longitudinal data to confirm patterns between water mass characteristics and diversity over time. Melting of Antarctic ice shelves may also influence biodiversity of Coral

seamount. The recent melting of ice shelves on the Antarctic Peninsula for example, has revealed 23,000 square kilometres of new seafloor that acts as an additional nutrient source for existing benthic communities, resulting in expansion of glass sponge populations (Fillinger et al., 2013).

Overall, findings presented here support the designation of Coral seamount as a Benthic Protected Area by SIODFA, and as an EBSA (Ecologically or Biologically Significant Area) by the Convention on Biological Diversity (CBD) (Dunn et al., 2014). Our results show high levels of VME richness on this seamount compared with others, supported by extensive coral frameworks of *Solensomilia variabilis.* Trawling is currently prohibited on Coral by SIODFA vessels, however video data used here showed evidence of lost fishing gear including large lengths of rope and gill nets. Since states outside of the SIODFA agreement also fish in the region, notably Japanese fishing vessels, increased protection of this habitat is warranted to prevent further degradation.

Strengths and Limitations of Work

Data Collection

Video data used in this project was collected via cameras mounted on a Remotely Operated Vehicle (ROV). Over the past 4 decades, the adaptation of Remotely Operated Vehicles (ROVs), originally designed for national defence and oil exploration (Macreadie et al., 2018) have proved particularly useful in the field of deep sea research. The fitting of ROVs with high-definition cameras, sensors and

robotic arms for sample collection have allowed scientists to explore deep sea habitats and their inhabitants in unprecedented detail.

Historically, deep-sea sampling has been conducted using invasive sampling methods such as grabs, box-corers, or trawls (Clark et al., 2016b). However, in recent years, underwater imagery has become a preferred method of data collection for deep sea research, offering several advantages. While firstly being non-destructive (Mallet and Pelletier, 2014) these methods allow researchers to capture large amounts of information over a shorter time, reaching sites that may otherwise be inaccessible (e.g due to depth, seafloor characteristics) using traditional sampling methods. Overall, this allows for a more comprehensive understanding of biodiversity and functional structures in deep sea communities (Jac et al., 2021).

Study Design

Given that the video data had already been collected prior to this work, changing sampling design or effort to better suit analysis objectives was not an option for this project. As a result, there was unequal sampling across depth zones on Melville Bank and across all seamounts. Such unequal sampling with depth is a common situation in deep sea science (Menegotto and Rangel 2018). In addition, data for different depth zones was sampled during different dive events on distinct sections of the seamount, rather than a continuous depth profile, introducing spatial heterogeneity. Though the analysis would have benefited from a more balanced sample design, it is acknowledged that logistical challenges of deep-sea research cruises, where factors like research budgets, currents, visibility, and weather conditions complicate this.

Limitations of Biological Dataset

Community data used in this thesis was generated through annotation of video footage in Biigle (Langenkämper et al., 2017). Standard approaches for determining taxonomy are not applicable to video data, and so taxonomic level has to be resolved to morphospecies which could correspond to a species, genus, family or higher taxonomic level. It is therefore likely that diversity is underestimated due to the presence of cryptic species that could not be visually distinguished (Grupstra et al. 2024). Moreover, organisms below a size threshold of ~3cm were not annotated, and so smaller species were overlooked. This exclusion leads to underestimation of the true diversity and density of species within these deep-sea communities, underscoring a limitation in capturing the full spectrum of marine life through video-based surveys. Moreover, this dataset did not take into account the different sizes of organisms belonging to the same morphospecies. Size information can shed light on the available habitat space provided by organisms, or even give information about recruitment following a disturbance event (Althaus et al., 2009). These aspects are ignored when considering abundance alone.

Lack of Ecological Baselines

One of the primary challenges faced in this study was the absence of baseline ecological data on the benthic diversity of South-West Indian Ocean Ridge (SWIOR) seamounts before their exposure to fishing activities. This gap complicates our ability to determine whether observed diversity patterns reflect the natural ecological state of these environments or are alterations resulting from human disturbance. This issue is

common in deep sea studies (Paulus, 2021), and underscores the urgent need for more comprehensive deep-sea biodiversity surveys before extensive human exploitation occurs.

Limitations of Environmental Dataset

The CTD-recorded environmental parameters of temperature and salinity used in this thesis capture conditions at a single point in time, which will not fully reflect the complex and fluctuating hydrodynamics of the region. Ideally, longitudinal environmental data, collated over time, would provide a more detailed understanding of how these environmental metrics influence seamount VME diversity. However, obtaining such data through repeated deployments of CTD instruments or long-term drifter arrays involves significant financial and logistical challenges. Using satellite data could provide an alternative, however, to obtain measurements at depth, interpolations are used which are not always reliable (Castro et al., 2018). Moreover, taking *in situ* environmental metrics (productivity, dissolved molecular oxygen, organic nutrients) that can be directly linked to community data from transects should be considered for future ecological expeditions in the region.

Measuring Diversity

This thesis focused on using richness (number of species) as the primary diversity metric. This is the simplest measure for characterising the diversity and features heavily in foundational models for community ecology. Even when abundance information is available, species count is still often the most relevant diversity metric in conservation analyses (Chao, 2006). However, it is worth noting that in nearly all

studies of biodiversity, compilation of a complete species inventory requires immense sampling efforts, which is challenging enough in terrestrial settings, let alone in extremely remote and largely inaccessible deep-sea areas. Consequently, for deep sea habitats, richness is an appropriate measure to use as most species are rare (McClain 2021). Practically speaking, establishing an exhaustive list of species from an environment is therefore an unattainable goal. As a result, species counts in a sample will nearly always underestimate the true species richness. This thesis aimed to address this through non-asymptotic approaches.

It is also important to recognise that taxonomic diversity reflects just one aspect of biodiversity. Functional diversity, which reports the range of functional traits of organisms in an ecosystem (Goswami et al., 2017), can offer additional insights into ecosystem processes such as nutrient cycling and productivity (McKinley et al., 2022; Pastor and Cohen, 1997). Genetic diversity can also provide information on the potential adaptability of communities to change (Selkoe et al., 2018) although this cannot be investigated using imagery alone.

Future research

Future work building on this research could incorporate assessment of additional environmental factors onto richness of VME indicator taxa along the SWIOR, notably productivity and nutrient regimes (Sonnekus et al., 2017). Furthermore, investigating the impact of fishing on specific taxonomic groups could reveal how bottom contact fisheries differentially affect species based on their unique morphology and life

histories (Goode et al., 2020). Investigation into community differences between seamounts would also shed light onto how species composition is distributed along this ocean ridge. The data collected in this project will contribute to the Smartar-ID online image reference database (Howell et al., 2019) which also opens avenues for comparative studies, enabling a broader comparison of seamount biodiversity across different ocean basins.

Conclusion

Protecting communities of VME indicator taxa on seamounts is an essential aspect of biodiversity conservation efforts on the High Seas. Whilst our understanding of life on seamounts has progressed greatly over the last 30 years, so have the multitude of anthropogenic threats that these ecosystems now face. These threats include overfishing, destructive fishing techniques, marine litter, future deep-sea mining, and the impacts of a warming climate. Establishing biological inventories of key habitat building species on seamounts and their spatial gradients across fishing grounds is essential to inform management that can limit the damage to seamount ecosystems from human activities. This thesis contributes towards closing the knowledge gap regarding seamount benthic biodiversity in the South-west Indian Ocean. Future work to extend surveys of seamount benthic fauna along this ridge is urged to further characterise benthic communities and thus build a more comprehensive picture of biodiversity along this ocean ridge.

Supplementary Materials

All code for collation of environmental metadata, community analyses and datasets used in this project are publicly available on the GitHub repository: https://github.com/CeliaHanna/Seamount_VMEs_SWIOR/tree/main

Chapter 1 Supplementary Materials

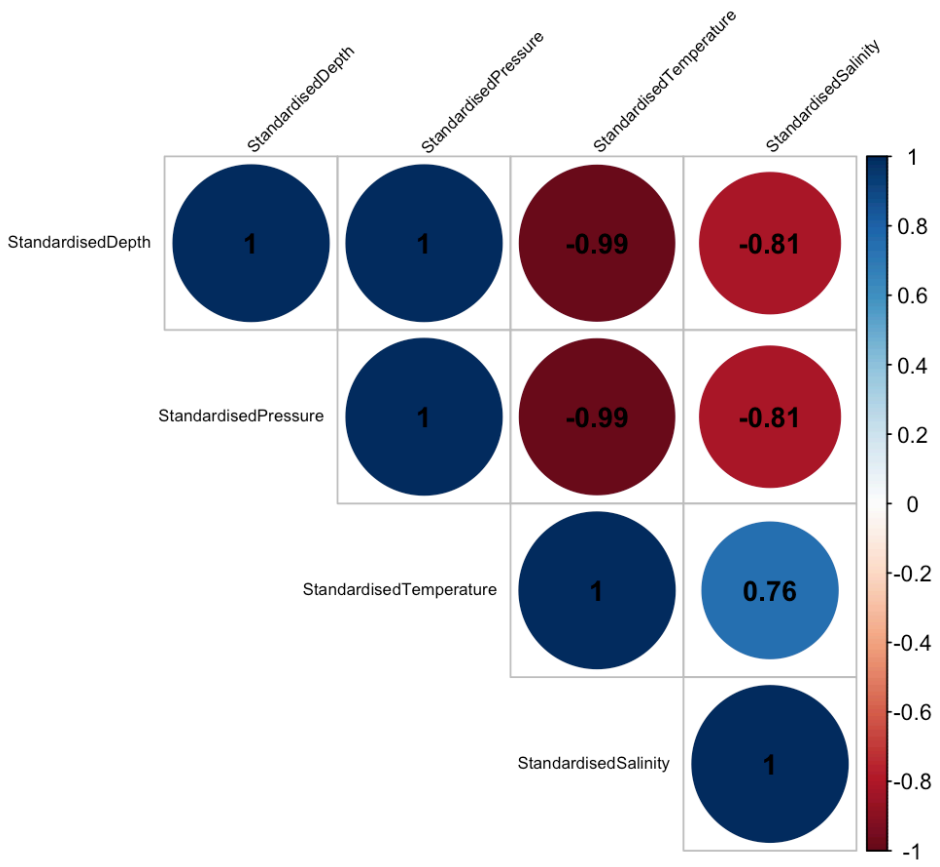


Figure S1.1: Matrix showing Pearson's correlation analysis of CTD collected variables (salinity, temperature, pressure) with depth.

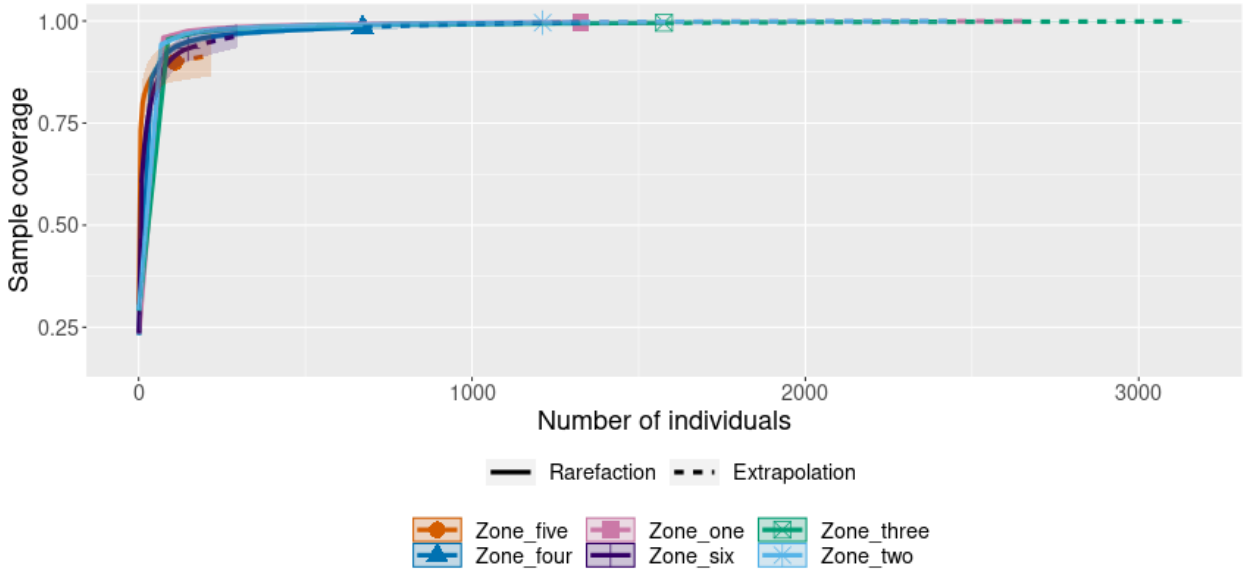


Figure S1.2. Sample completeness curve for each depth zone on Melville Bank generated using iNEXT.

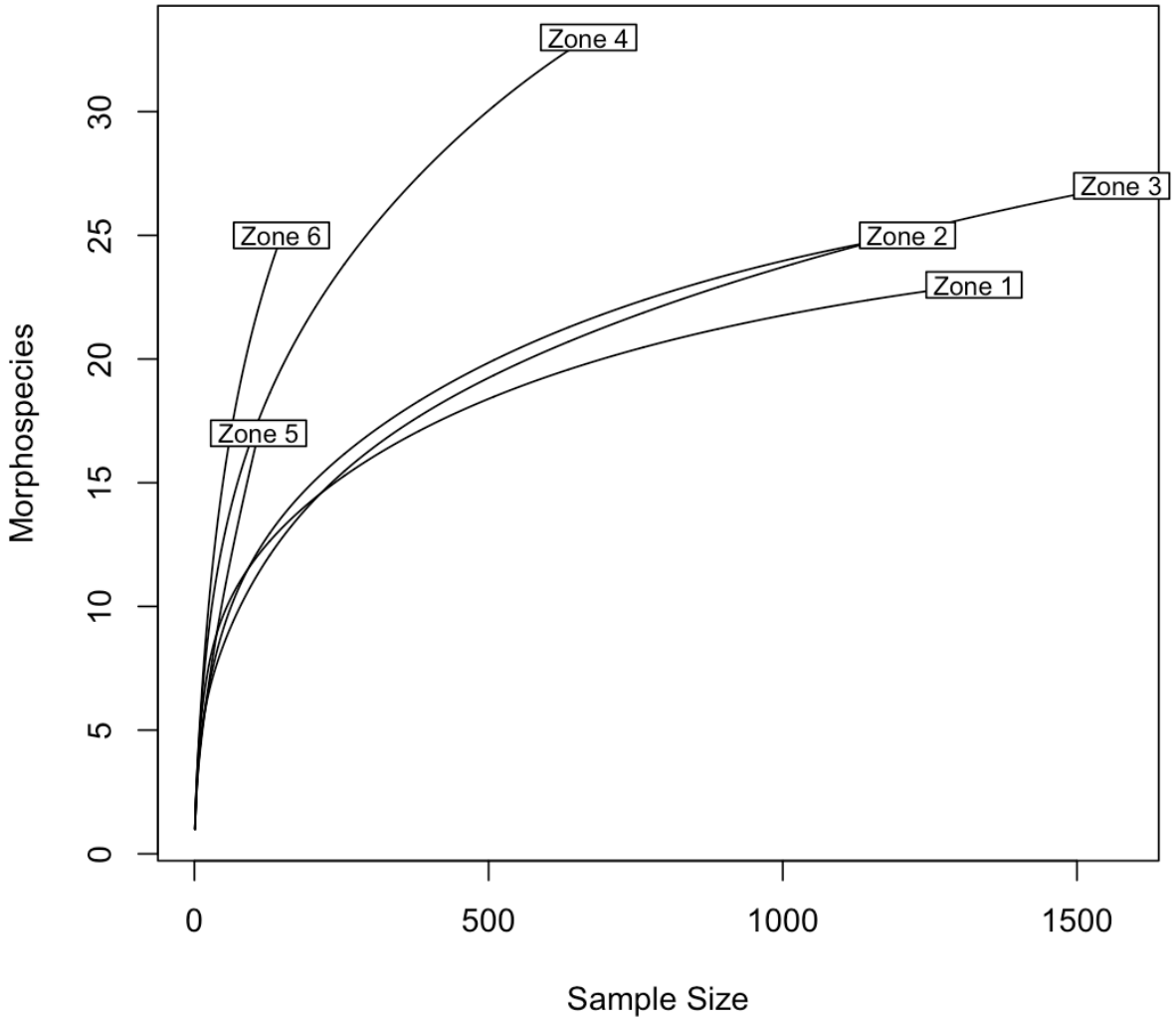


Figure S1.3: Rarefaction curves for VME morphospecies collected across different depth zones on Melville Bank.

Table S1.1. Model output of GLMM investigating effect of depth zone on morphospecies richness on Melville Bank, controlling for dive number.

```
Family: nbinom2  ( log )
Formula:          richness ~ depth_zone + (1 | dive_number)
Data: transect_info

     AIC      BIC   logLik deviance df.resid
   295.8    312.1   -139.9    279.8       49

Random effects:

Conditional model:
 Groups      Name        Variance  Std.Dev.
 dive_number (Intercept) 1.515e-10 1.231e-05
Number of obs: 57, groups:  dive_number, 4

Dispersion parameter for nbinom2 family (): 23.1

Conditional model:
                Estimate Std. Error z value Pr(>|z|)
(Intercept)      1.72277    0.12164  14.163  < 2e-16 ***
depth_zoneZone 2  0.09885    0.18287   0.541  0.58884
depth_zoneZone 3  0.02643    0.18139   0.146  0.88414
depth_zoneZone 4  0.59400    0.18728   3.172  0.00152 **
depth_zoneZone 5  0.70498    0.24220   2.911  0.00361 **
depth_zoneZone 6  0.37047    0.18252   2.030  0.04238 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Table S1.2. Summary of GLMM output investigating effect of depth zone on morphospecies abundance, controlling for dive.

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
 Family: poisson  ( log )
Formula: abundance ~ depth_zone + (1 | dive_number)
   Data: transect_info

     AIC      BIC   logLik deviance df.resid
  1820.3   1834.6   -903.1   1806.3       50

Scaled residuals:
    Min      1Q  Median      3Q     Max
-9.7560 -2.6693 -0.3107  2.3411 16.7812

Random effects:
 Groups      Name        Variance Std.Dev.
 dive_number (Intercept) 0        0
Number of obs: 57, groups:  dive_number, 4

Fixed effects:
                Estimate Std. Error z value Pr(>|z|)
(Intercept)      5.04256    0.02075 243.039  < 2e-16 ***
depth_zoneZone 2  0.09163    0.03108   2.948   0.0032 **
depth_zoneZone 3  0.18363    0.02964   6.196 5.79e-10 ***
depth_zoneZone 4 -0.29144    0.04080  -7.142 9.18e-13 ***
depth_zoneZone 5 -0.38543    0.05996  -6.428 1.29e-10 ***
depth_zoneZone 6 -0.75821    0.04429 -17.118  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Table S1.3. Output of ANOSIM investigating statistical similarity in community composition between depth zones on Melville Bank.

Call:
anosim(x = comm_data, grouping = final_df$depth_zone, permutations = 9999, distance = "jaccard")
Dissimilarity: jaccard

ANOSIM statistic **R: 0.3959**
Significance: **1e-04**

Permutation: free
Number of permutations: 9999

Upper quantiles of permutations (null model):
90% 95% 97.5% 99%
0.0571 0.0767 0.0937 0.1132

Dissimilarity ranks between and within classes:

	0%	25%	50%	75%	100%	N
Between	4	415.500	758.00	1207.500	1207.5	1125
zone_1	2	244.500	543.00	973.000	1207.5	91
zone_2	3	368.125	592.75	859.750	1207.5	66
zone_3	1	117.500	207.00	383.250	571.5	55
zone_4	51	193.750	297.75	591.125	923.5	28
zone_5	31	101.000	171.00	187.000	203.0	3
zone_6	89	146.625	171.00	196.625	261.5	10

Table S1.4: GLMM output investigating the effect of SAI evidence on morphospecies richness.

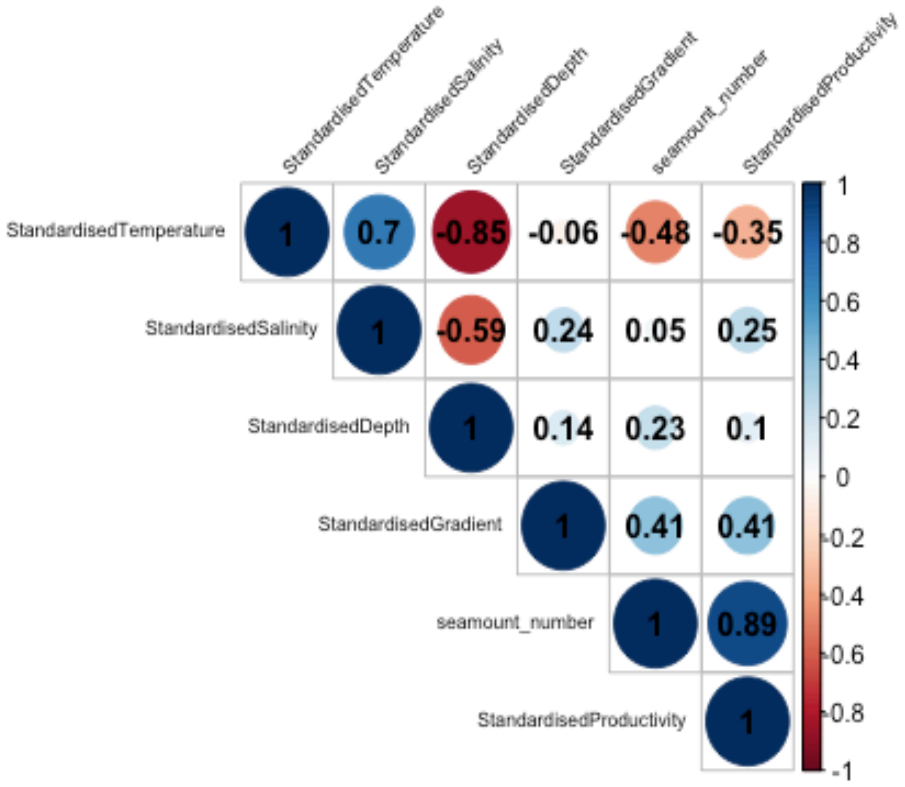
```
Family: nbinom2  ( log )
Formula:          species_richness ~ SAI_Evidence + (1 | depth_zone) + (1 |
dive_number)
Data: final_df

     AIC      BIC   logLik deviance df.resid
   292.5    302.3   -141.2    282.5       48

Random effects:

Conditional model:
 Groups      Name        Variance  Std.Dev.
 depth_zone  (Intercept) 2.661e-10 1.631e-05
 dive_number (Intercept) 1.691e-11 4.112e-06
Number of obs: 53, groups:  depth_zone, 6; dive_number, 4

Dispersion parameter for nbinom2 family (): 13.6

Conditional model:
             Estimate Std. Error z value Pr(>|z|)
(Intercept)     2.3848     0.1088  21.911   <2e-16 ***
SAI_EvidenceY  -0.3854     0.1312  -2.938   0.0033 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Table S1.5. Table showing top 3 morphospecies contributing to the differences for each depth zone comparison identified by SIMPER analysis and Bray-Curtis dissimilarity metrics (msp = 'morphospecies').

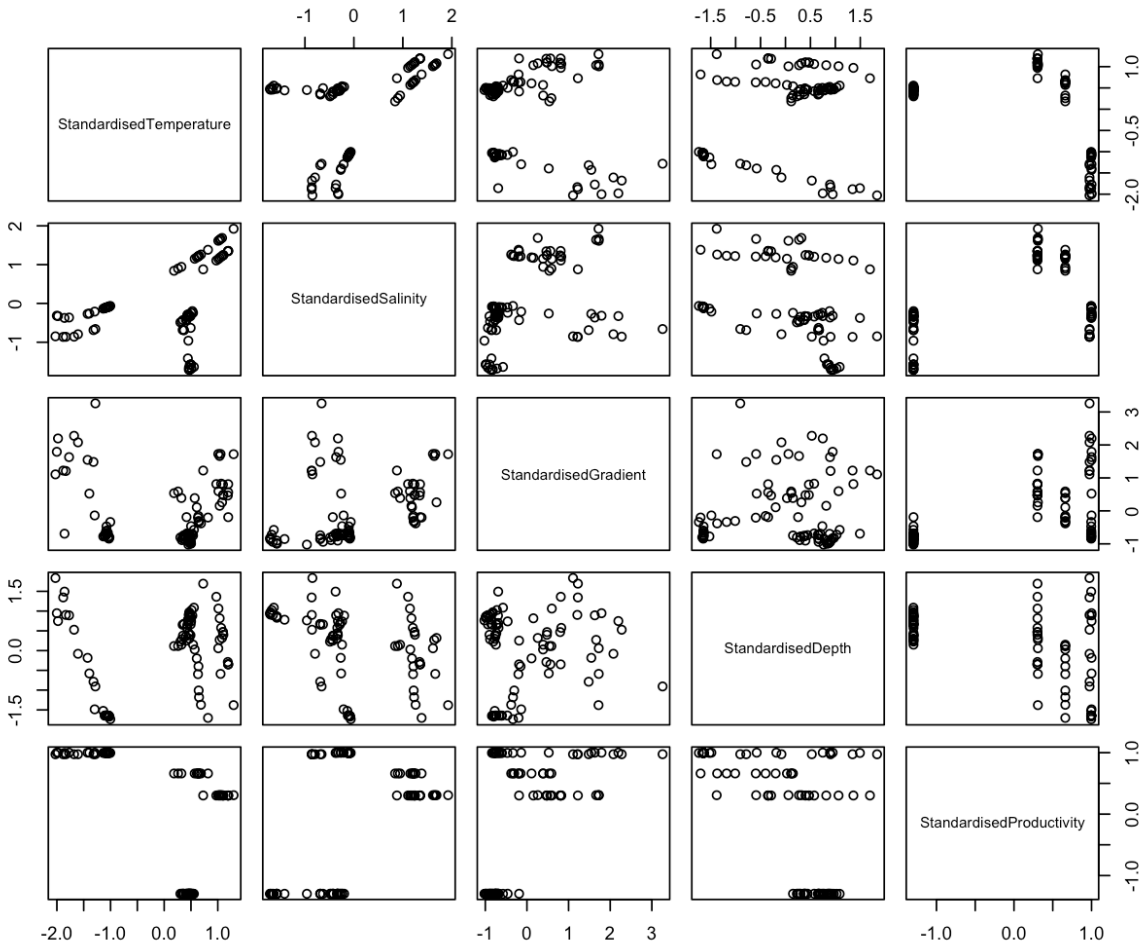
Depth zone comparison	Bray-Curtis Dissimilarity	Top contributing morphospecies identified by SIMPER analysis
Zone 1 : 6 (100 - 300m : 1100 - 1300m)	0.99	• *Acanthogorgia* octocoral fan • Branching glass sponge: *Sarostegia oculata* • *Plexauridae* octocoral fan
Zone 1:5 (100 - 300m 900 - 1100m)	0.99	• *Acanthogorgia* octocoral fan • Primnoidae octocoral: *Primnoides flagellum* • *Plexauridae* octocoral fan
Zone 1:4 (100 - 300m: 700 - 900m)	0.56	• Stylasteridae msp.1 • 2D lamellate sponge msp. • *Plexauridae* octocoral fan
Zone 1:3 (100 - 300m: 500 - 700m)	0.53	• Stylasteridae msp.1 • *Plexauridae* octocoral fan • *Acanthogorgia* yellow fan
Zone 1:2 (100 - 300m: 300 - 500m)	0.72	• 2D lamellate sponge msp. • White elephant ear sponge msp. • *Acanthogorgia* yellow fan
Zone 2:6 (300-500m : 1100 - 1300m)	0.98	• Branching glass sponge: *Sarostegia oculata* • 2D lamellate sponge msp. • Elephant ear sponge msp.
Zone 2:5 (300-500m: 900 -1100m)	0.99	• *Acanthogorgia* octocoral fan • Branching glass sponge: *Sarostegia oculata* • Primnoidae octocoral: *Primnoides flagellum*
Zone 2:4 (300-500m : 500-700m)	0.79	• *Stylasteridae* msp.2 • Folding white sponge msp. • Elephant ear sponge msp.
Zone 4:6 (500-700m : 1100-1300m)	0.92	• Branching glass sponge: *Sarostegia oculata* • Primnoidae octocoral: *Primnoides flagellum* • *Acanthogorgia* octocoral fan

Zone 4:5 (500-700m : 900-1100m)	0.92	• Branching glass sponge: *Sarostegia oculata* • *Stylasteridae* msp.2 • *Plexauridae* yellow fan
Zone 5:6 (900-1100m: 1100:1300m)	0.59	• Branching glass sponge: *Sarostegia oculata* • Primnoides octocoral: msp.7 • Primnoidae octocoral: *Primnoides flagellum*

Chapter 2 Supplementary Materials



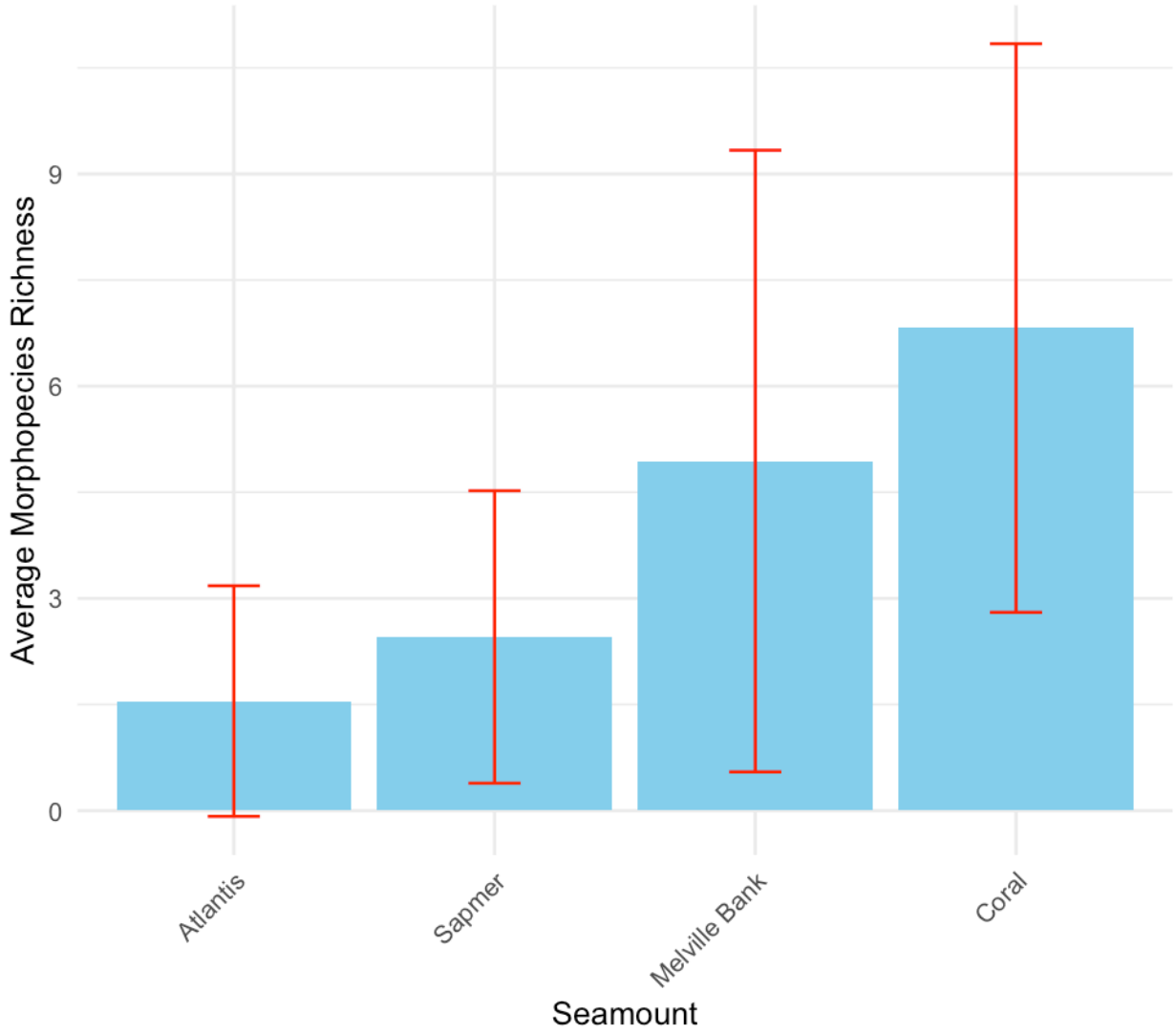
S2.1. Pearson's correlation analysis between scaled continuous environmental variables, using data from all transects.



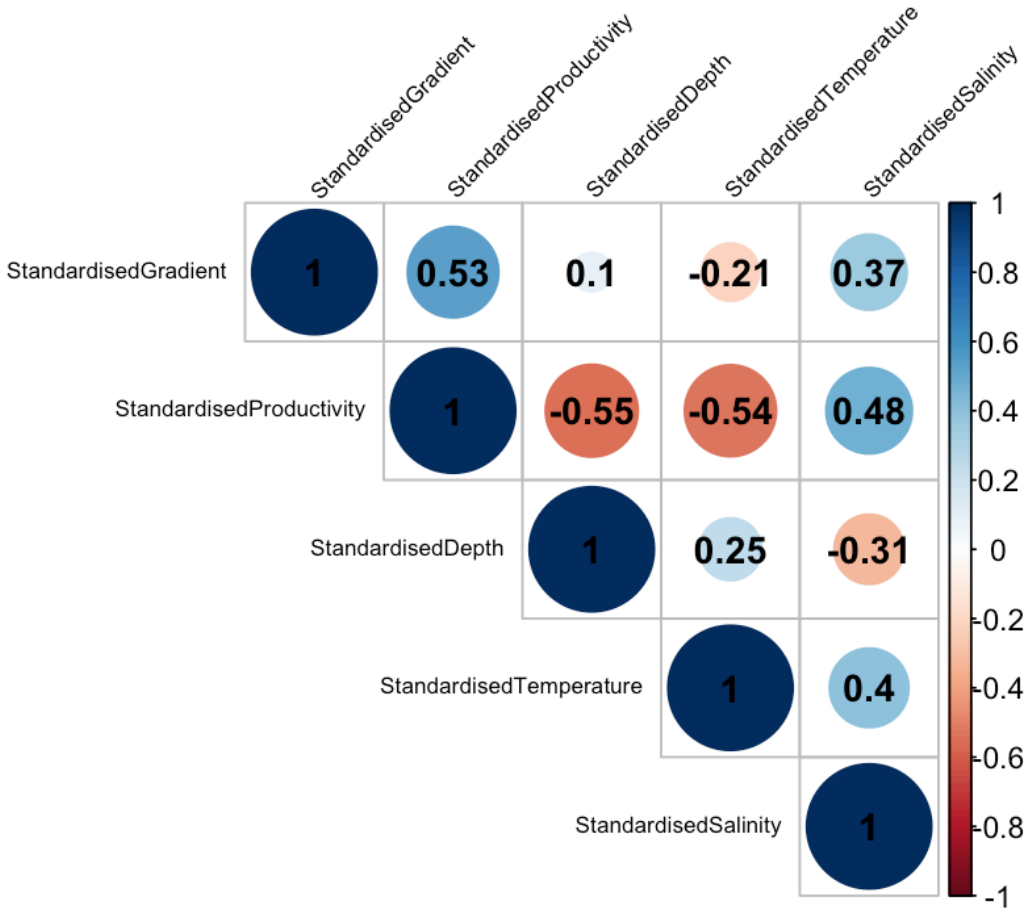
S2.2. Matrix of scatterplots of standardised continuous environmental variables used in GLMM.

S2.3. Model sensitivity analysis for GLMMs investigating richness drivers

Model Type	AIC	BIC	logLik	Deviance	df.resid	Variance of Random Effect	Std.Dev. of Random Effect	Number of Observations	Number of Groups	Dispersion Parameter (for nbinom2)
Poisson	1171.1	1215.2	-572.5	1145.1	207	0.1216	0.3487	220	12	-
Poisson with Zero Inflation	1166.4	1214.0	-569.2	1138.4	206	0.09978	0.3159	220	12	-
Negative Binomial	1115.0	1162.5	-543.5	1087.0	206	0.04226	0.2056	220	12	4.96
Negative Binomial with Zero Inflation	1117.0	1167.9	-543.5	1087.0	205	0.04226	0.2056	220	12	4.96



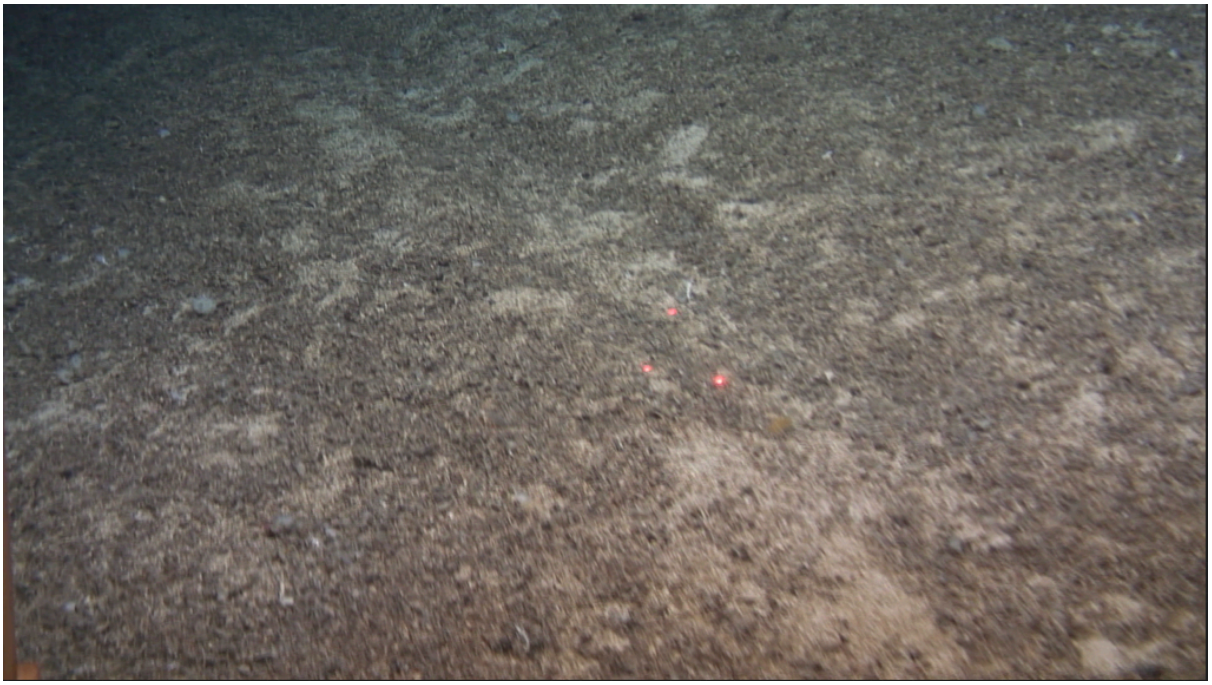
S2.4. Barplot of VME richness using data from 600 - 800m across all seamounts, standardised by transect number with error bars shown. (Code: barplot1.R)



S2.5. Pearson's correlation analysis between scaled continuous environmental variables, using only data from transects within a 600-800m depth range.

S2.6. Table showing sensitivity analysis of GLMM models investigating richness environmental drivers.

Model	AIC	BIC	logLik	Deviance	df.resid	Number of obs	Groups	Groups Number
Poisson	450.6	472.8	-216.3	432.6	78	87	dive	7
Poisson Zero Inflated	443.2	467.9	-211.6	423.2	77	87	dive	7
Negative Binomial	412.6	437.2	-196.3	392.6	77	87	dive	7
Negative Binomial Zero Inflated	414.6	441.7	-196.3	392.6	76	87	dive	7



S2.7. Trawling scars and coral rubble at the 600 - 800m depth zone on Sapmer seamount.

Bibliography

Agassiz, A., 1888. A Contribution to American Thalassography: Three Cruises of the United States Coast and Geodetic Survey Steamer “Blake”, in the Gulf of Mexico, in the Caribbean Sea, and Along the Atlantic Coast of the United States, from 1877 to 1880. Sampson Low, Marston, Searle & Rivington.

Aldea, C., Olabarria, C., Troncoso, J.S., 2008. Bathymetric zonation and diversity gradient of gastropods and bivalves in West Antarctica from the South Shetland Islands to the Bellingshausen Sea. Deep Sea Res. Part Oceanogr. Res. Pap. 55, 350–368. https://doi.org/10.1016/j.dsr.2007.12.002

Aller, J.Y., 1989. Quantifying sediment disturbance by bottom currents and its effect on benthic communities in a deep-sea western boundary zone. Deep Sea Res. Part Oceanogr. Res. Pap. 36, 901–934. https://doi.org/10.1016/0198-0149(89)90035-6

Althaus, F., Hill, N., Ferrari, R., Edwards, L., Przeslawski, R., Schönberg, C.H.L., Stuart-Smith, R., Barrett, N., Edgar, G., Colquhoun, J., Tran, M., Jordan, A., Rees, T., Gowlett-Holmes, K., 2015. A Standardised Vocabulary for Identifying Benthic Biota and Substrata from Underwater Imagery: The CATAMI Classification Scheme. PLOS ONE 10, e0141039. https://doi.org/10.1371/journal.pone.0141039

Althaus, F., Williams, A., Schlacher, T.A., Kloser, R.J., Green, M.A., Barker, B.A., Bax, N.J., Brodie, P., Schlacher-Hoenlinger, M.A., 2009. Impacts of bottom trawling on deep-coral ecosystems of seamounts are long-lasting. Mar. Ecol. Prog. Ser. 397, 279–294. https://doi.org/10.3354/meps08248

Anderson, O.F., Guinotte, J.M., Rowden, A.A., Clark, M.R., Mormede, S., Davies, A.J., Bowden, D.A., 2016. Field validation of habitat suitability models for vulnerable marine ecosystems in the South Pacific Ocean: Implications for the use of broad-scale models in fisheries management. Ocean Coast. Manag. 120, 110–126. https://doi.org/10.1016/j.ocecoaman.2015.11.025

Andrews, A.H., Cailliet, G.M., Kerr, L.A., Coale, K.H., Lundstrom, C., DeVogelaere, A.P., 2005. Investigations of age and growth for three deep-sea corals from the Davidson Seamount off central California, in: Freiwald, A., Roberts, J.M. (Eds.), Cold-Water Corals and Ecosystems. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 1021–1038. https://doi.org/10.1007/3-540-27673-4_51

Andrews, A.H., Stone, R.P., Lundstrom, C.C., DeVogelaere, A.P., 2009. Growth rate and age determination of bamboo corals from the northeastern Pacific Ocean using refined 210Pb dating. Mar. Ecol. Prog. Ser. 397, 173–185. https://doi.org/10.3354/meps08193

Armstrong, C.W., Foley, N.S., Tinch, R., van den Hove, S., 2012. Services from the deep: Steps towards valuation of deep sea goods and services. Ecosyst. Serv. 2, 2–13. https://doi.org/10.1016/j.ecoser.2012.07.001

Arrigo, K.R., Worthen, D., Schnell, A., Lizotte, M.P., 1998. Primary production in Southern Ocean waters. J. Geophys. Res. Oceans 103, 15587–15600. https://doi.org/10.1029/98JC00930

Ashford, O.S., Kenny, A.J., Barrio Froján, C.R.S., Downie, A.-L., Horton, T., Rogers, A.D., 2019. On the Influence of Vulnerable Marine Ecosystem Habitats on Peracarid Crustacean

Assemblages in the Northwest Atlantic Fisheries Organisation Regulatory Area. Front. Mar. Sci. 6. https://doi.org/10.3389/fmars.2019.00401
Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E.A., De Clerck, O., 2018. Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. Glob. Ecol. Biogeogr. 27, 277–284. https://doi.org/10.1111/geb.12693
Auster, P., Moore, J., Heinonen, K., Watling, L., 2005. A habitat classification scheme for seamount landscapes: assessing the functional role of deep-water corals as fish habitat. pp. 761–769. https://doi.org/10.1007/3-540-27673-4_40
Baco, A.R., Morgan, N.B., Roark, E.B., 2020. Observations of vulnerable marine ecosystems and significant adverse impacts on high seas seamounts of the northwestern Hawaiian Ridge and Emperor Seamount Chain. Mar. Policy 115, 103834. https://doi.org/10.1016/j.marpol.2020.103834
Baco, A.R., Roark, E.B., Morgan, N.B., 2019. Amid fields of rubble, scars, and lost gear, signs of recovery observed on seamounts on 30- to 40-year time scales. Sci. Adv. 5, eaaw4513. https://doi.org/10.1126/sciadv.aaw4513
Baletaud, F., Lecellier, G., Gilbert, A., Mathon, L., Côme, J.-M., Dejean, T., Dumas, M., Fiat, S., Vigliola, L., 2023. Comparing Seamounts and Coral Reefs with eDNA and BRUVS Reveals Oases and Refuges on Shallow Seamounts. Biology 12, 1446. https://doi.org/10.3390/biology12111446
Barnes, R., 2020. Fisheries and Areas beyond National Jurisdiction: Advancing and Enhancing Cooperation, in: New Knowledge and Changing Circumstances in the Law of the Sea. pp. 124–153.
Barnett, A., Abrantes, K.G., Seymour, J., Fitzpatrick, R., 2012. Residency and Spatial Use by Reef Sharks of an Isolated Seamount and Its Implications for Conservation. PLOS ONE 7, e36574. https://doi.org/10.1371/journal.pone.0036574
Barthel, D., Gutt, J., 1992. Sponge associations in the eastern Weddell Sea. Antarct. Sci. 4, 137–150. https://doi.org/10.1017/S0954102092000221
Beazley, L.I., Kenchington, E.L., Murillo, F.J., Sacau, M. del M., 2013. Deep-sea sponge grounds enhance diversity and abundance of epibenthic megafauna in the Northwest Atlantic. ICES J. Mar. Sci. 70, 1471–1490. https://doi.org/10.1093/icesjms/fst124
Bebber, D.P., Marriott, F.H.C., Gaston, K.J., Harris, S.A., Scotland, R.W., 2007. Predicting unknown species numbers using discovery curves. Proc. R. Soc. B Biol. Sci. 274, 1651–1658. https://doi.org/10.1098/rspb.2007.0464
Beijbom, O., Edmunds, P.J., Roelfsema, C., Smith, J., Kline, D.I., Neal, B.P., Dunlap, M.J., Moriarty, V., Fan, T.-Y., Tan, C.-J., Chan, S., Treibitz, T., Gamst, A., Mitchell, B.G., Kriegman, D., 2015. Towards Automated Annotation of Benthic Survey Images: Variability of Human Experts and Operational Modes of Automation. PLOS ONE 10, e0130312. https://doi.org/10.1371/journal.pone.0130312
Bell, K.L.C., Quinzin, M.C., Amon, D., Poulton, S., Hope, A., Sarti, O., Cañete, T.E., Smith, A.M., Baldwin, H.I., Lira, D.M., Cambronero-Solano, S., Chung, T.-R.A., Brady, B., 2023. Exposing inequities in deep-sea exploration and research: results of the 2022 Global Deep-Sea Capacity Assessment. Front. Mar. Sci. 10. https://doi.org/10.3389/fmars.2023.1217227
Bilan, M., Gori, A., Grinyó, J., Biel-Cabanelas, M., Puigcerver-Segarra, X., Santín, A., Piraino, S., Rossi, S., Puig, P., 2023. Vulnerability of six cold-water corals to sediment resuspension from bottom trawling fishing. Mar. Pollut. Bull. 196, 115423. https://doi.org/10.1016/j.marpolbul.2023.115423
Bodil, B.A., Ambrose, W.G., Bergmann, M., Clough, L.M., Gebruk, A.V., Hasemann, C., Iken, K., Klages, M., MacDonald, I.R., Renaud, P.E., Schewe, I., Soltwedel, T., Włodarska-Kowalczuk, M., 2011. Diversity of the arctic deep-sea benthos. Mar. Biodivers. 41, 87–107. https://doi.org/10.1007/s12526-010-0078-4

Boehlert, G.W., 1988. Current-topography interactions at mid-ocean seamounts and the impact on pelagic ecosystems. GeoJournal 16, 45–52. https://doi.org/10.1007/BF02626371
Bongiorni, L., Mea, M., Gambi, C., Pusceddu, A., Taviani, M., Danovaro, R., 2010. Deep-water scleractinian corals promote higher biodiversity in deep-sea meiofaunal assemblages along continental margins. Biol. Conserv., Conservation planning within emerging global climate and economic realities 143, 1687–1700. https://doi.org/10.1016/j.biocon.2010.04.009
Boschen, R.E., Rowden, A.A., Clark, M.R., Pallentin, A., Gardner, J.P.A., 2016. Seafloor massive sulfide deposits support unique megafaunal assemblages: Implications for seabed mining and conservation. Mar. Environ. Res. 115, 78–88. https://doi.org/10.1016/j.marenvres.2016.02.005
Bourque, J.R., Demopoulos, A.W.J., 2018. The influence of different deep-sea coral habitats on sediment macrofaunal community structure and function. PeerJ 6, e5276. https://doi.org/10.7717/peerj.5276
Bourrel, M., Thiele, T., Currie, D., 2018. The common of heritage of mankind as a means to assess and advance equity in deep sea mining. Mar. Policy 95, 311–316. https://doi.org/10.1016/j.marpol.2016.07.017
Boyd, C.E., McNevin, A.A., Davis, R.P., 2022. The contribution of fisheries and aquaculture to the global protein supply. Food Secur. 14, 805–827. https://doi.org/10.1007/s12571-021-01246-9
Brault, S., Stuart, C.T., Wagstaff, M.C., McClain, C.R., Allen, J.A., Rex, M.A., 2013. Contrasting patterns of α- and β-diversity in deep-sea bivalves of the eastern and western North Atlantic. Deep Sea Res. Part II Top. Stud. Oceanogr. 92, 157–164. https://doi.org/10.1016/j.dsr2.2013.01.018
Breitburg, D., Levin, L., Zhang, J., 2018. Declining oxygen in the global ocean and coastal waters. Science.
Brewin, P.E., Stocks, K.I., Menezes, G., 2007. A History of Seamount Research, in: Seamounts: Ecology, Fisheries & Conservation. John Wiley & Sons, Ltd, pp. 41–61. https://doi.org/10.1002/9780470691953.ch3
Bridges, A.E.H., Barnes, D.K.A., Bell, J.B., Ross, R.E., Howell, K.L., 2022. Depth and latitudinal gradients of diversity in seamount benthic communities. J. Biogeogr. 49, 904–915. https://doi.org/10.1111/jbi.14355
Bridges, A.E.H., Barnes, D.K.A., Bell, J.B., Ross, R.E., Howell, K.L., 2021. Benthic Assemblage Composition of South Atlantic Seamounts. Front. Mar. Sci. 8.
Buhl-Mortensen, L., Mortensen, P.B., 2004. Symbiosis in Deep-Water Corals.
Carney, R.S., 1998. Basing conservation policies for the deep-sea floor on current, diversity concepts: A consideration of rarity. Oceanogr. Lit. Rev. 6, 1041.
Cartes, J.E., Sardà, F., 1992. Abundance and diversity of decapod crustaceans in the deep-Catalan Sea (Western Mediterranean). J. Nat. Hist. 26, 1305–1323. https://doi.org/10.1080/00222939200770741
Cathalot, C., Van Oevelen, D., Cox, T.J.S., Kutti, T., Lavaleye, M., Duineveld, G., Meysman, F.J.R., 2015. Cold-water coral reefs and adjacent sponge grounds: hotspots of benthic respiration and organic carbon cycling in the deep sea. Front. Mar. Sci. 2.
Cattaneo-Vietti, R., Chiantore, M., Misic, C., Povero, P., Fabiano, M., 1999. The role of pelagic-benthic coupling in structuring littoral benthic communities at Terra Nova Bay (Ross Sea) and in the Straits of Magellan. Sci. Mar. 63, 113–121. https://doi.org/10.3989/scimar.1999.63s1113
Castro, S.L., Monzon, L.A., Wick, G.A., Lewis, R.D., Beylkin, G., 2018. Subpixel variability and quality assessment of satellite sea surface temperature data using a novel High Resolution Multistage Spectral Interpolation (HRMSI) technique. Remote Sens. Environ. 217, 292–308. https://doi.org/10.1016/j.rse.2018.08.019
Chao, A., 2006. Species Estimation and Applications. https://doi.org/10.1002/0471667196.ess5051

Chao, A., Jost, L., 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93, 2533–2547. https://doi.org/10.1890/11-1952.1
Chiu, C.-H., 2023. Sample coverage estimation, rarefaction, and extrapolation based on sample-based abundance data. Ecology 104, e4099. https://doi.org/10.1002/ecy.4099
Clark, M., 2001. Are deepwater fisheries sustainable? — the example of orange roughy (*Hoplostethus atlanticus*) in New Zealand. Fish. Res., Deep-water Fish and Fisheries: A Selection of Papers Presented at the ICES Annual Science Conference in Lisbon, Portugal. 16-18 September 1998. 51, 123–135. https://doi.org/10.1016/S0165-7836(01)00240-5
Clark, M., O'Driscoll, R., 2003. Deepwater Fisheries and Aspects of Their Impact on Seamount Habitat in New Zealand. J. Northwest Atl. Fish. Sci. 31, 441–458. https://doi.org/10.2960/J.v31.a34
Clark, M.R., 2009. Deep-sea seamount fisheries: a review of global status and future prospects. Lat. Am. J. Aquat. Res. 37, 501–512. https://doi.org/10.3856/vol37-issue3-fulltext-17
Clark, M.R., Althaus, F., Schlacher, T.A., Williams, A., Bowden, D.A., Rowden, A.A., 2016a. The impacts of deep-sea fisheries on benthic communities: a review. ICES J. Mar. Sci. 73, i51–i69. https://doi.org/10.1093/icesjms/fsv123
Clark, M.R., Bagley, N.W., Harley, B., 2016b. Trawls, in: Biological Sampling in the Deep Sea. John Wiley & Sons, Ltd, pp. 126–158. https://doi.org/10.1002/9781118332535.ch7
Clark, M.R., Bowden, D.A., 2015. Seamount biodiversity: high variability both within and between seamounts in the Ross Sea region of Antarctica. Hydrobiologia 761, 161–180. https://doi.org/10.1007/s10750-015-2327-9
Clark, M.R., Koslow, J.A., 2007. Impacts of Fisheries on Seamounts, in: Seamounts: Ecology, Fisheries & Conservation. John Wiley & Sons, Ltd, pp. 413–441. https://doi.org/10.1002/9780470691953.ch19
Clark, M.R., Rowden, A.A., Schlacher, T., Williams, A., Consalvey, M., Stocks, K.I., Rogers, A.D., O'Hara, T.D., White, M., Shank, T.M., Hall-Spencer, J.M., 2010. The Ecology of Seamounts: Structure, Function, and Human Impacts. Annu. Rev. Mar. Sci. 2, 253–278. https://doi.org/10.1146/annurev-marine-120308-081109
Clark, M.R., Schlacher, T.A., Rowden, A.A., Stocks, K.I., Consalvey, M., 2012. Science Priorities for Seamounts: Research Links to Conservation and Management. PLoS ONE 7, e29232. https://doi.org/10.1371/journal.pone.0029232
Clark, M.R., Vinnichenko, V.I., Gordon, J.D.M., Beck-Bulat, G.Z., Kukharev, N.N., Kakora, A.F., 2007. Large-Scale Distant-Water Trawl Fisheries on Seamounts, in: Seamounts: Ecology, Fisheries & Conservation. John Wiley & Sons, Ltd, pp. 361–399. https://doi.org/10.1002/9780470691953.ch17
Clark, M.R., Watling, L., Rowden, A.A., Guinotte, J.M., Smith, C.R., 2011. A global seamount classification to aid the scientific design of marine protected area networks. Ocean Coast. Manag. 54, 19–36. https://doi.org/10.1016/j.ocecoaman.2010.10.006
Clarke, Andrew., Crame, J.Alistair., 1997. Diversity, latitude and time: Patterns in the shallow sea, in: Gage, J.D., Angel, M.V., Ormond, R.F.G. (Eds.), Marine Biodiversity: Patterns and Processes. Cambridge University Press, Cambridge, pp. 122–147. https://doi.org/10.1017/CBO9780511752360.007
Clarke, J., Milligan, R.J., Bailey, D.M., Neat, F.C., 2015. A Scientific Basis for Regulating Deep-Sea Fishing by Depth. Curr. Biol. 25, 2425–2429. https://doi.org/10.1016/j.cub.2015.07.070
Collie, J.S., Hall, S.J., Kaiser, M.J., Poiner, I.R., 2000. A quantitative analysis of fishing impacts on shelf-sea benthos. J. Anim. Ecol. 69, 785–798. https://doi.org/10.1046/j.1365-2656.2000.00434.x
Corliss, B.H., Brown, C.W., Sun, X., Showers, W.J., 2009. Deep-sea benthic diversity linked to seasonality of pelagic productivity. Deep Sea Res. Part Oceanogr. Res. Pap. 56, 835–841. https://doi.org/10.1016/j.dsr.2008.12.009

Costello, M.J., Chaudhary, C., 2017. Marine Biodiversity, Biogeography, Deep-Sea Gradients, and Conservation. Curr. Biol. 27, R511–R527. https://doi.org/10.1016/j.cub.2017.04.060
Culver, S.J., Buzas, M.A., 2000. Global latitudinal species diversity gradient in deep-sea benthic foraminifera. Deep Sea Res. Part Oceanogr. Res. Pap. 47, 259–275. https://doi.org/10.1016/S0967-0637(99)00055-2
Da Ros, Z., Dell'Anno, A., Morato, T., Sweetman, A.K., Carreiro-Silva, M., Smith, C.J., Papadopoulou, N., Corinaldesi, C., Bianchelli, S., Gambi, C., Cimino, R., Snelgrove, P., Van Dover, C.L., Danovaro, R., 2019. The deep sea: The new frontier for ecological restoration. Mar. Policy 108, 103642. https://doi.org/10.1016/j.marpol.2019.103642
Danovaro, R., Corinaldesi, C., Dell'Anno, A., Snelgrove, P.V.R., 2017. The deep-sea under global change. Curr. Biol. 27, R461–R465. https://doi.org/10.1016/j.cub.2017.02.046
Danovaro, R., Dell'Anno, A., Pusceddu, A., 2004. Biodiversity response to climate change in a warm deep sea. Ecol. Lett. 7, 821–828. https://doi.org/10.1111/j.1461-0248.2004.00634.x
Danovaro, R., Gambi, C., Dell'Anno, A., Corinaldesi, C., Fraschetti, S., Vanreusel, A., Vincx, M., Gooday, A.J., 2008. Exponential Decline of Deep-Sea Ecosystem Functioning Linked to Benthic Biodiversity Loss. Curr. Biol. 18, 1–8. https://doi.org/10.1016/j.cub.2007.11.056
Davies, A.J., Guinotte, J.M., 2011. Global Habitat Suitability for Framework-Forming Cold-Water Corals. PLOS ONE 6, e18483. https://doi.org/10.1371/journal.pone.0018483
Davies, J.S., Stewart, H.A., Narayanaswamy, B.E., Jacobs, C., Spicer, J., Golding, N., Howell, K.L., 2015. Benthic Assemblages of the Anton Dohrn Seamount (NE Atlantic): Defining Deep-Sea Biotopes to Support Habitat Mapping and Management Efforts with a Focus on Vulnerable Marine Ecosystems. PLOS ONE 10, e0124815. https://doi.org/10.1371/journal.pone.0124815
Dayton, P.K., Hessler, R.R., 1972. Role of biological disturbance in maintaining diversity in the deep sea. Deep Sea Res. Oceanogr. Abstr. 19, 199–208. https://doi.org/10.1016/0011-7471(72)90031-9
Dayton, P.K., Robilliard, G.A., Paine, R.T., Dayton, L.B., 1974. Biological Accommodation in the Benthic Community at McMurdo Sound, Antarctica. Ecol. Monogr. 44, 105–128. https://doi.org/10.2307/1942321
Deasy, K., 2023. What we know about the new High Seas Treaty. Npj Ocean Sustain. 2, 1–3. https://doi.org/10.1038/s44183-023-00013-x
Dede, A., Öztürk, A.A., Tonay, A.M., Özsandıkçı, U., Gönülal, O., Öztürk, B., 2022. Cetacean sightings in the Finike Seamounts area and adjacent waters during the surveys in 2022.
Demopoulos, A., Smith, C., Tyler, P., 2003. The deep Indian Ocean floor.
Djurhuus, A., Boersch-Supan, P.H., Mikalsen, S.-O., Rogers, A.D., 2017. Microbe biogeography tracks water masses in a dynamic oceanic frontal system. R. Soc. Open Sci. 4, 170033. https://doi.org/10.1098/rsos.170033
Doi, H., Yasuhara, M., Ushio, M., 2021. Causal analysis of the temperature impact on deep-sea biodiversity. Biol. Lett. 17, 20200666. https://doi.org/10.1098/rsbl.2020.0666
Dover, C., Aronson, J., Pendleton, L., Smith, S., Arnaud-Haond, S., Moreno Mateos, D., Barbier, E., David, S.M., Bowers, K., Danovaro, R., Edwards, A., Kellert, S., Morato, T., Pollard, E., Rogers, A., Warner, R., 2014. Ecological restoration in the deep sea: Desiderata. Mar. Policy 44, 98–106. https://doi.org/10.1016/j.marpol.2013.07.006
Drazen, J.C., Smith, C.R., Gjerde, K.M., Haddock, S.H.D., Carter, G.S., Choy, C.A., Clark, M.R., Dutrieux, P., Goetze, E., Hauton, C., Hatta, M., Koslow, J.A., Leitner, A.B., Pacini, A., Perelman, J.N., Peacock, T., Sutton, T.T., Watling, L., Yamamoto, H., 2020. Midwater ecosystems must be considered when evaluating environmental risks of deep-sea mining. Proc. Natl. Acad. Sci. 117, 17455–17460. https://doi.org/10.1073/pnas.2011914117
Dulvy, N., Ellis, J., Goodwin, N., Grant, A., Reynolds, J., Jennings, S., 2004. Methods of assessing extinction risk in marine fishes. Fish Fish. 5, 255–276. https://doi.org/10.1111/j.1467-2679.2004.00158.x

Dunn, D.C., Ardron, J., Bax, N., Bernal, P., Cleary, J., Cresswell, I., Donnelly, B., Dunstan, P., Gjerde, K., Johnson, D., Kaschner, K., Lascelles, B., Rice, J., von Nordheim, H., Wood, L., Halpin, P.N., 2014. The Convention on Biological Diversity's Ecologically or Biologically Significant Areas: Origins, development, and current status. Mar. Policy 49, 137–145. https://doi.org/10.1016/j.marpol.2013.12.002

Dunstan, P.K., Althaus, F., Williams, A., Bax, N.J., 2012. Characterising and Predicting Benthic Biodiversity for Conservation Planning in Deepwater Environments. PLOS ONE 7, e36558. https://doi.org/10.1371/journal.pone.0036558

Durden et al., 2016. Perspectives in Visual Imaging for Marine Biology and Ecology: From Acquisition to Understanding.

Eerkes-Medrano, D., Drewery, J., Burns, F., Cárdenas, P., Taite, M., MKay, D.W., Stirling, D., Neat, F., 2020. A community assessment of the demersal fish and benthic invertebrates of the Rosemary Bank Seamount marine protected area (NE Atlantic). Deep Sea Res. Part Oceanogr. Res. Pap. 156, 103180. https://doi.org/10.1016/j.dsr.2019.103180

Eguíluz, V.M., Salazar, G., Fernández-Gracia, J., Pearman, J.K., Gasol, J.M., Acinas, S.G., Sunagawa, S., Irigoien, X., Duarte, C.M., 2019. Scaling of species distribution explains the vast potential marine prokaryote diversity. Sci. Rep. 9, 18710. https://doi.org/10.1038/s41598-019-54936-y

Elshkaki, A., Graedel, T.E., Ciacci, L., Reck, B., 2018. Resource Demand Scenarios for the Major Metals. Environ. Sci. Technol. https://doi.org/10.1021/acs.est.7b05154

Etnoyer, P.J., Wood, J., Shirley, T.C., 2010. BOX 12 | How Large Is the Seamount Biome? Oceanography 23, 206–209.

Etter, R.J., Rex, M.A., 1990. Population differentiation decreases with depth in deep-sea gastropods. Deep Sea Res. Part Oceanogr. Res. Pap. 37, 1251–1261. https://doi.org/10.1016/0198-0149(90)90041-S

Evans, K.L., Greenwood, J.J.D., Gaston, K.J., 2005. Dissecting the species–energy relationship. Proc. R. Soc. B Biol. Sci. 272, 2155–2163. https://doi.org/10.1098/rspb.2005.3209

Fallon, S.J., Thresher, R.E., Adkins, J., 2014. Age and growth of the cold-water scleractinian Solenosmilia variabilis and its reef on SW Pacific seamounts. Coral Reefs 33, 31–38. https://doi.org/10.1007/s00338-013-1097-y

FAO, 2009. Report of the Technical Consultation on International Guidelines for the Management of Deep-sea Fisheries in the High Seas. FAO Fisheries and Aquaculture Report, Rome.

Ferrier, S., 2002. Mapping Spatial Pattern in Biodiversity for Regional Conservation Planning: Where to from Here? Syst. Biol. 51, 331–363. https://doi.org/10.1080/10635150252899806

Fillinger, L., Janussen, D., Lundälv, T., Richter, C., 2013. Rapid Glass Sponge Expansion after Climate-Induced Antarctic Ice Shelf Collapse. Curr. Biol. 23, 1330–1334. https://doi.org/10.1016/j.cub.2013.05.051

Fisher, M.A., Vinson, J.E., Gittleman, J.L., Drake, J.M., 2018. The description and number of undiscovered mammal species. Ecol. Evol. 8, 3628–3635. https://doi.org/10.1002/ece3.3724

Fleishman, E., Noss, R.F., Noon, B.R., 2006. Utility and limitations of species richness metrics for conservation planning. Ecol. Indic. 6, 543–553. https://doi.org/10.1016/j.ecolind.2005.07.005

Freese, J.L., Wing, B.L., 2003. Juvenile Red Rockfish, Sebastes sp., Associations with Sponges in the Gulf of Alaska. Mar. Fish. Rev. 65, 38–42.

Froneman, P.W., Ansorge, I.J., Richoux, N., Blake, J., Daly, R., Sterley, J., Mostert, B., Heyns, E., Sheppard, J., Kuyper, B., Hart, N., George, C., Howard, J., Mustafa, E., Pey, F., Lutjeharms, J.R.E., 2007. Physical and biological processes at the Subtropical Convergence in the South-west Indian Ocean : research in action. South Afr. J. Sci. 103, 193–195. https://doi.org/10.10520/EJC96683

Fulton, B., Morato, T., Pitcher, T.J., 2007. Modelling Seamount Ecosystems and their Fisheries, in: Seamounts: Ecology, Fisheries & Conservation. John Wiley & Sons, Ltd, pp. 296–332. https://doi.org/10.1002/9780470691953.ch15

Gage, J.D., Lamont, P.A., Kroeger, K., Paterson, G.L.J., Vecino, J.L.G., 2000. Patterns in deep-sea macrobenthos at the continental margin: standing crop, diversity and faunal change on the continental slope off Scotland, in: Jones, M.B., Azevedo, J.M.N., Neto, A.I., Costa, A.C., Martins, A.M.F. (Eds.), Island, Ocean and Deep-Sea Biology. Springer Netherlands, Dordrecht, pp. 261–271. https://doi.org/10.1007/978-94-017-1982-7_24
Garrigue, C., Clapham, P.J., Geyer, Y., Kennedy, A.S., Zerbini, A.N., 2015. Satellite tracking reveals novel migratory patterns and the importance of seamounts for endangered South Pacific humpback whales. R. Soc. Open Sci. 2, 150489. https://doi.org/10.1098/rsos.150489
Genin, A., 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. J. Mar. Syst., The Role of Biophysical Coupling in Concentrating Marine Organisms Around Shallow Topographies 50, 3–20. https://doi.org/10.1016/j.jmarsys.2003.10.008
Genin, A., Dower, J., 2007. Seamounts: Ecology, Fisheries & Conservation | Wiley Online Books. Blackwell Publishing Ltd.
Georgian, S.E., Kramer, K., Saunders, M., Shedd, W., Roberts, H., Lewis, C., Fisher, C., Cordes, E., 2020. Habitat suitability modelling to predict the spatial distribution of cold-water coral communities affected by the Deepwater Horizon oil spill. J. Biogeogr. 47, 1455–1466. https://doi.org/10.1111/jbi.13844
Gershanovich, D.Ye., Dubinets, G.A., 1991. Geomorphology of Indian Ocean Seamounts. Int. Geol. Rev. 33, 903–913. https://doi.org/10.1080/00206819109465733
Gibson, R., Atkinson, R., Gordon, J., Editors, T., In, F., Carney, R., 2005. Zonation of Deep Biota on Continental Margins. Annu. Rev. 43, 211–278.
Gibson, R.N., Atkinson, R.J.A., Gordon, J.D.M., 2005. Oceanography and Marine Biology: An annual review. Volume 43. CRC Press.
Goldthwait, S., Carlson, C., Henderson, G., Alldredge, A., 2005. Effects of physical fragmentation on remineralization of marine snow. Mar. Ecol. Prog. Ser. 305, 59–65. https://doi.org/10.3354/meps305059
Goode, S.L., Rowden, A.A., Bowden, D.A., Clark, M.R., 2020. Resilience of seamount benthic communities to trawling disturbance. Mar. Environ. Res. 161, 105086. https://doi.org/10.1016/j.marenvres.2020.105086
Goode, S.L., Rowden, A.A., Bowden, D.A., Clark, M.R., Stephenson, F., 2021. Fine-Scale Mapping of Mega-Epibenthic Communities and Their Patch Characteristics on Two New Zealand Seamounts. Front. Mar. Sci. 8. https://doi.org/10.3389/fmars.2021.765407
Goren, L., Idan, T., Shefer, S., Ilan, M., 2021. Macrofauna Inhabiting Massive Demosponges From Shallow and Mesophotic Habitats Along the Israeli Mediterranean Coast. Front. Mar. Sci. 7. https://doi.org/10.3389/fmars.2020.612779
Goswami, M., Bhattacharyya, P., Mukherjee, I., Tribedi, P., 2017. Functional Diversity: An Important Measure of Ecosystem Functioning. Adv. Microbiol. 7, 82–93. https://doi.org/10.4236/aim.2017.71007
Grassle, J.F., Maciolek, N.J., 1992. Deep-Sea Species Richness: Regional and Local Diversity Estimates from Quantitative Bottom Samples. Am. Nat. 139, 313–341. https://doi.org/10.1086/285329
Grattarola, F., Bowler, D.E., Keil, P., 2023. Integrating presence-only and presence–absence data to model changes in species geographic ranges: An example in the Neotropics. J. Biogeogr. 50, 1561–1575. https://doi.org/10.1111/jbi.14622
Griffiths, H.J., 2010. Antarctic Marine Biodiversity – What Do We Know About the Distribution of Life in the Southern Ocean? PLOS ONE 5, e11683. https://doi.org/10.1371/journal.pone.0011683
Grinyó, J., Gori, A., Greenacre, M., Requena, S., Canepa, A., Lo Iacono, C., Ambroso, S., Purroy, A., Gili, J.-M., 2018. Megabenthic assemblages in the continental shelf edge and upper slope of the Menorca Channel, Western Mediterranean Sea. Prog. Oceanogr. 162, 40–51. https://doi.org/10.1016/j.pocean.2018.02.002

Gruber, N., Clement, D., Carter, B.R., Feely, R.A., van Heuven, S., Hoppema, M., Ishii, M., Key, R.M., Kozyr, A., Lauvset, S.K., Lo Monaco, C., Mathis, J.T., Murata, A., Olsen, A., Perez, F.F., Sabine, C.L., Tanhua, T., Wanninkhof, R., 2019. The oceanic sink for anthropogenic CO2 from 1994 to 2007. Science 363, 1193–1199. https://doi.org/10.1126/science.aau5153

Haney, J.C., Haury, L.R., Mullineaux, L.S., Fey, C.L., 1995. Sea-bird aggregation at a deep North Pacific seamount. Mar. Biol. 123, 1–9. https://doi.org/10.1007/BF00350317

Harris, P.T., Macmillan-Lawler, M., Rupp, J., Baker, E.K., 2014. Geomorphology of the oceans. Mar. Geol., 50th Anniversary Special Issue 352, 4–24. https://doi.org/10.1016/j.margeo.2014.01.011

Harrison, T.D., Whitfield, A.K., 2006. Temperature and salinity as primary determinants influencing the biogeography of fishes in South African estuaries. Estuar. Coast. Shelf Sci. 66, 335–345. https://doi.org/10.1016/j.ecss.2005.09.010

Hartwell, A.M., Wheat, A.E., Dijkstra, J.A., 2024. Natural warming differentiates communities and increases diversity in deep-sea Ridge Flank Hydrothermal Systems. Commun. Biol. 7, 1–11. https://doi.org/10.1038/s42003-024-06070-3

Hein, J.R., Conrad, T.A., Staudigel, H., 2010. Seamount Mineral Deposits: A SOURCE OF RARE METALS FOR HIGH-TECHNOLOGY INDUSTRIES. Oceanography 23, 184–189.

Henry, L.-A., Frank, N., Hebbeln, D., Wienberg, C., Robinson, L., de Flierdt, T. van, Dahl, M., Douarin, M., Morrison, C.L., Correa, M.L., Rogers, A.D., Ruckelshausen, M., Roberts, J.M., 2014. Global ocean conveyor lowers extinction risk in the deep sea. Deep Sea Res. Part Oceanogr. Res. Pap. 88, 8–16. https://doi.org/10.1016/j.dsr.2014.03.004

Henry, L.-A., Vad, J., Findlay, H.S., Murillo, J., Milligan, R., Roberts, J.M., 2014. Environmental variability and biodiversity of megabenthos on the Hebrides Terrace Seamount (Northeast Atlantic). Sci. Rep. 4, 5589. https://doi.org/10.1038/srep05589

Hestetun, J.T., Rapp, H.T., Xavier, J., 2017. Carnivorous sponges (Porifera, Cladorhizidae) from the Southwest Indian Ocean Ridge seamounts. Deep Sea Res. Part II Top. Stud. Oceanogr., Advances in deep-sea biology: biodiversity, ecosystem functioning and conservation 137, 166–189. https://doi.org/10.1016/j.dsr2.2016.03.004

Hiddink, J.G., Jennings, S., Kaiser, M.J., 2017. Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance | PNAS. PNAS.

Hillebrand, H., 2004. On the Generality of the Latitudinal Diversity Gradient. Am. Nat. https://doi.org/10.1086/381004

Hillier, J.K., Watts, A.B., 2007. Global distribution of seamounts from ship-track bathymetry data. Geophys. Res. Lett. 34. https://doi.org/10.1029/2007GL029874

Hogg, M., Tendal, O., Conway, S., Pomponi, S., Krautter, M., 2010. Deep-sea sponge grounds: reservoirs of biodiversity., UNEP-WCMC Biodiversity Series, 32.

Holland, Kim, Kleiber, Kajiura, 1999. Different residence times of yellowfin tuna, Thunnus albacares, and bigeye tuna, T. obesus, found in mixed aggregations over a seamount. Fishery Bulletin-National Oceanic and Atmospheric Administration 392–395.

Hopkinson, C.S., Vallino, J.J., 2005. Efficient export of carbon to the deep ocean through dissolved organic matter. Nature 433, 142–145. https://doi.org/10.1038/nature03191

Howell, K.L., Davies, J.S., Allcock, A.L., Braga-Henriques, A., Buhl-Mortensen, P., Carreiro-Silva, M., Dominguez-Carrió, C., Durden, J.M., Foster, N.L., Game, C.A., Hitchin, B., Horton, T., Hosking, B., Jones, D.O.B., Mah, C., Marchais, C.L., Menot, L., Morato, T., Pearman, T.R.R., Piechaud, N., Ross, R.E., Ruhl, H.A., Saeedi, H., Stefanoudis, P.V., Taranto, G.H., Thompson, M.B., Taylor, J.R., Tyler, P., Vad, J., Victorero, L., Vieira, R.P., Woodall, L.C., Xavier, J.R., Wagner, D., 2019. A framework for the development of a global standardised marine taxon reference image database (SMarTaR-ID) to support image-based analyses. PLOS ONE 14, e0218904. https://doi.org/10.1371/journal.pone.0218904

Howell, K.L., Pond, D.W., Billett, D.S.M., Tyler, P.A., 2003. Feeding ecology of deep-sea seastars (Echinodermata: Asteroidea): a fatty-acid biomarker approach. Mar. Ecol. Prog. Ser. 255, 193–206. https://doi.org/10.3354/meps255193
Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol. Evol. 7, 1451–1456. https://doi.org/10.1111/2041-210X.12613
Hu, Z., Hu, J., Hu, H., Zhou, Y., 2020. Predictive habitat suitability modeling of deep-sea framework-forming scleractinian corals in the Gulf of Mexico. Sci. Total Environ. 742, 140562. https://doi.org/10.1016/j.scitotenv.2020.140562
Huang, S., Hall, P.S., Jackson, M.G., 2011. Geochemical zoning of volcanic chains associated with Pacific hotspots. Nat. Geosci. 4, 874–878. https://doi.org/10.1038/ngeo1263
Hunt, J.C., Lindsay, D.J., Shahalemi, R.R., 2011. A nursery site of the golden skate (Rajiformes: Rajidae: Bathyraja smirnovi) on the Shiribeshi Seamount, Sea of Japan. Mar. Biodivers. Rec. 4, e70. https://doi.org/10.1017/S1755267211000728
Huvenne, V.A.I., Bett, B.J., Masson, D.G., Le Bas, T.P., Wheeler, A.J., 2016. Effectiveness of a deep-sea cold-water coral Marine Protected Area, following eight years of fisheries closure. Biol. Conserv. 200, 60–69. https://doi.org/10.1016/j.biocon.2016.05.030
Ingram, T., 2011. Speciation along a depth gradient in a marine adaptive radiation. Proc. R. Soc. B Biol. Sci. 278, 613–618. https://doi.org/10.1098/rspb.2010.1127
Jac, C., Desroy, N., Duchêne, J.-C., Foveau, A., Labrune, C., Lescure, L., Vaz, S., 2021. Assessing the impact of trawling on benthic megafauna: comparative study of video surveys vs. scientific trawling. ICES J. Mar. Sci. 78, 1636–1649. https://doi.org/10.1093/icesjms/fsab033
Jouffray, J.-B., Blasiak, R., Norström, A.V., Österblom, H., Nyström, M., 2020. The Blue Acceleration: The Trajectory of Human Expansion into the Ocean. One Earth 2, 43–54. https://doi.org/10.1016/j.oneear.2019.12.016
Kaiser, M.J., Collie, J.S., Hall, S.J., Jennings, S., Poiner, I.R., 2002. Modification of marine habitats by trawling activities: prognosis and solutions. Fish Fish. 3, 114–136. https://doi.org/10.1046/j.1467-2979.2002.00079.x
Kaufmann, R.S., Wakefield, W.W., Genin, A., 1989. Distribution of epibenthic megafauna and lebensspuren on two central North Pacific seamounts. Deep Sea Res. Part Oceanogr. Res. Pap. 36, 1863–1896. https://doi.org/10.1016/0198-0149(89)90116-7
Kenchington, E., Power, D., Koen-Alonso, M., 2013. Associations of demersal fish with sponge grounds on the continental slopes of the northwest Atlantic. Mar. Ecol. Prog. Ser. 477, 217–230. https://doi.org/10.3354/meps10127
Kennedy, B., 2016. Deepwater Wonders of Wake: Exploring the Pacific Remote Islands Marine National Monument.
Kersken, D., Feldmeyer, B., Janussen, D., 2016. Sponge communities of the Antarctic Peninsula: influence of environmental variables on species composition and richness. Polar Biol. 39, 851–862. https://doi.org/10.1007/s00300-015-1875-9
Kimball, L., 2004. Deep-Sea Fisheries of the High Seas: The Management Impasse. Int. J. Mar. Coast. Law 19, 259–287. https://doi.org/10.1163/1571808042886011
Kitchingman, A., Lai, S., 2004. Inferences on Potential Seamount Locations from Mid-Resolution Bathymetric Data. Seamounts: Biodiversity and Fisheries 7.
Kitchingman, A., Lai, S., Morato, T., Pauly, D., 2007. How Many Seamounts are There and Where are They Located?, in: Seamounts: Ecology, Fisheries & Conservation. John Wiley & Sons, Ltd, pp. 26–40. https://doi.org/10.1002/9780470691953.ch2
Klimley, A., Butler, S., Nelson, D., Stull, A., 1988. Diel movements of scalloped hammerhead sharks, Sphyrna lewini Griffith and Smith, to and from a seamount in the Gulf of California. Journal of Fish Biology.
Koleff, P., Gaston, K.J., Lennon, J.J., 2003. Measuring beta diversity for presence–absence data. J. Anim. Ecol. 72, 367–382. https://doi.org/10.1046/j.1365-2656.2003.00710.x

Koslow, J.A., 1996. Energetic and life-history patterns of deep-sea benthic, benthopelagic and seamount-associated fish. J. Fish Biol. 49, 54–74. https://doi.org/10.1111/j.1095-8649.1996.tb06067.x
Koslow, J.A., Gowlett-Holmes, K., Lowry, J.K., O'Hara, T., Poore, G.C.B., Williams, A., 2001. Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. Mar. Ecol. Prog. Ser. 213, 111–125. https://doi.org/10.3354/meps213111
Kuhnz, L.A., Ruhl, H.A., Huffard, C.L., Smith, K.L., 2014. Rapid changes and long-term cycles in the benthic megafaunal community observed over 24 years in the abyssal northeast Pacific. Prog. Oceanogr. 124, 1–11. https://doi.org/10.1016/j.pocean.2014.04.007
Kung, A., Svobodova, K., Lèbre, E., Valenta, R., Kemp, D., Owen, J.R., 2021. Governing deep sea mining in the face of uncertainty. J. Environ. Manage. 279, 111593. https://doi.org/10.1016/j.jenvman.2020.111593
Kvile, K.Ø., Taranto, G.H., Pitcher, T.J., Morato, T., 2014. A global assessment of seamount ecosystems knowledge using an ecosystem evaluation framework. Biol. Conserv. 173, 108–120. https://doi.org/10.1016/j.biocon.2013.10.002
La Bianca, G., Rees, S., Attrill, M.J., Lombard, A.T., McQuaid, K.A., Niner, H.J., van Rein, H., Sink, K.J., Howell, K.L., 2023. A standardised ecosystem services framework for the deep sea. Front. Mar. Sci. 10. https://doi.org/10.3389/fmars.2023.1176230
Lacharité, M., Metaxas, A., 2017. Hard substrate in the deep ocean: How sediment features influence epibenthic megafauna on the eastern Canadian margin. Deep Sea Res. Part Oceanogr. Res. Pap. 126, 50–61. https://doi.org/10.1016/j.dsr.2017.05.013
Lambshead, P., Tietjen, J., Moncrieff, C., Ferrero, T., 2001. North Atlantic latitudinal diversity patterns in deep-sea marine nematode data: a reply to Rex et al. Mar. Ecol. Prog. Ser. 210, 299–301. https://doi.org/10.3354/meps210299
Lambshead, P.J.D., Brown, C.J., Ferrero, T.J., Mitchell, N.J., Smith, C.R., Hawkins, L.E., Tietjen, J., 2002. Latitudinal diversity patterns of deep-sea marine nematodes and organic fluxes : a test from the central equatorial Pacific. Mar. Ecol. Prog. Ser. 236, 129–135. https://doi.org/10.3354/meps236129
Langenkämper, D., Zurowietz, M., Schoening, T., Nattkemper, T.W., 2017. BIIGLE 2.0 - Browsing and Annotating Large Marine Image Collections. Front. Mar. Sci. 4.
Laptikhovsky, V., Boersch-Supan, P., Bolstad, K., Kemp, K., Letessier, T., Rogers, A.D., 2017. Cephalopods of the Southwest Indian OceanRidge: A hotspot of biological diversity and absence of endemism. Deep Sea Res. Part II Top. Stud. Oceanogr., The Pelagic Ecology of Seamounts of the South West Indian Ocean 136, 98–107. https://doi.org/10.1016/j.dsr2.2015.07.002
Lavelle, J.W., Thurnherr, A.M., Ledwell, J.R., McGillicuddy Jr., D.J., Mullineaux, L.S., 2010. Deep ocean circulation and transport where the East Pacific Rise at 9–10°N meets the Lamont seamount chain. J. Geophys. Res. Oceans 115. https://doi.org/10.1029/2010JC006426
Le Danois, 1948. Le profondeurs de la mer. Paris.
Leduc, D., Rowden, A.A., Bowden, D.A., Probert, P.K., Pilditch, C.A., Nodder, S.D., 2012. Unimodal relationship between biomass and species richness of deep-sea nematodes: implications for the link between productivity and diversity. Mar. Ecol. Prog. Ser. 454, 53–64. https://doi.org/10.3354/meps09609
Leitner, A.B., Neuheimer, A.B., Drazen, J.C., 2020. Evidence for long-term seamount-induced chlorophyll enhancements. Sci. Rep. 10, 12729. https://doi.org/10.1038/s41598-020-69564-0
Levin, L., Etter, R., Rex, M., Gooday, A., Smith, C., Pineda, J., Stuart, C., Hessler, R., Pawson, D., 2003. Environmental Influences on Regional Deep-Sea Species Diversity 1. Annu. Rev. Ecol. Syst. 32, 51–93. https://doi.org/10.1146/annurev.ecolsys.32.081501.114002
Levin, L.A., Gage, J.D., 1998. Relationships between oxygen, organic matter and the diversity of bathyal macrofauna. Deep Sea Res. Part II Top. Stud. Oceanogr. 45, 129–163. https://doi.org/10.1016/S0967-0645(97)00085-4

Lively, J.A., Good, T.P., 2019. Chapter 10 - Ghost Fishing, in: Sheppard, C. (Ed.), World Seas: An Environmental Evaluation (Second Edition). Academic Press, pp. 183–196. https://doi.org/10.1016/B978-0-12-805052-1.00010-3
Llodra, E.R., 2006. Deep-Sea Ecosystems: Pristine Biodiversity Reservoir and Technological Challenges.
Lockhart, S.J., Hocevar, J., 2021. Combined Abundance of All Vulnerable Marine Ecosystem Indicator Taxa Inadequate as Sole Determiner of Vulnerability, Antarctic Peninsula. Front. Mar. Sci. 8. https://doi.org/10.3389/fmars.2021.577761
Lutjeharms, J.R.E., 2007. Three decades of research on the greater Agulhas Current. Ocean Sci. 3, 129–147. https://doi.org/10.5194/os-3-129-2007
MacLeod, N., Benfield, M., Culverhouse, P., 2010. Time to automate identification. Nature 467, 154–155. https://doi.org/10.1038/467154a
Macpherson, E., 2002. Large–scale species–richness gradients in the Atlantic Ocean. Proc. R. Soc. Lond. B Biol. Sci. 269, 1715–1720. https://doi.org/10.1098/rspb.2002.2091
Macreadie, P.I., McLean, D.L., Thomson, P.G., Partridge, J.C., Jones, D.O.B., Gates, A.R., Benfield, M.C., Collin, S.P., Booth, D.J., Smith, L.L., Techera, E., Skropeta, D., Horton, T., Pattiaratchi, C., Bond, T., Fowler, A.M., 2018. Eyes in the sea: Unlocking the mysteries of the ocean using industrial, remotely operated vehicles (ROVs). Sci. Total Environ. 634, 1077–1091. https://doi.org/10.1016/j.scitotenv.2018.04.049
Magnusson, A., Skaug, H.J., Nielsen, A., Berg., C.W., Kristensen, K., Maechler, M., van Bentham, K.J., Bolker, B.M., Brooks, M.E., 2017. {glmmTMB}: Generalized Linear Mixed Models using Template Model Builder.
Maguire, K., O'Neill, H., Althaus, F., White, W., Williams, A., 2023. Seamount coral reefs are egg case nurseries for deep-sea skates. J. Fish Biol. 102, 1455–1469. https://doi.org/10.1111/jfb.15376
Mallet, D., Pelletier, D., 2014. Underwater video techniques for observing coastal marine biodiversity: A review of sixty years of publications (1952–2012). Fish. Res. 154, 44–62. https://doi.org/10.1016/j.fishres.2014.01.019
Manjón-Cabeza, M.E., Ríos, P., García-Guillén, L.M., Macías-Ramírez, A., Sánchez, F., Rodríguez-Básalo, A., Ibarrola, T.P., Cristobo, J., 2021. Asteroids and Ophiuroids Associated With Sponge Aggregations as a Key to Marine Habitats. A Comparative Analysis Between Avilés Canyons System and El Cachucho, Marine Protected Area. Front. Mar. Sci. 7. https://doi.org/10.3389/fmars.2020.606749
Marques da Silva, H., Pinho, M., 2007. Small-scale fishing on seamounts, in: Seamount: Ecology, Fisheries & Conservation. https://doi.org/10.1002/9780470691953
Marsac, F., Galletti, F., Ternon, J.-F., Romanov, E.V., Demarcq, H., Corbari, L., Bouchet, P., Roest, W.R., Jorry, S.J., Olu, K., Loncke, L., Roberts, M.J., Ménard, F., 2020. Seamounts, plateaus and governance issues in the southwestern Indian Ocean, with emphasis on fisheries management and marine conservation, using the Walters Shoal as a case study for implementing a protection framework. Deep Sea Res. Part II Top. Stud. Oceanogr., Bio-Physical coupling around three shallow seamounts in the South Western Indian Ocean, with regional comparisons based on modelling, remote sensing and observational studies 176, 104715. https://doi.org/10.1016/j.dsr2.2019.104715
Martini, S., Kuhnz, L., Mallefet, J., Haddock, S.H.D., 2019. Distribution and quantification of bioluminescence as an ecological trait in the deep sea benthos. https://doi.org/10.1038/s41598-019-50961-z
Maxwell, S.M., 2011. Benthic Foraging on seamounts: A specialised foraging behaviour in a deep-diving pinniped. Marine Mammal Science. https://doi.org/10.1111/j.1748-7692.2011.00527.x
Maynou, F., Cartes, J.E., 2012. Effects of trawling on fish and invertebrates from deep-sea coral facies of Isidella elongata in the western Mediterranean. J. Mar. Biol. Assoc. U. K. 92, 1501–1507. https://doi.org/10.1017/S0025315411001603

McClain, C.R., 2021. The commonness of rarity in a deep-sea taxon. Oikos 130, 863–878. https://doi.org/10.1111/oik.07602
McClain, C.R., Lundsten, L., 2015. Assemblage structure is related to slope and depth on a deep offshore Pacific seamount chain. Mar. Ecol. 36, 210–220. https://doi.org/10.1111/maec.12136
McClain, C.R., Lundsten, L., Barry, J., DeVogelaere, A., 2010. Assemblage structure, but not diversity or density, change with depth on a northeast Pacific seamount. Mar. Ecol. 31, 14–25. https://doi.org/10.1111/j.1439-0485.2010.00367.x
McClain, C.R., Rex, M.A., 2015. Toward a Conceptual Understanding of β-Diversity in the Deep-Sea Benthos. Annu. Rev. Ecol. Evol. Syst. 46, 623–642. https://doi.org/10.1146/annurev-ecolsys-120213-091640
McKinley, S.J., Saunders, B.J., Rastoin-Laplane, E., Salinas-de-León, P., Harvey, E.S., 2022. Functional diversity of reef fish assemblages in the Galapagos Archipelago. J. Exp. Mar. Biol. Ecol. 549, 151695. https://doi.org/10.1016/j.jembe.2022.151695
McManus, J.W., Polsenberg, J.F., 2004. Coral–algal phase shifts on coral reefs: Ecological and environmental aspects. Prog. Oceanogr. 60, 263–279. https://doi.org/10.1016/j.pocean.2004.02.014
Mello-Rafter, K., Sowers, D., Malik, M., Watling, L., Mayer, L.A., Dijkstra, J.A., 2021. Environmental and Geomorphological Effects on the Distribution of Deep-Sea Canyon and Seamount Communities in the Northwest Atlantic. Front. Mar. Sci. 8.
Melo-Merino, S., Reyes-Bonilla, H., Lira-Noriega, A., 2020. Ecological niche models and species distribution models in marine environments: A literature review and spatial analysis of evidence. Ecol. Model. 415, 108837. https://doi.org/10.1016/j.ecolmodel.2019.108837
Mestre, N.C., Brown, A., Thatje, S., 2013. Temperature and pressure tolerance of larvae of Crepidula fornicata suggest thermal limitation of bathymetric range. Mar. Biol. 160, 743–750. https://doi.org/10.1007/s00227-012-2128-x
Menegotto, A., Rangel, T.F., 2018. Mapping knowledge gaps in marine diversity reveals a latitudinal gradient of missing species richness. Nat. Commun. 9, 4713. https://doi.org/10.1038/s41467-018-07217-7
Meyssignac, B., Boyer, T., Zhao, Z., Hakuba, M.Z., Landerer, F.W., Stammer, D., Köhl, A., Kato, S., L'Ecuyer, T., Ablain, M., Abraham, J.P., Blazquez, A., Cazenave, A., Church, J.A., Cowley, R., Cheng, L., Domingues, C.M., Giglio, D., Gouretski, V., Ishii, M., Johnson, G.C., Killick, R.E., Legler, D., Llovel, W., Lyman, J., Palmer, M.D., Piotrowicz, S., Purkey, S.G., Roemmich, D., Roca, R., Savita, A., Schuckmann, K. von, Speich, S., Stephens, G., Wang, G., Wijffels, S.E., Zilberman, N., 2019. Measuring Global Ocean Heat Content to Estimate the Earth Energy Imbalance. Front. Mar. Sci. 6. https://doi.org/10.3389/fmars.2019.00432
Mienis, F., Duineveld, G.C.A., Davies, A.J., Lavaleye, M.M.S., Ross, S.W., Seim, H., Bane, J., van Haren, H., Bergman, M.J.N., de Haas, H., Brooke, S., van Weering, T.C.E., 2014. Cold-water coral growth under extreme environmental conditions, the Cape Lookout area, NW Atlantic. Biogeosciences 11, 2543–2560. https://doi.org/10.5194/bg-11-2543-2014
Miller, K.A., Thompson, K.F., Johnston, P., Santillo, D., 2018. An Overview of Seabed Mining Including the Current State of Development, Environmental Impacts, and Knowledge Gaps. Front. Mar. Sci. 4. https://doi.org/10.3389/fmars.2017.00418
Moore, J., Vecchione, M., Gibbons, R., Galbraith, J.K., Turnipseed, M., Southworth, M., Watkins, E., 2003. Biodiversity of Bear Seamount, New England Seamount chain: Results of exploratory trawling. J. Northwest Atl. Fish. Sci. 31, 363–372.
Morato, T., Cheung, W.W.L., Pitcher, T.J., 2006. Vulnerability of seamount fish to fishing: fuzzy analysis of life-history attributes. J. Fish Biol. 68, 209–221. https://doi.org/10.1111/j.0022-1112.2006.00894.x
Morato, T., González-Irusta, J.-M., Dominguez-Carrió, C., Wei, C.-L., Davies, A., Sweetman, A.K., Taranto, G.H., Beazley, L., García-Alegre, A., Grehan, A., Laffargue, P., Murillo, F.J., Sacau, M., Vaz, S., Kenchington, E., Arnaud-Haond, S., Callery, O., Chimienti, G., Cordes, E.,

Egilsdottir, H., Freiwald, A., Gasbarro, R., Gutiérrez-Zárate, C., Gianni, M., Gilkinson, K., Wareham Hayes, V.E., Hebbeln, D., Hedges, K., Henry, L.-A., Johnson, D., Koen-Alonso, M., Lirette, C., Mastrototaro, F., Menot, L., Molodtsova, T., Durán Muñoz, P., Orejas, C., Pennino, M.G., Puerta, P., Ragnarsson, S.Á., Ramiro-Sánchez, B., Rice, J., Rivera, J., Roberts, J.M., Ross, S.W., Rueda, J.L., Sampaio, Í., Snelgrove, P., Stirling, D., Treble, M.A., Urra, J., Vad, J., van Oevelen, D., Watling, L., Walkusz, W., Wienberg, C., Woillez, M., Levin, L.A., Carreiro-Silva, M., 2020. Climate-induced changes in the suitable habitat of cold-water corals and commercially important deep-sea fishes in the North Atlantic. Glob. Change Biol. 26, 2181–2202. https://doi.org/10.1111/gcb.14996

Morato, T., Hoyle, S.D., Allain, V., Nicol, S.J., 2010. Seamounts are hotspots of pelagic biodiversity in the open ocean. Proc. Natl. Acad. Sci. 107, 9707–9711. https://doi.org/10.1073/pnas.0910290107

Morgan, N.B., Goode, S., Roark, E.B., Baco, A.R., 2019. Fine Scale Assemblage Structure of Benthic Invertebrate Megafauna on the North Pacific Seamount Mokumanamana. Front. Mar. Sci. 6.

Mortensen, P.B., Buhl-Mortensen, L., 2005. Morphology and growth of the deep-water gorgonians Primnoa resedaeformis and Paragorgia arborea. Mar. Biol. 147, 775–788. https://doi.org/10.1007/s00227-005-1604-y

Mountains in the Sea [WWW Document], 2012. . Magazine. URL https://www.nationalgeographic.com/magazine/article/seamounts (accessed 1.8.24).

O'Driscoll, R.L., Clark, M.R., 2005. Quantifying the relative intensity of fishing on New Zealand seamounts. N. Z. J. Mar. Freshw. Res. 39, 839–850. https://doi.org/10.1080/00288330.2005.9517356

O'Leary, B.C., Hoppit, G., Townley, A., Allen, H.L., McIntyre, C.J., Roberts, C.M., 2020. Options for managing human threats to high seas biodiversity. Ocean Coast. Manag. 187, 105110. https://doi.org/10.1016/j.ocecoaman.2020.105110

Obura, D., 2017. Reviving the Western Indian Ocean Economy: Actions for A Sustainable Future. WWF.

Oksanen J et al., 2022. vegan: Community Ecology Package, R.

Olabarria, C., 2005. Patterns of bathymetric zonation of bivalves in the Porcupine Seabight and adjacent Abyssal plain, NE Atlantic. Deep Sea Res. Part Oceanogr. Res. Pap. 52, 15–31. https://doi.org/10.1016/j.dsr.2004.09.005

Oliver, T.H., Heard, M.S., Isaac, N.J.B., Roy, D.B., Procter, D., Eigenbrod, F., Freckleton, R., Hector, A., Orme, C.D.L., Petchey, O.L., Proença, V., Raffaelli, D., Suttle, K.B., Mace, G.M., Martín-López, B., Woodcock, B.A., Bullock, J.M., 2015. Biodiversity and Resilience of Ecosystem Functions. Trends Ecol. Evol. 30, 673–684. https://doi.org/10.1016/j.tree.2015.08.009

Palacio, R.D., Negret, P.J., Velásquez-Tibatá, J., Jacobson, A.P., 2021. A data-driven geospatial workflow to map species distributions for conservation assessments. Divers. Distrib. 27, 2559–2570. https://doi.org/10.1111/ddi.13424

Pastor, J., Cohen, Y., 1997. Herbivores, the Functional Diversity of Plants Species, and the Cycling of Nutrients in Ecosystems. Theor. Popul. Biol. 51, 165–179. https://doi.org/10.1006/tpbi.1997.1327

Patel, K., 2023. Scientists uncover the secret of the deep-sea "octopus garden". Wash. Post NA-NA.

Paulus, E., 2021. Shedding Light on Deep-Sea Biodiversity—A Highly Vulnerable Habitat in the Face of Anthropogenic Change. Front. Mar. Sci. 8. https://doi.org/10.3389/fmars.2021.667048

Payne, P., 2015. Taxonomy and diversity of the sponge fauna from Walters Shoal, a shallow seamount in the Western Indian Ocean region. University of the Western Cape.

Petersen, S., Hannington, M., Krätschell, A., 2017. Technology developments in the exploration and evaluation of deep-sea mineral resources. Ann. Mines - Responsab. Environ. 85, 14–18. https://doi.org/10.3917/re1.085.0014

Pham, C.K., Vandeperre, F., Menezes, G., Porteiro, F., Isidro, E., Morato, T., 2015. The importance of deep-sea vulnerable marine ecosystems for demersal fish in the Azores. Deep Sea Res. Part Oceanogr. Res. Pap. 96, 80–88. https://doi.org/10.1016/j.dsr.2014.11.004
Pile, A.J., Young, C.M., 2006. The natural diet of a hexactinellid sponge: Benthic–pelagic coupling in a deep-sea microbial food web. Deep Sea Res. Part Oceanogr. Res. Pap. 53, 1148–1156. https://doi.org/10.1016/j.dsr.2006.03.008
Pitcher, T.J., Clark, M.R., Morato, T., Watson, R., 2010. Seamount Fisheries: Do They Have a Future? Oceanography 23, 134–144.
Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., Santos, R.S. (Eds.), 2007. Seamounts: Ecology, Fisheries & Conservation. Blackwell Publishing Ltd, Oxford, UK. https://doi.org/10.1002/9780470691953
Pollard, R., Read, J., 2017. Circulation, stratification and seamounts in the Southwest Indian Ocean. Deep Sea Res. Part II Top. Stud. Oceanogr., The Pelagic Ecology of Seamounts of the South West Indian Ocean 136, 36–43. https://doi.org/10.1016/j.dsr2.2015.02.018
Powers, J.E., 2010. Measuring biodiversity in marine ecosystems. Nature 468, 385–386. https://doi.org/10.1038/468385a
Prada, C., Hellberg, M.E., 2021. Speciation-by-depth on coral reefs: Sympatric divergence with gene flow or cryptic transient isolation? J. Evol. Biol. 34, 128–137. https://doi.org/10.1111/jeb.13731
Preez, C.D., Curtis, J.M.R., Clarke, M.E., 2016. The Structure and Distribution of Benthic Communities on a Shallow Seamount (Cobb Seamount, Northeast Pacific Ocean). PLOS ONE 11, e0165513. https://doi.org/10.1371/journal.pone.0165513
Puerta, P., Johnson, C., Carreiro-Silva, M., Henry, L.-A., Kenchington, E., Morato, T., Kazanidis, G., Rueda, J.L., Urra, J., Ross, S., Wei, C.-L., González-Irusta, J.M., Arnaud-Haond, S., Orejas, C., 2020. Influence of Water Masses on the Biodiversity and Biogeography of Deep-Sea Benthic Ecosystems in the North Atlantic. Front. Mar. Sci. 7. https://doi.org/10.3389/fmars.2020.00239
Pusceddu, A., Bianchelli, S., Martín, J., Puig, P., Palanques, A., Masqué, P., Danovaro, R., 2014. Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. Proc. Natl. Acad. Sci. 111, 8861–8866. https://doi.org/10.1073/pnas.1405454111
Quintanar-Retama, O., Vázquez-Bader, A.R., Gracia, A., 2023. Macrofauna abundance and diversity patterns of deep sea southwestern Gulf of Mexico. Front. Mar. Sci. 9. https://doi.org/10.3389/fmars.2022.1033596
R Core Team., 2022. R: A language and environment for statistical computing.
Ramirez-Llodra, E., Tyler, P.A., Baker, M.C., Bergstad, O.A., Clark, M.R., Escobar, E., Levin, L.A., Menot, L., Rowden, A.A., Smith, C.R., Van Dover, C.L., 2011. Man and the Last Great Wilderness: Human Impact on the Deep Sea. PLoS ONE 6, e22588. https://doi.org/10.1371/journal.pone.0022588
Ramiro-Sánchez, B., Martin, A., Leroy, B., 2023. The epitome of data paucity: Deep-sea habitats of the Southern Indian Ocean. Biol. Conserv. 283, 110096. https://doi.org/10.1016/j.biocon.2023.110096
Read, J., Pollard, R., 2017. An introduction to the physical oceanography of six seamounts in the southwest Indian Ocean. Deep Sea Res. Part II Top. Stud. Oceanogr. 136, 44–58. https://doi.org/10.1016/j.dsr2.2015.06.022
Read, J.F., Lucas, M.I., Holley, S.E., Pollard, R.T., 2000. Phytoplankton, nutrients and hydrography in the frontal zone between the Southwest Indian Subtropical gyre and the Southern Ocean. Deep Sea Res. Part Oceanogr. Res. Pap. 47, 2341–2367. https://doi.org/10.1016/S0967-0637(00)00021-2
Reiss, H., Birchenough, S., Borja, A., Buhl-Mortensen, L., Craeymeersch, J., Dannheim, J., Darr, A., Galparsoro, I., Gogina, M., Neumann, H., Populus, J., Rengstorf, A.M., Valle, M., van Hoey, G., Zettler, M.L., Degraer, S., 2015. Benthos distribution modelling and its relevance for

marine ecosystem management. ICES J. Mar. Sci. 72, 297–315. https://doi.org/10.1093/icesjms/fsu107
Remia, A., Taviani, M., 2005. Shallow-buried Pleistocene Madrepora-dominated coral mounds on a muddy continental slope, Tuscan Archipelago, NE Tyrrhenian Sea. Facies 50, 419–425. https://doi.org/10.1007/s10347-004-0029-2
Rengstorf, A.M., Yesson, C., Brown, C., Grehan, A.J., 2013. High-resolution habitat suitability modelling can improve conservation of vulnerable marine ecosystems in the deep sea. J. Biogeogr. 40, 1702–1714. https://doi.org/10.1111/jbi.12123
Rex, M., Etter, R., Morris, J., Crouse, J., McClain, C., Johnson, N., Stuart, C., Deming, J., Thies, R., Avery, R., 2006. Global bathymetric patterns of standing stock and body size in the deep-sea benthos. Mar. Ecol. Prog. Ser. 317, 1–8. https://doi.org/10.3354/meps317001
Rex, M.A., Crame, J.A., Stuart, C.T., Clarke, A., 2005. Large-Scale Biogeographic Patterns in Marine Mollusks: A Confluence of History and Productivity? Ecology 86, 2288–2297. https://doi.org/10.1890/04-1056
Rex, M.A., Stuart, C.T., Coyne, G., 2000. Latitudinal gradients of species richness in the deep-sea benthos of the North Atlantic. Proc. Natl. Acad. Sci. U. S. A. 97, 4082–4085.
Rex, M.A., Stuart, C.T., Hessler, R.R., Allen, J.A., Sanders, H.L., Wilson, G.D.F., 1993. Global-scale latitudinal patterns of species diversity in the deep-sea benthos. Nature 365, 636–639. https://doi.org/10.1038/365636a0
Richer de Forges, B., Koslow, J.A., Poore, G.C.B., 2000. Diversity and endemism of the benthic seamount fauna in the southwest Pacific. Nature 405, 944–947. https://doi.org/10.1038/35016066
Roberts, C.M., Hawkins, J.P., Roberts, C.M., Hawkins, J.P., 1999. Extinction risk in the sea. Trends Ecol. Evol. 14, 241–246. https://doi.org/10.1016/S0169-5347(98)01584-5
Roberts, E.M., Mienis, F., Rapp, H.T., Hanz, U., Meyer, H.K., Davies, A.J., 2018. Oceanographic setting and short-timescale environmental variability at an Arctic seamount sponge ground. Deep Sea Res. Part Oceanogr. Res. Pap. 138, 98–113. https://doi.org/10.1016/j.dsr.2018.06.007
Roberts, J.M., Cairns, S.D., 2014. Cold-water corals in a changing ocean. Curr. Opin. Environ. Sustain., Environmental change issues 7, 118–126. https://doi.org/10.1016/j.cosust.2014.01.004
Roberts, J.M., Wheeler, A.J., Freiwald, A., 2006. Reefs of the Deep: The Biology and Geology of Cold-Water Coral Ecosystems. Science 312, 543–547. https://doi.org/10.1126/science.1119861
Robinson, R.A., Crick, H.Q.P., Learmonth, J.A., Maclean, I.M.D., Thomas, C.D., Bairlein, F., Forchhammer, M.C., Francis, C.M., Gill, J.A., Godley, B.J., Harwood, J., Hays, G.C., Huntley, B., Hutson, A.M., Pierce, G.J., Rehfisch, M.M., Sims, D.W., Santos, M.B., Sparks, T.H., Stroud, D.A., Visser, M.E., 2009. Travelling through a warming world: climate change and migratory species. Endanger. Species Res. 7, 87–99. https://doi.org/10.3354/esr00095
Rogers et al., 2009. Final cruise report: Southern Indian Ocean Seamounts 2009.
Rogers, A., 2004. The Biology, Ecology and Vulnerability of Deep-Water Coral Reefs.
Rogers, A., 2016. Pelagic ecology of the South West Indian Ocean Ridge seamounts: introduction and overview. Deep Sea Res. Part II Top. Stud. Oceanogr. 136.
Rogers, A., 2018. The Biology of Seamounts: 25 Years on, in: Advances in Marine Biology. https://doi.org/10.1016/bs.amb.2018.06.001
Rogers, A., Taylor, M.L., 2012. Benthic biodiversity of seamounts in the southwest Indian Ocean. Cruise report – R/V James Cook 066. November 7th–December 21st, 2011., Proceedings of the Southwest Indian Ocean Seamounts Expedition – November 7th–December 21st, 2011.
Rogers, A.D., 1994. The Biology of Seamounts, in: Blaxter, J.H.S., Southward, A.J. (Eds.), Advances in Marine Biology. Academic Press, pp. 305–350. https://doi.org/10.1016/S0065-2881(08)60065-6

Rogers, A.D., Alvheim, O., Bemanaja, E., Benivary, D., Boersch-Supan, P., Bornman, T.G., Cedras, R., Du Plessis, N., Gotheil, S., Høines, A., Kemp, K., Kristiansen, J., Letessier, T., Mangar, V., Mazungula, N., Mørk, T., Pinet, P., Pollard, R., Read, J., Sonnekus, T., 2017. Pelagic communities of the South West Indian Ocean seamounts: R/V Dr *Fridtjof Nansen* Cruise 2009-410. Deep Sea Res. Part II Top. Stud. Oceanogr., The Pelagic Ecology of Seamounts of the South West Indian Ocean 136, 5–35. https://doi.org/10.1016/j.dsr2.2016.12.010

Rogers, A.D., Baco, A., Griffiths, H., Hart, T., Hall-Spencer, J.M., 2007. Corals on Seamounts, in: Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., Santos, R.S. (Eds.), Seamounts: Ecology, Fisheries & Conservation. Blackwell Publishing Ltd, Oxford, UK, pp. 141–169. https://doi.org/10.1002/9780470691953.ch8

Rohde, K., 1992. Latitudinal Gradients in Species Diversity: The Search for the Primary Cause. Oikos 65, 514–527. https://doi.org/10.2307/3545569

Romanov, E.V., 2003. Summary and review of Soviet and Ukrainian scientific and commercial fishing operations on the deepwater ridges of the southern Indian Ocean. FAO Fisheries Circular.

Romoth, K., Darr, A., Papenmeier, S., Zettler, M.L., Gogina, M., 2023. Substrate Heterogeneity as a Trigger for Species Diversity in Marine Benthic Assemblages. Biology 12, 825. https://doi.org/10.3390/biology12060825

Rosa, R., Dierssen, H.M., Gonzalez, L., Seibel, B.A., 2008. Large-Scale Diversity Patterns of Cephalopods in the Atlantic Open Ocean and Deep Sea. Ecology 89, 3449–3461. https://doi.org/10.1890/08-0638.1

Ross, R.E., Howell, K.L., 2013. Use of predictive habitat modelling to assess the distribution and extent of the current protection of 'listed' deep-sea habitats. Divers. Distrib. 19, 433–445. https://doi.org/10.1111/ddi.12010

Ross, T., Du Preez, C., Ianson, D., 2020. Rapid deep ocean deoxygenation and acidification threaten life on Northeast Pacific seamounts. Glob. Change Biol. 26, 6424–6444. https://doi.org/10.1111/gcb.15307

Rowden, A.A., Clark, M.R., Wright, I.C., 2005. Physical characterisation and a biologically focused classification of "seamounts" in the New Zealand region. N. Z. J. Mar. Freshw. Res. 39, 1039–1059. https://doi.org/10.1080/00288330.2005.9517374

Rowden, A.A., Dower, J.F., Schlacher, T.A., Consalvey, M., Clark, M.R., 2010. Paradigms in seamount ecology: fact, fiction and future. Mar. Ecol. 31, 226–241. https://doi.org/10.1111/j.1439-0485.2010.00400.x

Rowe, G.T., 1983. The Sea, Volume 8: Deep-Sea Biology. Harvard University Press.

Rowe, G.T., Menzies, R.J., 1969. Zonation of large benthic invertebrates in the deep-sea off the Carolinas. Deep Sea Res. Oceanogr. Abstr. 16, 531–537. https://doi.org/10.1016/0011-7471(69)90041-2

Roy, K., Jablonski, D., Valentine, J.W., Rosenberg, G., 1998. Marine latitudinal diversity gradients: Tests of causal hypotheses. Proc. Natl. Acad. Sci. 95, 3699–3702. https://doi.org/10.1073/pnas.95.7.3699

Rueda, J.L., Urra, J., Aguilar, R., Angeletti, L., Bo, M., García-Ruiz, C., González-Duarte, M.M., López, E., Madurell, T., Maldonado, M., Mateo-Ramírez, Á., Megina, C., Moreira, J., Moya, F., Ramalho, L.V., Rosso, A., Sitjà, C., Taviani, M., 2019. 29 Cold-Water Coral Associated Fauna in the Mediterranean Sea and Adjacent Areas, in: Orejas, C., Jiménez, C. (Eds.), Mediterranean Cold-Water Corals: Past, Present and Future, Coral Reefs of the World. Springer International Publishing, Cham, pp. 295–333. https://doi.org/10.1007/978-3-319-91608-8_29

Saeedi, H., Costello, M.J., Warren, D., Brandt, A., 2019. Latitudinal and bathymetrical species richness patterns in the NW Pacific and adjacent Arctic Ocean. Sci. Rep. 9, 9303. https://doi.org/10.1038/s41598-019-45813-9

Saito, T., Uchida, I., Takeda, M., 2002. Skeletal growth of the deep-sea hexactinellid sponge Euplectella oweni, and host selection by the symbiotic shrimp Spongicola japonica (Crustacea: Decapoda: Spongicolidae). J. Zool. 258, 521–529. https://doi.org/10.1017/S0952836902001681
Sala, E., Aburto-Oropeza, O., Paredes, G., Thompson, G., 2003. Spawning aggregations and reproductive behavior of reef fishes in the Gulf of California. Bull. Mar. Sci. 72, 103–121.
Salazar, G., Cornejo-Castillo, F.M., Benítez-Barrios, V., Fraile-Nuez, E., Álvarez-Salgado, X.A., Duarte, C.M., Gasol, J.M., Acinas, S.G., 2016. Global diversity and biogeography of deep-sea pelagic prokaryotes. ISME J. 10, 596–608. https://doi.org/10.1038/ismej.2015.137
Samadi, S., Bottan, L., Macpherson, E., De Forges, B.R., Boisselier, M.-C., 2006. Seamount endemism questioned by the geographic distribution and population genetic structure of marine invertebrates. Mar. Biol. 149, 1463–1475. https://doi.org/10.1007/s00227-006-0306-4
Sanders, H.L., Hessler, R.R., 1969. Ecology of the Deep-Sea Benthos: More detailed recent sampling has altered our concepts about the animals living on the deep-ocean floor. Science 163, 1419–1424. https://doi.org/10.1126/science.163.3874.1419
Sauter, D., Cannat, M., 2010. The ultraslow spreading Southwest Indian Ridge, in: Rona, P.A., Devey, C.W., Dyment, J., Murton, B.J. (Eds.), Geophysical Monograph Series. American Geophysical Union, Washington, D. C., pp. 153–173. https://doi.org/10.1029/2008GM000843
Sauter, D., Cannat, M., Rouméjon, S., Andreani, M., Birot, D., Bronner, A., Brunelli, D., Carlut, J., Delacour, A., Guyader, V., MacLeod, C.J., Manatschal, G., Mendel, V., Ménez, B., Pasini, V., Ruellan, E., Searle, R., 2013. Continuous exhumation of mantle-derived rocks at the Southwest Indian Ridge for 11 million years. Nat. Geosci. 6, 314–320. https://doi.org/10.1038/ngeo1771
Sautya, S., Ingole, B., Ray, D., Stöhr, S., Samudrala, K., Raju, K.A.K., Mudholkar, A., 2011. Megafaunal Community Structure of Andaman Seamounts Including the Back-Arc Basin – A Quantitative Exploration from the Indian Ocean. PLoS ONE 6, e16162. https://doi.org/10.1371/journal.pone.0016162
Scales, H., 2023. The Deep Sea, in: Obaidullah, F. (Ed.), The Ocean and Us. Springer International Publishing, Cham, pp. 163–173. https://doi.org/10.1007/978-3-031-10812-9_15
Schlacher, T.A., Rowden, A.A., Dower, J.F., Consalvey, M., 2010. Seamount science scales undersea mountains: new research and outlook. Mar. Ecol. 31, 1–13. https://doi.org/10.1111/j.1439-0485.2010.00396.x
Schmidt, R., 1999. Seamounts and Island Building. Academic Press.
Schmidtko, S., Stramma, L., Visbeck, M., 2017. Decline in global oceanic oxygen content during the past five decades. Nature. https://doi.org/10.1038/nature21399
Schoening, T., Bergmann, M., Ontrup, J., Taylor, J., Dannheim, J., Gutt, J., Purser, A., Nattkemper, T.W., 2012. Semi-Automated Image Analysis for the Assessment of Megafaunal Densities at the Arctic Deep-Sea Observatory HAUSGARTEN. PLoS ONE 7, e38179. https://doi.org/10.1371/journal.pone.0038179
Schönke, M., Clemens, D., Feldens, P., 2022. Quantifying the Physical Impact of Bottom Trawling Based on High-Resolution Bathymetric Data. Remote Sens. 14, 2782. https://doi.org/10.3390/rs14122782
Sciberras, M., Hiddink, J.G., Jennings, S., Szostek, C.L., Hughes, K.M., Kneafsey, B., Clarke, L.J., Ellis, N., Rijnsdorp, A.D., McConnaughey, R.A., Hilborn, R., Collie, J.S., Pitcher, C.R., Amoroso, R.O., Parma, A.M., Suuronen, P., Kaiser, M.J., 2018. Response of benthic fauna to experimental bottom fishing: A global meta-analysis. Fish Fish. 19, 698–715. https://doi.org/10.1111/faf.12283
Sedberry, G., Loefer, J., 2001. Satellite telemetry tracking of swordfish, Xiphias gladius, off the eastern United States. Mar. Biol. 139, 355–360. https://doi.org/10.1007/s002270100593
Selkoe, K.A., Gaggiotti, O., Treml, E., 2018. The DNA of coral reef biodiversity: predicting and protecting genetic diversity of reef assemblages. https://doi.org/10.1098/rspb.2016.0354

Serpetti, N., Taylor, M.L., Brennan, D., Green, D.H., Rogers, A.D., Paterson, G.L.J., Narayanaswamy, B.E., 2017. Ecological adaptations and commensal evolution of the Polynoidae (Polychaeta) in the Southwest Indian Ocean Ridge: A phylogenetic approach. Deep Sea Res. Part II Top. Stud. Oceanogr., Advances in deep-sea biology: biodiversity, ecosystem functioning and conservation 137, 273–281. https://doi.org/10.1016/j.dsr2.2016.06.004

Serrano, A., González-Irusta, J.M., Punzón, A., García-Alegre, A., Lourido, A., Ríos, P., Blanco, M., Gómez-Ballesteros, M., Druet, M., Cristobo, J., Cartes, J.E., 2017. Deep-sea benthic habitats modeling and mapping in a NE Atlantic seamount (Galicia Bank). Deep Sea Res. Part Oceanogr. Res. Pap. 126, 115–127. https://doi.org/10.1016/j.dsr.2017.06.003

Sharifian, S., Kamrani, E., Saeedi, H., 2021. Global biodiversity and biogeography of mangrove crabs: Temperature, the key driver of latitudinal gradients of species richness. J. Therm. Biol. 92, 102692.

Sharma, R., 2015. Environmental Issues of Deep-Sea Mining. Procedia Earth Planet. Sci., Global Challenges, Policy Framework & Sustainable Development for Mining of Mineral and Fossil Energy Resources (GCPF:2015–20) 11, 204–211. https://doi.org/10.1016/j.proeps.2015.06.026

Shen, C., Lu, B., Li, Z., Zhang, R., Chen, W., Xu, P., Yao, H., Chen, Z., Pang, J., Wang, C., Zhang, D., 2021. Community structure of benthic megafauna on a seamount with cobalt-rich ferromanganese crusts in the northwestern Pacific Ocean. Deep Sea Res. Part Oceanogr. Res. Pap. 178, 103661. https://doi.org/10.1016/j.dsr.2021.103661

SIODFA, 2015. Southern Indian Ocean Deepwater Fisheries Association (SIODFA) Benthic Protected Areas in the Southern Indian Ocean.

SIOFA, 2018. Conservation and Management Measure for the Interim Management of Bottom Fishing in the Agreement Area (Interim Management of Bottom Fishing).

Soetaert, K., Heip, C., 1990. Sample-size dependence of diversity indices and the determination of sufficient sample size in a high-diversity deep-sea environment. Mar. Ecol. Prog. Ser. 59, 305–307. https://doi.org/10.3354/meps059305

Sogin, M.L., Morrison, H.G., Huber, J.A., Welch, D.M., Huse, S.M., Neal, P.R., Arrieta, J.M., Herndl, G.J., 2006. Microbial diversity in the deep sea and the underexplored “rare biosphere.” Proc. Natl. Acad. Sci. 103, 12115–12120. https://doi.org/10.1073/pnas.0605127103

Somerfield, P., 2008. Identification of the Bray-Curtis similarity index: Comment on Yoshioka (2008). Mar. Ecol. Prog. Ser. 372, 303–306. https://doi.org/10.3354/meps07841

Somoza, L., Ercilla, G., Urgorri, V., León, R., Medialdea, T., Paredes, M., Gonzalez, F.J., Nombela, M.A., 2014. Detection and mapping of cold-water coral mounds and living Lophelia reefs in the Galicia Bank, Atlantic NW Iberia margin. Mar. Geol. 349, 73–90. https://doi.org/10.1016/j.margeo.2013.12.017

Sonnekus, M.J., Bornman, T.G., Campbell, E.E., 2017. Phytoplankton and nutrient dynamics of six South West Indian Ocean seamounts. Deep Sea Res. Part II Top. Stud. Oceanogr., The Pelagic Ecology of Seamounts of the South West Indian Ocean 136, 59–72. https://doi.org/10.1016/j.dsr2.2016.12.008

Staudigel, H., Koppers, A., Lavelle, W., Pitcher, T., Shank, T.M., 2010. Defining the Word “Seamount.” Oceanography 23.

Steiner, A., 2011. UNEP Year Book 2011: Emerging Issues in Our Global Environment. UNEP/Earthprint.

Stocks, K.I., Clark, M.R., Rowden, A.A., Consalvey, M., Schlacher, T.A., 2012. CenSeam, an International Program on Seamounts within the Census of Marine Life: Achievements and Lessons Learned. PLOS ONE 7, e32031. https://doi.org/10.1371/journal.pone.0032031

Stratmann, T., Simon-Lledó, E., Morganti, T.M., de Kluijver, A., Vedenin, A., Purser, A., 2022. Habitat types and megabenthos composition from three sponge-dominated high-Arctic seamounts. Sci. Rep. 12, 20610. https://doi.org/10.1038/s41598-022-25240-z

Sumaila, U.R., Zeller, D., Watson, R., Alder, J., Pauly, D., 2007. Potential costs and benefits of marine reserves in the high seas. Mar. Ecol. Prog. Ser. 345, 305–310. https://doi.org/10.3354/meps07065
Swanborn, D.J.B., Huvenne, V.A.I., Malpas, T., Pittman, S.J., Rogers, A.D., Taylor, M.L., Woodall, L.C., 2023. Seamount seascape composition and configuration shape Southwest Indian Ridge fish assemblages. Deep Sea Res. Part Oceanogr. Res. Pap. 191, 103921. https://doi.org/10.1016/j.dsr.2022.103921
Swanborn, Huvenne, V.A.I., Pittman, S.J., Rogers, A.D., Taylor, M.L., Woodall, L.C., 2023. Mapping, quantifying and comparing seascape heterogeneity of Southwest Indian Ridge seamounts. Landsc. Ecol. 38, 185–203. https://doi.org/10.1007/s10980-022-01541-6
Sweetman, A.K., Thurber, A.R., Smith, C.R., Levin, L.A., Mora, C., Wei, C.-L., Gooday, A.J., Jones, D.O.B., Rex, M., Yasuhara, M., Ingels, J., Ruhl, H.A., Frieder, C.A., Danovaro, R., Würzberg, L., Baco, A., Grupe, B.M., Pasulka, A., Meyer, K.S., Dunlop, K.M., Henry, L.-A., Roberts, J.M., 2017. Major impacts of climate change on deep-sea benthic ecosystems. Elem. Sci. Anthr. 5, 4. https://doi.org/10.1525/elementa.203
Taylor, M.L., Gwinnett, C., Robinson, L.F., Woodall, L.C., 2016. Plastic microfibre ingestion by deep-sea organisms. Sci. Rep. 6, 33997. https://doi.org/10.1038/srep33997
Taylor, M.L., Rogers, A.D., 2017. Primnoidae (Cnidaria: Octocorallia) of the SW Indian Ocean: new species, genus revisions and systematics. Zool. J. Linn. Soc. 181, 70–97. https://doi.org/10.1093/zoolinnean/zlx003
Teixidó, N., Garrabou, J., Arntz, W.E., 2002. Spatial pattern quantification of Antarctic benthic communities using landscape indices. Mar. Ecol. Prog. Ser. 242, 1–14. https://doi.org/10.3354/meps242001
Thomson, C.W., 1878. The Voyage of the “Challenger.”: The Atlantic; a Preliminary Account of the General Results of the Exploring Voyage of H.M.S. “Challenger” During the Year 1873 and the Early Part of the Year 1876. Harper & Brothers.
Tietjen, J.H., 1984. Distribution and species diversity of deep-sea nematodes in the Venezuela Basin. Deep Sea Res. Part Oceanogr. Res. Pap. 31, 119–132. https://doi.org/10.1016/0198-0149(84)90019-0
Tillin, H.M., Hiddink, J.G., Jennings, S., Kaiser, M.J., 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. Mar. Ecol. Prog. Ser. 318, 31–45. https://doi.org/10.3354/meps318031
Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Berghe, E.V., Worm, B., 2010. Global patterns and predictors of marine biodiversity across taxa. Nature 466, 1098–1101. https://doi.org/10.1038/nature09329
Tracey, D.M., Horn, P.L., 1999. Background and review of ageing orange roughy (Hoplostethus atlanticus, Trachichthyidae) from New Zealand and elsewhere. N. Z. J. Mar. Freshw. Res. 33, 67–86. https://doi.org/10.1080/00288330.1999.9516858
Tsukamoto, K., Otake, T., Mochioka, N., Lee, T.-W., Fricke, H., Inagaki, T., Aoyama, J., Ishikawa, S., Kimura, S., Miller, M., Hasumoto, H., Oya, M., Suzuki, Y., 2003. Seamounts, New Moon and eel Spawning: The Search for the Spawning Site of the Japanese eel. Environ. Biol. Fishes 66, 221–229. https://doi.org/10.1023/A:1023926705906
Turley, C.M., Roberts, J.M., Guinotte, J.M., 2007. Corals in deep-water: will the unseen hand of ocean acidification destroy cold-water ecosystems? Coral Reefs 26, 445–448. https://doi.org/10.1007/s00338-007-0247-5
Tyler, P.A., 2003. Ecosystems of the Deep Oceans. Elsevier.
Ugland, K.I., Gray, J.S., Ellingsen, K.E., 2003. The species–accumulation curve and estimation of species richness. J. Anim. Ecol. 72, 888–897. https://doi.org/10.1046/j.1365-2656.2003.00748.x
Valdemarsen, J.W., 2001. Technological trends in capture fisheries. Ocean Coast. Manag., Trends in Ocean Industries 44, 635–651. https://doi.org/10.1016/S0964-5691(01)00073-4

Valle-Levinson, A., Trasviña Castro, A., Gutiérrez de Velasco, G., González Armas, R., 2004. Diurnal vertical motions over a seamount of the southern Gulf of California. J. Mar. Syst., The Role of Biophysical Coupling in Concentrating Marine Organisms Around Shallow Topographies 50, 61–77. https://doi.org/10.1016/j.jmarsys.2003.09.016
van Denderen, P.D., Holah, H., Robson, L.M., Hiddink, J.G., Menot, L., Pedreschi, D., Kazanidis, G., Llope, M., Turner, P.J., Stirling, D., Murillo, F.J., Kenny, A., Campbell, N., Allcock, A.L., Braga-Henriques, A., González-Irusta, J.M., Johnston, G., Orejas, C., Serrano, A., Xavier, J.R., Hopkins, P., Kenchington, E., Nixon, E., Valanko, S., 2022. A policy-based framework for the determination of management options to protect vulnerable marine ecosystems under the EU deep-sea access regulations. ICES J. Mar. Sci. 79, 34–49. https://doi.org/10.1093/icesjms/fsab237
van der Elst, R., Everett, B., 2015. Offshore Fisheries of the Southwest Indian Ocean: their status and the impact on vulnerable species (No. 10). South African Association for Marine Biological Research.
Vedenin, A., Galkin, S., Gebruk, A.V., Mironov, A., 2021. Vertical zonation of the Siberian Arctic benthos: bathymetric boundaries from coastal shoals to deep-sea Central Arctic. PeerJ. https://doi.org/10.7717/peerj.11640
Victorero, L., Robert, K., Robinson, L.F., Taylor, M.L., Huvenne, V.A.I., 2018. Species replacement dominates megabenthos beta diversity in a remote seamount setting. Sci. Rep. 8, 4152. https://doi.org/10.1038/s41598-018-22296-8
Vinogradova, N.G., 1958. The zoogeographical distribution of the deep-water bottom fauna in the abyssal zone of the ocean. Deep Sea Res. 1953 5, 205–208. https://doi.org/10.1016/0146-6313(58)90012-1
Wafar, M., Venkataraman, K., Ingole, B., Khan, S.A., LokaBharathi, P., 2011. State of Knowledge of Coastal and Marine Biodiversity of Indian Ocean Countries. PLOS ONE 6, e14613. https://doi.org/10.1371/journal.pone.0014613
Walker, S., B., D., Machler, M, B., B., 2015. Fitting Linear Mixed-Effects Models Using {lme4}}.
Watling, L., Auster, P., 2020. Seamounts, VMEs and Spatial management.
Watling, L., Auster, P.J., 2017. Seamounts on the High Seas Should Be Managed as Vulnerable Marine Ecosystems. Front. Mar. Sci. 4.
Watling, L., Auster, P.J., 2021. Vulnerable Marine Ecosystems, Communities, and Indicator Species: Confusing Concepts for Conservation of Seamounts. Front. Mar. Sci. 8.
Watling, L., France, S.C., Pante, E., Simpson, A., 2011. Chapter Two - Biology of Deep-Water Octocorals, in: Lesser, M. (Ed.), Advances in Marine Biology, Advances in Marine Biology. Academic Press, pp. 41–122. https://doi.org/10.1016/B978-0-12-385529-9.00002-0
Watson, R., Kitchingman, A., Cheung, W.W., 2007. Catches from World Seamount Fisheries, in: Seamounts: Ecology, Fisheries & Conservation. John Wiley & Sons, Ltd, pp. 400–412. https://doi.org/10.1002/9780470691953.ch18
Watson, R., Morato, T., 2004. Exploitation patterns in seamount fisheries: A preliminary analysis. Fish. Cent. Res. Rep. 12, 61–66.
Weaver, P.P.E., Billett, D.S.M., Van Dover, C.L., 2018. Environmental Risks of Deep-sea Mining, in: Salomon, M., Markus, T. (Eds.), Handbook on Marine Environment Protection : Science, Impacts and Sustainable Management. Springer International Publishing, Cham, pp. 215–245. https://doi.org/10.1007/978-3-319-60156-4_11
Wessel, P., Sandwell, D., Kim, S.-S., 2010a. The Global Seamount Census. Oceanography 23. https://doi.org/10.5670/oceanog.2010.60
Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30, 279–338. https://doi.org/10.2307/1943563
Wijffels, S., Roemmich, D., Monselesan, D., Church, J., Gilson, J., 2016. Ocean temperatures chronicle the ongoing warming of Earth. Nat. Clim. Change 6, 116–118. https://doi.org/10.1038/nclimate2924

Williams, A., Althaus, F., Maguire, K., Green, M., Untiedt, C., Alderslade, P., Clark, M.R., Bax, N., Schlacher, T.A., 2020. The Fate of Deep-Sea Coral Reefs on Seamounts in a Fishery-Seascape: What Are the Impacts, What Remains, and What Is Protected? Front. Mar. Sci. 7. https://doi.org/10.3389/fmars.2020.567002
Williams, A., Schlacher, T.A., Rowden, A.A., Althaus, F., Clark, M.R., Bowden, D.A., Stewart, R., Bax, N.J., Consalvey, M., Kloser, R.J., 2010. Seamount megabenthic assemblages fail to recover from trawling impacts. Mar. Ecol. 31, 183–199. https://doi.org/10.1111/j.1439-0485.2010.00385.x
Willis, A.D., 2019. Rarefaction, Alpha Diversity, and Statistics. Front. Microbiol. 10. https://doi.org/10.3389/fmicb.2019.02407
Woodall, L.C., Robinson, L.F., Rogers, A.D., Narayanaswamy, B.E., Paterson, G.L.J., 2015. Deep-sea litter: a comparison of seamounts, banks and a ridge in the Atlantic and Indian Oceans reveals both environmental and anthropogenic factors impact accumulation and composition. Front. Mar. Sci. 2.
Woolley, S.N.C., Tittensor, D.P., Dunstan, P.K., Guillera-Arroita, G., Lahoz-Monfort, J.J., Wintle, B.A., Worm, B., O'Hara, T.D., 2016. Deep-sea diversity patterns are shaped by energy availability. Nature 533, 393–396. https://doi.org/10.1038/nature17937
Woulds, C., Cowie, G.L., Levin, L.A., Andersson, J.H., Middelburg, J.J., Vandewiele, S., Lamont, P.A., Larkin, K.E., Gooday, A.J., Schumacher, S., Whitcraft, C., Jeffreys, R.M., Schwartz, M., 2007. Oxygen as a control on sea floor biological communities and their roles in sedimentary carbon cycling. Limnol. Oceanogr. 52, 1698–1709. https://doi.org/10.4319/lo.2007.52.4.1698
Wright, D.H., 1983. Species-Energy Theory: An Extension of Species-Area Theory. Oikos 41, 496–506. https://doi.org/10.2307/3544109
Wyrtki, K., 1973. Physical Oceanography of the Indian Ocean, in: The Biology of the Indian Ocean. pp. 18–36.
Yasuhara, M., Danovaro, R., 2016. Temperature impacts on deep-sea biodiversity. Biol. Rev. 91, 275–287. https://doi.org/10.1111/brv.12169
Yasuhara, M., Hunt, G., Cronin, T.M., Okahashi, H., 2009. Temporal latitudinal-gradient dynamics and tropical instability of deep-sea species diversity. Proc. Natl. Acad. Sci. 106, 21717–21720. https://doi.org/10.1073/pnas.0910935106
Yesson, C., Clark, M.R., Taylor, M.L., Rogers, A.D., 2011. The global distribution of seamounts based on 30 arc seconds bathymetry data. Deep Sea Res. Part Oceanogr. Res. Pap. 58, 442–453. https://doi.org/10.1016/j.dsr.2011.02.004
Zeller, D., Ansell, M., Andreoli, V., Heidrich, K., 2023. Trends in Indian Ocean marine fisheries since 1950: synthesis of reconstructed catch and effort data. Mar. Freshw. Res. 74, 301–319. https://doi.org/10.1071/MF22148
Zhou, S., Huang, P., Wang, L., Hu, K., Huang, G., Hu, P., 2024. Robust changes in global subtropical circulation under greenhouse warming. Nat. Commun. 15, 96. https://doi.org/10.1038/s41467-023-44244-5