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ECOLOGICAL STUDIES OF THE SOUTH ATLANTIC DEEP SEA TO INFORM SUSTAINABLE MANAGEMENT

by

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This thesis is dedicated to my loving Nan.

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At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Doctoral College Quality Sub-Committee. Work submitted for this research degree at the University of Plymouth has not formed part of any other degree either at the University of Plymouth or at another establishment. This study was principally financed by the Centre for Environment, Fisheries and Aquaculture Science and the University of Plymouth, with contributions from British Antarctic Survey, National Geographic, and personal funding. It was carried out as a collaboration between the University of Plymouth, Centre for Environment, Fisheries and Aquaculture Science, British Antarctic Survey and the Institute of Marine Research, Norway.

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- Chapter 5 may form part of a broader publication comparing two habitat classification methodologies to be submitted to a suitable conservation journal

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2018 Centre for Environment, Fisheries and Aquaculture Science, Lowestoft, UK

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2020 **Public talk**: St Helena Nature Conservation Group Talk, St Helena, "*Mapping the deep: conserving Earth's largest ecosystem*"

2019 **Public talk**: 'Pints, Pies & PhDs', Plymouth, UK, "*Mapping the Deep… there be dragons?*"

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ABSTRACT

ECOLOGICAL STUDIES OF THE SOUTH ATLANTIC DEEP SEA TO INFORM SUSTAINABLE MANAGEMENT

Amelia Elizabeth Henrietta Bridges

Although deep-sea science continues to progress, the southern hemisphere represents a vast and yet understudied area, and the South Atlantic is no exception to this. However, as with other ocean basins, blue growth and the potential for expansion of new and emerging industries mean that information is required to characterise the ecology of the basin to inform sustainable management. Furthermore, novel tools will be required to assist in translating ecological knowledge into usable products that can facilitate marine spatial planning.

The aims of this thesis were to contribute to our understanding of the benthic ecology of seamount and oceanic island ecosystems in the South Atlantic, and to trial new methodologies for the development of tools to facilitate sustainable management of the deep sea. The results of this thesis show that productivity and substrate hardness are both significant drivers of α-diversity on seamount and oceanic island ecosystems, manifesting in significantly higher α-diversity in temperate latitudes. Interestingly, no consistent relationship between α-diversity and depth was identified, upon further exploration, significant bathymetric β-diversity (turnover) gradients were identified. Further developing our ecological understanding of the basin, similarities and dissimilarities in community structure across the South Atlantic were explored, again linking ecological distributions with environmental parameters. Significant differences between deep-sea communities from temperate and tropical latitudes were identified, with latitude and depth considered the key environmental drivers of community composition. Vulnerable Marine Ecosystems (VMEs) were identified in both tropical and temperate latitudes, often displaying strong similarities to faunal assemblages described in the North Atlantic. These findings suggest that South Atlantic seamounts and oceanic islands may harbour significant abundance and diversity of deep-sea species and assemblages including those protected through various legal instruments.

This thesis also addresses how to appropriately inform sustainable management of data-poor ocean basins in multiple ways: the first explores the use of a model transfer approach across a data gradient from rich to poor and ascertains the ecological relevance of modelled predictions through independent validation using data from the South Atlantic. The second uses ecological variables known to drive species distributions to develop a global habitat classification. The final output is evaluated against faunal zonation literature and other modelled outputs, considering both our current understanding of drivers of global species and habitat distribution, and the drivers and distributions identified within this thesis for the South Atlantic.

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LIST OF ACRONYMS AND ABBREVIATIONS

ABMTs	Area-based management tools
ABNJ	Areas beyond national jurisdiction
AIC	Akaike information criterion
ANOVA	Analysis of variance

APEI	Area of particular environmental interest
ASW	Average silhouette width
AUC	Area under curve
BAS	British Antarctic Survey
BBNJ	Biodiversity beyond national jurisdiction
BBPI	Broad-scale bathymetric position index
BDG	Bathymetric diversity gradient
BODC	British Oceanographic Data Centre
BPI	Bathymetric position index
CBD	Convention on Biological Diversity
CCAMLR	Convention on the Conservation of Antarctic Marine Living Resources
CCZ	Clarion-Clipperton Zone
CEFAS	Centre for Environment, Fisheries and Aquaculture Science
CH	Calinski-Harabasz
CLARA	Clustering Large Applications
CLCS	Commission on the Limits of the Continental Shelf
CLUSTER	Hierarchical cluster analysis
CWC	Cold-water coral
dbRDA	Distance-based redundancy analysis
DistLM	Distance-based linear model

EBSA	Ecologically or biologically significant marine areas
EEZ	Exclusive Economic Zone
EIA	Environmental impact assessment
EU	European Union
EUNIS	European nature information system
FAO	Food and Agriculture Organization of the United Nations
FBPI	Fine-scale bathymetric position index
GAM	Generalised additive model
GEBCO	General Bathymetric Chart of the Oceans
GLM	Generalised linear model
GMRT	Global Multi-Resolution Topography
HBCCF	Hard-bottom cup coral field
HSD	[Tukey’s] honest significant difference
HSM	Habitat suitability model/modelling
ICCAT	International Commission for the Conservation of Atlantic Tunas
ILBI	International legally binding instrument
IMR	Norwegian Institute of Marine Research
ISA	International Seabed Authority
IUCN	International Union for Conservation of Nature
IUU	Illegal, unreported and unregulated

LDG	Latitudinal diversity gradient
MAR	Mid-Atlantic ridge
MaxEnt	Maximum Entropy modelling
MMO	Marine Management Organisation
MoU	Memorandum of understanding
MPA	Marine protected area
MPZ	Marine protection zone
MSP	Marine spatial planning
Nm	Nautical mile
nMDS	Non-metric multidimensional scaling
OBIS	Ocean Biodiversity Information System
OECM	Other effective area-based conservation measures
OTU	Operational taxonomic unit
PCC	Percent correctly classified
POC	Particulate organic carbon
PRZ	Preservation reference zone
REMP	Regional environmental management plan
RFMO	Regional fisheries management organisation
ROV	Remotely operated vehicle
SAG	South Atlantic gyre

SAI	Significant adverse impact
SDM	Species distribution model/modelling
SEAFO	South East Atlantic Fisheries Organisation
SIMPER	Similarity Percentage Routines
SIMPROF	Similarity Profile Analysis
STCF	Subtropical Convergence Front
STF	Subtropical front
SUCS	Shallow Underwater Camera System
TSS	True skills statistics
UBRE	Un-biased risk estimator
UKOT	United Kingdom Overseas Territory
UN	United Nations
UNCLOS	United Nations Convention on the Law of the Sea
UNEP	United Nations Environment Programme
UNGA	United Nations General Assembly
USBL	Ultra-short baseline
VME	Vulnerable Marine Ecosystem
VMS	Vessel monitoring system
VTC	Vitória-Trindade seamount chain
WGDEC	Working Group on Deep-water Ecology

CHAPTER 1: GENERAL INTRODUCTION

1.1 The South Atlantic Ocean

The South Atlantic Ocean is confined by Africa to the east and South America to the west, but latitudinally extends from the equator to 60°S between 70°W and 50°W, and 50°S between 50°W and 30°E (Figure 1.1

This southern boundary differs based on the Southern Ocean as defined by the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). The South Atlantic covers 37 million km2 of the world's ocean, with an average depth of 3,977 m and a maximum of 7,770 m (GEBCO Compilation Group, 2020).).

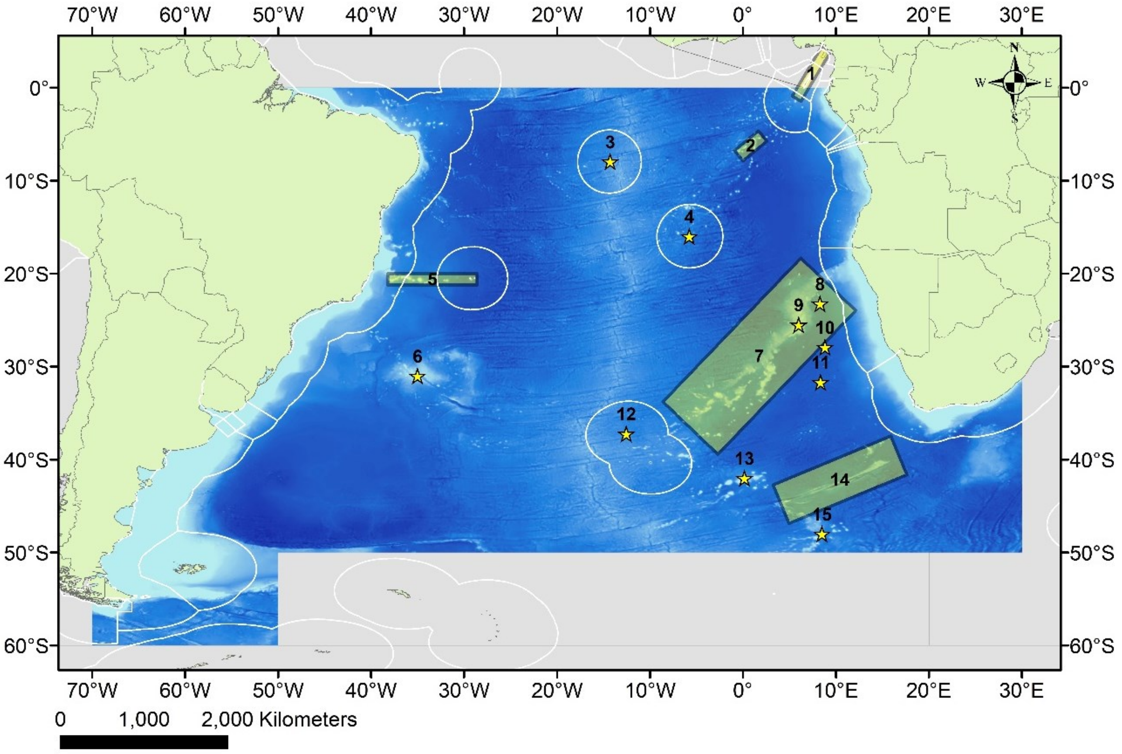

Figure 1.1: Map depicting the South Atlantic, with the southern boundary being defined by the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR); the white line depicts the Exclusive Economic Zones of bordering nations. Key features referred to in Chapter 1 are plotted: 1 = Cameroon Line, 2 = Guinea Seamount Chain, 3 = Ascension Island, 4 = Saint Helena, 5 = Vitória-Trindade Seamount Chain, 6 = Rio Grande Rise, 7 = Walvis Ridge, 8 = Ewing Seamount, 9 = Valdivia Bank,

10 = Molloy Seamount, 11 = Vema Seamount, 12 = Tristan da Cunha, 13 = Discovery Seamount, 14 = Algulhas Ridge, 15 = Meteor Seamount. Bathymetry provided by GEBCO 2020 Grid. Map drawn in WGS84.

This southern boundary differs based on the Southern Ocean as defined by the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). The South Atlantic covers 37 million km^2 of the world’s ocean, with an average depth of 3,977 m and a maximum of 7,770 m (GEBCO Compilation Group, 2020).

The Mid-Atlantic Ridge (MAR) runs the length the entire South Atlantic, roughly along 15˚W. Other prominent ridge systems include the Walvis and Agulhas, both running in a southwesterly direction from 18˚S and 35˚S respectively (Figure 1.1
This southern boundary differs based on the Southern Ocean as defined by the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). The South Atlantic covers 37 million km2 of the world’s ocean, with an average depth of 3,977 m and a maximum of 7,770 m (GEBCO Compilation Group, 2020).). The southeast Atlantic is home to multiple seamounts and seamount complexes, many of which are still un-sampled. The Cameroon Line and adjacent Guinea Seamount Chain form a line/cluster of seamounts from the Gulf of Guinea towards Saint Helena, with the southern-most end of the chain located just south of the equator. Other prominent complexes include Vema, Discovery and Meteor; Valdivia Bank is also located in the eastern part of the South Atlantic on the Walvis Ridge. These features, along with some more isolated seamount complexes such as Ewing and Molloy, are target areas for deep-sea fisheries in this region (FAO, 2009). The Angola and the Cape basins are the two major basins in the southeast Atlantic, separated by the Walvis Ridge (Pérez-Díaz & Eagles, 2017).

The southwest Atlantic is characterized by less rugose terrain and is home to one of the largest continental slope regions on the planet. The two major basins are the Brazil and Argentine basins, separated by the Rio Grande Rise (Pérez-Díaz & Eagles, 2017). The Vitória-Trindade Seamount Chain extends off the Brazilian coast in an easterly direction at 20°S.

States that border the South Atlantic include Brazil, Uruguay, and Argentina to the west, and Gabon, Congo Republic, Democratic Republic of the Congo, Angola, Namibia and South Africa to the east. In addition, there are a number of Overseas Territories in the South Atlantic: Trindade and Martin Vaz, an archipelago claimed by Brazil and located roughly 1,100 km from its coast, and the United Kingdom Overseas Territories (UKOTs) of the Falkland Islands and Saint Helena, Ascension and Tristan da Cunha, the latter of which is formed of three separate oceanic islands (Figure 1.1
This southern boundary differs based on the Southern Ocean as defined by the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). The South Atlantic covers 37 million km2 of the world's ocean, with an average depth of 3,977 m and a maximum of 7,770 m (GEBCO Compilation Group, 2020).). Equatorial Guinea is also responsible for an area in the northeastern corner of the South Atlantic due to its governance over Annobón Island (the southernmost island in the Cameroon Line).

In 1982, the 200 nautical mile (nm) Exclusive Economic Zone (EEZ) was formally adopted as part of the United Nations Convention on the Law of the Sea (UNCLOS). This dictates that coastal states can exercise sovereign rights for the purposes of exploring, exploiting, conserving and managing natural resources over the 200 nm of water column and seabed adjacent to their coastline. Areas beyond national jurisdiction (ABNJ) represent the majority of the ocean where no single state has authority and constitute the 'High Seas' and 'the Area'. The former refers to the water column in ABNJ, and the latter to the seabed and subsoil. The value of 200 nm for EEZs was chosen because in most scenarios, this covers the continental shelf. However, where the continental shelf extends further than 200 nm, states may submit a request to the Commission on the Limits of the Continental Shelf (CLCS) to extend their EEZ. Approval of this submission would result in the state exercising sovereign rights over the new area of seabed, but *not* the water column above it; there is currently no legal framework for states to make sovereign claims over the water column adjacent to their 200 nm EEZ.

The only two countries bordering the South Atlantic that have *not* made submissions to the CLCS are the Congo Republic and the Democratic Republic of the Congo. Of the remaining seven countries that have made submissions, those sponsored by Argentina, South Africa and Namibia have the largest spatial coverage (Figure 1.2). Most nations have requested extensions that run relatively parallel to their current EEZ boundary. Although the Namibian claim of an extra ~380,000 km^2 equates to a smaller area than both Argentina and South Africa, it is significant as the submission requests that the entire Walvis Ridge system be incorporated into Namibia's EEZ (Figure 1.2).

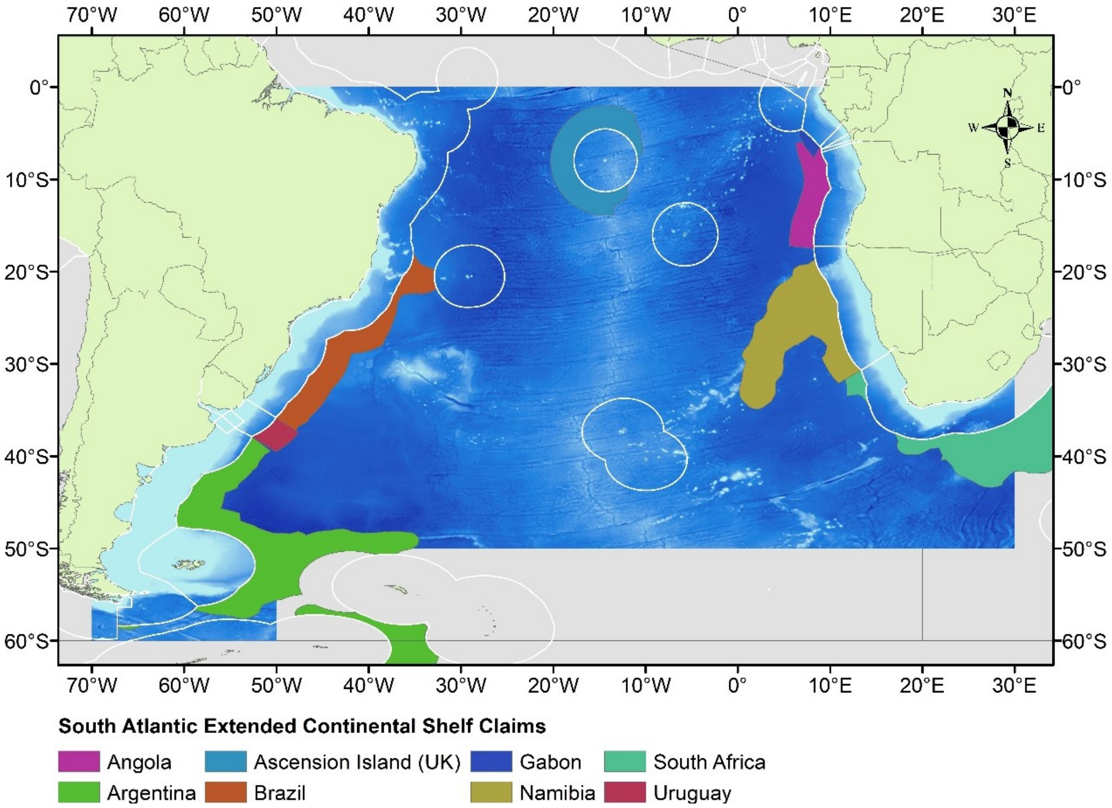

Figure 1.2: Claims submitted by South Atlantic bordering nations to the Commission on the Limits of the Continental Shelf. Bathymetry provided by GEBCO 2020 Grid. Map drawn in WGS84. Brazil have recently submitted an addendum to their application to include the Rio Grande Rise region.

1.2 Biodiversity of the South Atlantic

1.2.1 Broad-scale ecological trends

The southern hemisphere is extremely data-poor compared to the northern hemisphere (Howell *et al.*, 2020b), and the South Atlantic is no exception to this. This said, there are some inter-basin comparisons that have suggested the South Atlantic deep sea is more speciose than the North Atlantic due to its geological history and openness to immigration from the Indo-Pacific area (Wilson, 1998; Culver & Buzas, 2000; Gage, 2004).

Studies that have characterised broad-scale distribution patterns of the South Atlantic have typically done so as part of an inter-basin comparison (e.g. Culver & Buzas, 2000). A frequent result is that latitudinal diversity gradients observed in the North Atlantic are less clear in the South Atlantic, somewhat due to a lack of data, but also due to strong interregional variation (e.g. Rex *et al.*, 1993; Gage, 2004). For example, the southwest Atlantic (Argentine Basin) displays exceptionally high diversity compared to other regions and basins across a range of taxa (Rex *et al.*, 1993; Dos Santos *et al.*, 2020).

Studies that have collected data from the South Atlantic typically report the tropical deep sea to be more diverse than temperate and polar regions (Rex *et al.*, 1993; Culver & Buzas, 2000), although there have been disputes as to whether Antarctic deep-sea diversity is truly low (Brey *et al.*, 1994; Brandt *et al.*, 2007; Ellingsen *et al.*, 2007). The presence and/or direction of a latitudinal diversity gradient also appears to be somewhat dependent on the taxonomic group from which the gradients are described, and individual studies. For example, bivalves and benthic foraminifera display significant poleward decline in diversity from tropical latitudes (Rex *et al.*, 1993; Culver & Buzas, 2000); gastropods display both a poleward decline (Rex *et al.*, 1993) and incline (Schrödl *et al.*, 2011) in diversity from the tropics towards Antarctica; and Cumacea diversity displays no significant relationship with latitude (Gage, 2004). One factor that all these studies have in common is that, as with most studies with similar objectives, they are all based on data collected from epibenthic sledge deployments and thus report gradients of macro- and/or meio- faunal communities of soft-sediment areas.

Thorson (1957) first described the differences in latitudinal diversity gradients of assemblages from hard *versus* soft substrate areas, finding them to differ in shallow water ecosystems. In the deep sea, hard substrate features such as seamounts and oceanic islands have be theorised to harbour diverse ranges of communities as they provide rocky habitat in otherwise soft sediment areas (Samadi *et al.*, 2006; Clark *et al.*, 2010). However, broad-scale ecological patterns of communities from hard substrate features in the South Atlantic deep sea represents a current data gap.

1.2.2 Fine-scale biodiversity

At a finer scale, some recent studies have focused on describing the diversity and ecology of particular geomorphological features in the South Atlantic that are typically dominated by hard substrate such as oceanic islands and seamounts (e.g. Caselle *et al.*, 2018). On these structures, many studies have elucidated records of Vulnerable Marine Ecosystems (VMEs). The following sections focus on VMEs and their distribution in the South Atlantic.

1.2.2.1 What are Vulnerable Marine Ecosystems?

VME is a term adopted by the United Nations General Assembly (UNGA) to refer to areas where the biology is vulnerable to damage from bottom fishing, and thus are protected under various UNGA resolutions (see Section 1.4.1.2). The Food and Agriculture Organisation (FAO) developed the International Guidelines for the Management of Deep-Sea Fisheries in the High Seas (FAO, 2009) which lists five characteristics that lead to the designation of marine ecosystems as VMEs: (1) uniqueness or rarity; (2) functional significance of the habitat; (3) fragility; (4) life-history traits of component species that make recovery difficult and (5) structural complexity. Multiple deep-sea habitats are listed as examples of VMEs, including cold-water coral (CWC) reefs, coral gardens, deep-sea sponge aggregations and sea pen and burrowing megafaunal communities. In 2013, the South East Atlantic Fisheries Organisation (SEAFO) Scientific Committee agreed upon a provisional list of benthic invertebrates as VME-indicator taxa within the SEAFO Convention Area (Table 1.1; Figure 1.3).

Table 1.1: Extended list of VME-indicator species adopted by SEAFO.

Taxon	**Taxonomic rank**	**Common name**	**Number of South Atlantic records (200m+) in Ocean Biodiversity Information System (OBIS, May 2021)**
Porifera Grant, 1836	Phylum	Sponges	884
Bryozoa Ehrenberg, 1831	Phylum	Erect bryozoans	338
Cyrtocrinida Sieverts-Doreck, 1952	Order	Sea lilies	41
Hyocrinida Rasmussen, 1978	Order		
Isocrinida Sieverts-Doreck, 1952	Order		
Gorgonocephalidae Ljungman, 1867	Family	Basket stars	426
Ascidiacea Blainville, 1824	Class	Sea squirts	107
Alcyonacea Lamouroux, 1816	Order	Gorgonian corals	436
Anthoathecata Cornelius, 1992	Order	Hydrocorals	409
Scleractinia Bourne, 1900	Order	Stony corals	1099
Antipatharia Milne-Edwards & Haime, 1857	Order	Black corals	40
Zoantharia Gray, 1832	Order	Zoanthids	28
Pennatulacea Verrill, 1865	Order	Sea pens	120
Serpulidae Rafinesque, 1815	Family	Tube worms	26

To be designated a VME, one of the five FAO criteria needs to be met. In the deep sea where most of the environment comprises abyssal plain, areas suitable for the development of, for example, CWC reefs are relatively rare due to the requirement of hard substrate for larvae to successfully settle and recruit. However, many reef-forming species of CWCs are described as having cosmopolitan distributions in the sense that they occur across the world *in suitable habitat*. This can lead to confusion as having a rare species/ecosystem with a cosmopolitan distribution is somewhat counterintuitive. The same principle of limited suitable habitat being available applies to depth too, where much of the deep sea may be too deep for some VME-indicator taxa. This means that some taxa, despite being described as having cosmopolitan distributions, are still considered comparatively rare.

There is a large body of scientific literature on which the FAO (2009) criteria are based that justifies the importance of different VMEs. For example, deep-sea sponge aggregations are clusters of individual sponges that form biogenic reefs (Rice *et al.*, 1990). Studies have suggested that shallow water sponge aggregations play important functional roles in biogeochemical cycling of silicon, nitrogen and carbon (Reiswig, 1971, 1974; Maldonado *et al.*, 2005, 2017; Bell, 2008); provision of refugia for fish and invertebrate species; and increasing biodiversity by increasing habitat complexity (Bo *et al.*, 2012; Maldonado *et al.*, 2017). There is evidence that deep-sea sponge aggregations play similar roles to their shallow water counterparts (Howell *et al.*, 2016). Studies focusing on CWC reefs suggest they play analogous ecological roles to deep-sea sponge aggregations due to their comparable effects on the physical environment (Roberts *et al.*, 2006). This has led to them also being recognized as essential fish habitat (Kaiser, 2004; Kutti *et al.*, 2014), and as nursery grounds for fish larvae (Baillon *et al.*, 2012).

1.2.2.2 Vulnerable Marine Ecosystem distribution in the South Atlantic

Southeast Atlantic

Deep-sea benthic communities of seamounts and oceanic islands in the southeast Atlantic are diverse, often comprising many filter-feeding VME-indicator taxa such as scleractinian and gorgonian corals (Durán Muñoz *et al.*, 2014; Caselle *et al.*, 2018; Bergstad *et al.*, 2019a; FAO, 2019). Similarly, the continental shelves and slopes off west Africa harbour diverse benthic communities including CWC reef and coral gardens (Zibrowius & Gili, 1990; Hanz *et al.*, 2019; Sink *et al.*, 2019).

Zibrowius & Gili (1990) compiled a list of the deep-sea Scleractinia found in the southeast Atlantic off the coast of southern Namibia, the northernmost coast of South Africa, and on the Walvis Ridge. The three cruises they reported on were carried out during 1982 – 1984, and sampled 22 stations. Six-hundred specimens across 11 species were collected from depths between 145 and 1,398 m, including reef-forming corals such as *Desmophyllum pertusum* (Linnaeus, 1758) and *Enallopsammia rostrata* (Pourtalès, 1878). The species found were unequally represented from 1 – 300 specimens per trawl. The Walvis Ridge was the most diverse area with 9 out of 11 species obtained there. These data suggest that, although spatially heterogeneous, cold-water scleractinians may be found in the deep waters off the whole coast of the southwest African continent.

More recently in the southeast Atlantic, Spanish and Namibian scientists collaborated on the Rap-Sur project, one of four Atlantic projects with aims to: map the seabed; identify VMEs; study the interaction with bottom fisheries; and select suitable areas to preserve VMEs (Durán Muñoz *et al.*, 2014). The Rap-Sur project ran three multi-disciplinary cruises during 2008 – 2010 focused around Ewing Seamount and Valdivia

Bank, surveying depths between 218 and 3,000 m with bottom trawls, rock dredges and box corers. The benthic fauna associated with VMEs consisted mainly of Antipatharia and colonial scleractinians that formed coral gardens (a type of VME). The larger, reef-forming corals provide substrate for solitary scleractinians, octocorals, and small sessile organisms, thus drastically increasing the biodiversity within the area. Of the samples collected, a large proportion of the Scleractinia were found dead, although *E. rostrata* retained live polyps (Durán Muñoz *et al.*, 2012).

In 2015, the FAO lead a 29-day research cruise in the SEAFO Convention Area focusing on several seamounts and prominent features including Ewing seamount, Valdivia Bank and Vema seamount (FAO, 2016; Bergstad *et al.*, 2019a, b; see Figure 4.3 for locations). Similarly to the Rap-Sur project, the cruise devoted time to multibeam mapping; benthic video mapping of VME-indicator taxa on seamounts; hydrographic sampling using CTDs; and physical sample collection using a variety of grabs and trawls (FAO, 2016). Physical specimens were preserved and later identified by taxonomic experts; Arthropoda and Cnidaria were found to be the two most speciose phyla respectively, and reef-building corals were collected, with *E. rostrata* identified (Ramil, 2015). FAO (2016) details the individual seamount data, with some video dives recording large amounts of dead scleractinian coral rubble, suggesting past extensive densities of reef-building corals and VMEs; live coral was relatively patchy on the surveyed locations (FAO, 2016; Bergstad *et al.*, 2019a). Of the five features/seamounts surveyed, Valdivia Bank, located on the Walvis Ridge (~25.5° S, 6° E; see Figure 1.1

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This southern boundary differs based on the Southern Ocean as defined by the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). The South Atlantic covers 37 million km2 of the world’s ocean, with an average depth of 3,977 m and a maximum of 7,770 m (GEBCO Compilation Group, 2020).), including two subareas closed to fishing (FAO, 2019).

The British Antarctic Survey (BAS) and the Centre for Environment, Fisheries and Aquaculture Science (CEFAS), both based in the UK, have jointly led mid-Atlantic cruises focusing on the UKOT of Saint Helena, Ascension and Tristan da Cunha. Five research cruises were undertaken ranging 2013 – 2019 (Barnes *et al.*, 2013, 2015, 2019; Morley *et al.*, 2018; Whomersley *et al.*, 2019). Surveys in 2013, 2015 and 2018 sampled within the EEZs of Tristan da Cunha and Saint Helena, whilst the 2015 and 2017 surveys sampled around Ascension Island. VMEs in the form of *D. pertusum* reef, *Solenosmilia variabilis* Duncan, 1873 reef, coral gardens and hard-bottom cup coral fields comprising solitary scleractinians were all observed. Although relatively pelagically focused, Caselle *et al.* (2018) report that species richness differed significantly between the four oceanic islands at Tristan da Cunha. High habitat heterogeneity between relatively close features is also reported by Bergstad *et al.* (2019a) along the Walvis Ridge.

Southwest Atlantic

Work in the southwest Atlantic suggests a diverse range of benthic assemblages are also present here including multiple types of CWC reef (Pires, 2007; Barbosa *et al.*, 2020; Kitahara *et al.*, 2020), coral gardens (Durán Muñoz *et al.*, 2012; Portela *et al.*, 2012; Cordeiro *et al.*, 2020) and deep-sea sponge aggregations (Portela *et al.*, 2012; Durán Muñoz *et al.*, 2014; Hajdu *et al.*, 2017).

Pires (2007) investigated coral faunal diversity and distribution off the coast of Brazil with data compiled from the literature as well as newly collected data. Fifty-six species were reported, translating into a 4:1 ratio between azooxanthellate to zooxanthellate corals for Brazilian waters; higher than the usual ratio from the tropical-warm temperate western Atlantic (2:1) and the worldwide ratio (1:1). This suggests that Brazilian waters, and likely a large proportion of the South Atlantic, represent an area of high biodiversity of CWCs. This study found that the most dominant reef-forming CWCs in Brazilian waters are *D. pertusum* and *S. variabilis*.

Between 2007 and 2010, the ATLANTIS project studied ABNJ in the southwest Atlantic between 42˚S and 48˚S, to the east of Argentina and north of the Falkland Islands. The project was one of the four on VMEs in the Atlantic, and was overseen by the Spanish Institute of Oceanography and the General Secretariat of Fisheries of the Spanish Ministry of Agriculture, Food and Environment. The multidisciplinary work involved collecting high-resolution multibeam bathymetry data for the area, as well as performing a series of biologically-focused benthic surveys (rock dredges, boxcorers, bottom trawls and sediment collections) on the Patagonian shelf and adjacent slope (both popular fishing areas, see Section 1.3.2). Four type of VME were identified in the study area: (1) deep-sea sponge aggregations; (2) CWC reefs; (3) coral gardens, and (4) deep-sea rocky environments; the majority of which were located between 400 and 1,000 m. Cnidaria and Porifera, both VME-indicator taxa, dominated the benthic megafaunal catch during the cruises. Of the Cnidaria collected, 33.7% were octocorals (Muñoz *et al.*, 2012). The ATLANTIS Project led to the identification of nine VME candidate areas for protection in the High Seas.

In 2016, Pires *et al.* investigated the existence of deep-sea coral reefs along the Brazilian coast using records of occurrence of coral reef builder species (*D. pertusum, Madrepora oculata* Linnaeus, 1758*, S. variabilis, Dendrophyllia alternata* Pourtalès, 1880*, and E. rostrata*). The study determined that Brazil had an almost continuous latitudinal distribution of CWC species along its entire ~7,000 km coast, and therefore the potential of widespread VMEs.

The South Atlantic is home to many seamount/seamount complexes. Clark *et al.* (2006) found that CWC are likely to be found in association with seamounts within fishable depths (<2,000 m) between 20˚S and 60˚S. A study conducted by the European Commission concluded that within fished areas bordering the Argentine EEZ, the seabed falls abruptly from 200 to 1,000 m, concurrent with the conditions favourable for CWC reef and deep-sea sponge aggregations (Portel*a et al.*, 2010).

1.3 Extraction activities in the South Atlantic

Although it is clear that the South Atlantic supports a diverse range of species and habitats including VMEs, and despite little being known about the connectivity of ecosystems and their environmental drivers, human industries that extract resources from the natural environment are also present in the South Atlantic.

1.3.1 Fishing in the southeast Atlantic

The South East Atlantic Fisheries Organisation (SEAFO) was established in 2003 and is the RFMO responsible for sustainably managing fisheries and marine life resources in the southeast Atlantic within its Convention Area (Figure 1.3**Error! Reference source not found.**). The Convention Area does not encompass the EEZs of the bordering countries (Angola, Namibia, South Africa and the United Kingdom), only ABNJ, which includes both The Area and the High Seas.

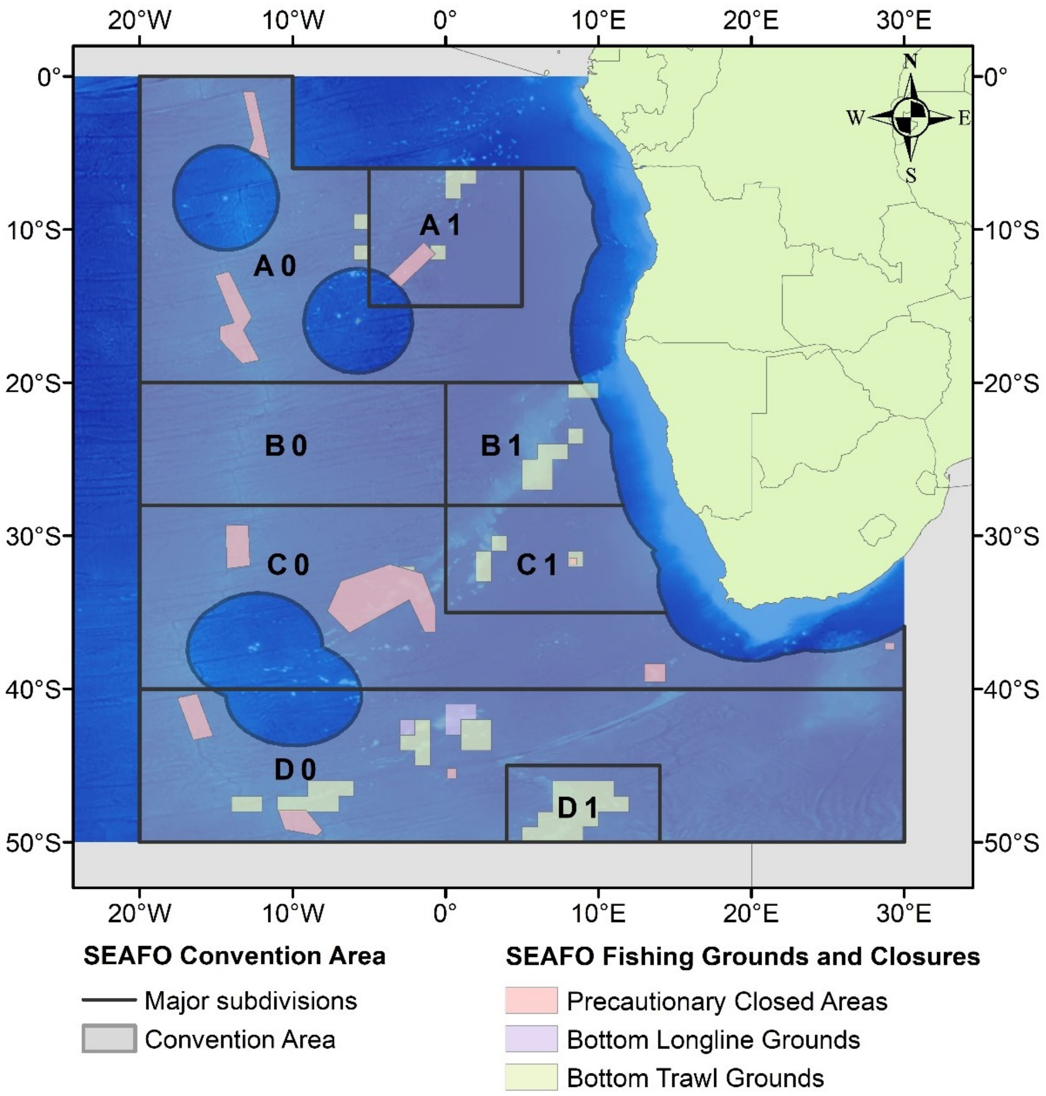

Figure 1.3: The South East Atlantic Fisheries Organisation (SEAFO) Convention Area. Grey lines depict the four major divisions of the FAO Major Fishing Area 47 (A0-D0), as well as the four major sub-divisions, where the majority of bottom fishing takes place (A1-D1). Current bottom fishing areas and closures are also shown. A small VME Closed Area on Valdivia Bank is not shown due to scale. Underlying bathymetry from GEBCO 2020 Grid. Map drawn in WGS84.

Over recent decades, the southeast Atlantic has been the subject of increasing fisheries exploitation due to its rich nature and relatively short commercial fishing history (1950s+) when compared to other oceanic regions (Thompson *et al.*, 2017). All present fisheries in the SEAFO Convention Area (Figure 1.3) occur on or around seamounts (Thompson *et al.*, 2017), with the majority of bottom fishing activity falling into three distinct areas: the Valdivia Bank seamount complex, the Discovery seamounts, and the Meteor seamounts.

Alfonsino (mainly *Beryx splendens* Lowe, 1834) and southern boarfish (*Pseudopentaceros richardsoni* (Smith, 1844)) are caught using bottom and mid-water trawls on the top and along the slopes of Valdivia Bank between 200 and 700 m. Anchored lines of 400 Japanese beehive pots (roughly 7.7 km long) are used to catch deep-sea red crab in the region (mainly *Chaceon erytheiae* (Macpherson, 1984)); again, this is largely focused around Valdivia Bank between 280 and 1,150 m. For a 10-year period from 1995, bottom trawls were used to target orange roughy (*Hoplostethus atlanticus* Collett, 1889) on Valdivia Bank, Ewing Seamount and the northeastern section of the Walvis Ridge. These areas have all been identified as hotspots of biodiversity, with ecosystems including CWC reefs being recorded (see Section 1.2.2). Although fishing effort has been increasing and catches are highly variable, the annual catches for all species have been declining since 2010 (Thompson *et al.*, 2017) in-line with many global fisheries (Froese *et al.*, 2012).

SEAFO has adopted measures to ensure that illegal, unregulated and unreported (IUU) fisheries are limited in their Convention Area, by implementing an authorised vessel list, and has added to the IUU vessel list compiled by the North East Atlantic Fisheries Commission, the Northwest Atlantic Fisheries Organisation and the CCAMLR. IUU fishing is likely to affect VMEs as the lack of adherence to rules suggests the reporting of VME bycatch and location data would not be shared. However, it is worth noting that although SEAFO contribute to the list, instances of non-compliance (and therefore

IUU fishing) are not actively searched for and it is therefore likely that IUU fishing in the region is underestimated. Since 2005, SEAFO has also mandatorily implemented a vessel monitoring system (VMS). Additionally, it has adopted a protocol for the retrieval and reporting of lost gear, a source of damage to some VMEs (Roberts & Hirshfield, 2004).

Within EEZs, many West African nations bordering the South Atlantic rely heavily on inshore fisheries for food provision, although some have expanded their fleets to allow for the creation of deep-water fisheries. Off southwest Africa, key deep-water fisheries include the: Namibian-South African *Merluccius* spp. Rafinesque, 1810 (hake) fishery (Paterson *et al.*, 2013); large-eye dentex (*Dentex macrophthalmus* (Blotch, 1791)) fishery (Potts *et al.*, 2010) and deep-water shrimp fisheries (Konda, 2008). Additionally, communities on the small oceanic islands of Ascension Island, Saint Helena and Tristan da Cunha are very isolated, and therefore a large portion of their economies rely on fishing (Glass, 2014; St Helena Government, 2016; Ascension Island Government, 2021).

1.3.2 Fishing in the southwest Atlantic

Unlike the southeast, there is no RFMO for the southwest Atlantic, and therefore responsibility falls upon bordering states to cooperate in the management of High Seas fisheries (FAO, 2009); mainly on the Patagonian Shelf, Rio Grande Rise and some isolated seamounts. The major High Seas bottom fisheries in the region principally target Argentine hake (*Merluccius hubbsi* Marini, 1933) and Argentine shortfin squid (*Illex argentinus* (Castellanos, 1960)), mainly undertaken by Spanish and Taiwanese vessels, respectively (Portela *et al.*, 2010; Vilela *et al.*, 2018). Although the fisheries in this area target Argentine squid and hake on sandy bottoms, some trawls may extend beyond the shelf break and therefore pose a threat to VMEs (European Commission, 2007). A number of nations actively fishing the area have reported large catches of non-target species including elasmobranchs (FAO, 2009).

Other current bottom fisheries in the region include a longline fishery on the Patagonian Shelf for the Patagonian toothfish (*Dissostichus eleginoides* Smitt, 1898), and fisheries on individual seamounts, for which data are not available (Clark *et al.*, 2007). Brazil have been targeting demersal fish stocks in the deep High Seas for more than a decade, and yet still only little is known about the impacts caused by bottom-towed gear in the region (Pires *et al.*, 2016). However, findings from the ATLANTIS project determined that 99% of fishing effort in their study area was targeted at <300 m, assessed using commercial fishing data and VMS.

The fisheries within EEZs of countries bordering the southwest Atlantic are similar to those in ABNJ, largely targeting hake species (*Merluccius* spp.), monkfish (*Lophius gastrophysus*, Miranda Ribeiro, 1915), Patagonian toothfish and deep-water crustaceans (Pezzut*o et al.*, 2006; Perez *et al.*, 2009).

1.3.3 Deep seabed mining

Deep seabed mining usually refers to one of three extraction activities whereby natural resources are removed from the seabed: seafloor massive sulfides (often referred to as hydrothermal events), polymetallic nodules and cobalt-rich ferromanganese crusts. The impacts of deep-sea mining on biodiversity will depend on the type of mining and the proximity of certain ecosystems, although it is understood that it will likely drive overall losses in biodiversity (Van Dover *et al.*, 2017).

The southwest Atlantic is currently a key focus area for exploration for mining activities, with the Companhia De Pesquisa de Recursos Minerais of Brazil being granted a 15-year contract for exploration of cobalt-rich ferromanganese crusts on the Rio Grande Rise area in November 2015. Although this seamount complex is the only area with a current exploratory licence in the South Atlantic, Hein *et al.* (2013) identified areas of seabed at which conditions were viable for the production of polymetallic nodules and cobalt-rich ferromanganese crusts (Figure 1.4). With regards to seafloor massive sulfide mining, the MAR that runs down the basin is home to a large number of hydrothermal vents due to its high volcanic activity, although the suitability of these for mining exploration has yet to be affirmed.

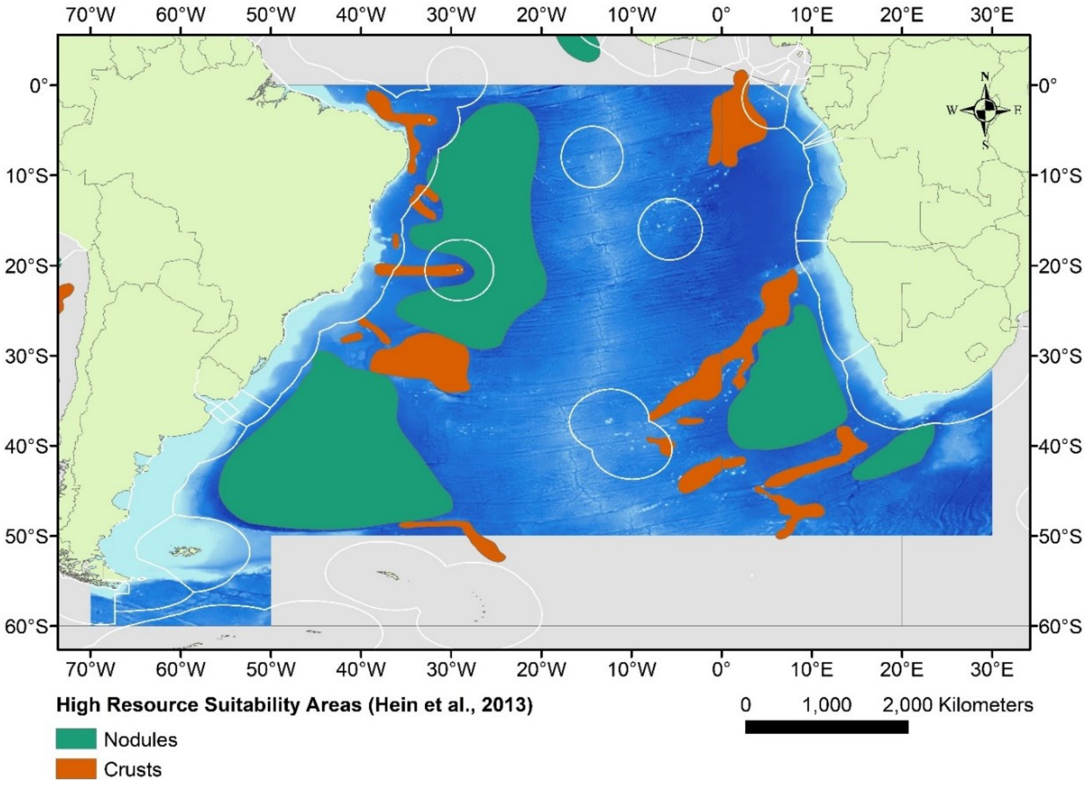

Figure 1.4: Map depicting permissive areas for the development of manganese nodules and cobalt-rich ferromanganese crusts as identified by Hein et al. (2013). White lines depict national Exclusive Economic Zones. Underlying bathymetry provided by GEBCO 2020 Grid. Map drawn in WGS84.

1.4 Area-based management of the South Atlantic

Area-based management tools (ABMTs) represent one way of spatially regulating where particular industries can work, of which Marine Protected Areas (MPAs) are an example. MPA is an umbrella term for which the definition varies depending upon the level of protection given, the activities/threats it is designed to protect against and the defining body. The number of MPAs across the world's ocean has increased dramatically in the last five decades, although coverage in the South Atlantic has lagged behind global efforts (Figure 1.5) However, whilst the usefulness of MPAs in some circumstances is demonstrable, their use has been criticized by some for providing the illusion of protection when no active protection is occurring (Agardy *et al.*, 2011).

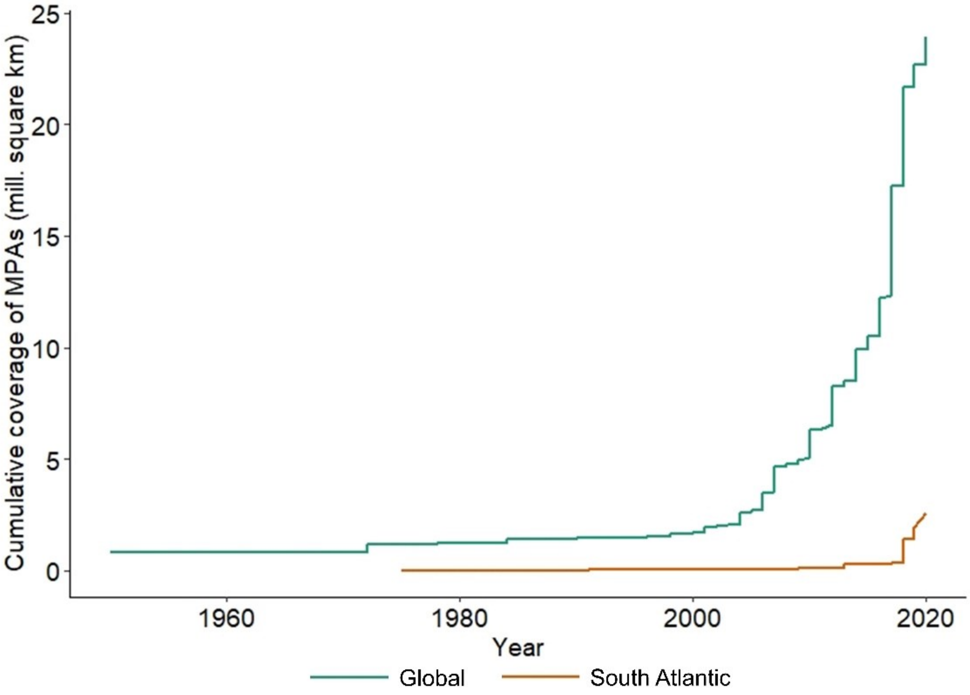

Figure 1.5: Cumulative coverage of MPAs globally and in the South Atlantic from 1950 to 2020. Data from UNEP-WCMC & IUCN (2021).

The International Union for the Conservation of Nature (IUCN) categorizes protected areas into various types dependent upon the level of protection it is deemed to provide (Table 1.2). Most MPAs fall into category V, allowing for sustainable use of natural resources (e.g. certain fisheries), although there are a number of designated no take zones (category I).

Table 1.2: IUCN Protected Area categories and allowed extraction/use.

IUCN Category	**Description**	**Use**
Ia	Strict Nature Reserve	No resource extraction
Ib	Wilderness Area	First Nations traditional harvesting and collection for scientific research allowed
II	National Park	First Nations traditional harvesting and collection for scientific research allowed
III	Natural Monument or Feature	First Nations traditional harvesting and collection for scientific research allowed
IV	Habitat/Species Management Area	Sustainable resource extraction allowed
V	Protected Landscape/Seascape	Sustainable resource extraction allowed
VI	Protected Area with Sustainable Use of Natural Resources	Sustainable resource extraction allowed

1.4.1 Area-based management in areas beyond national jurisdiction

UNCLOS outlines the rights and responsibility of member states regarding the oceans. Although it contains clauses pertaining to the conservation of living resources in ABNJ (Part Y, Section 2), the Convention lacks the legal framework from which to implement ABMT, including but not limited to, MPAs. However, other pieces of legislation focusing on specific sectors do have the legal capability to 'close' areas to specific activities e.g. fisheries closures in RFMO Convention Areas, but these are often not considered MPAs because they can only protect from damage caused by individual sectors.

1.4.1.1 Ecologically or Biologically Significant Marine Areas

The Convention on Biological Diversity (CBD) was signed by the international community in Rio de Janeiro, Brazil, in 1992 and came into force in December 1993. It has three main objectives: (1) the conservation of biological diversity; (2) the sustainable use of the components of biological diversity, and; (3) the fair and equitable sharing of the benefits arising out of the use of genetic resources. In 2010, the Aichi Biodiversity Targets were adopted under the CBD, number 11 of which stipulates that "*by 2020, at least 17 per cent of terrestrial and inland water areas and 10 per cent of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscape and seascape*". To ensure that the protected areas will be scientifically influenced, the CBD held regional workshops and invited scientists to identify Ecologically or Biologically Significant Marine Areas (EBSAs) that were "*in need of protection in open ocean waters and deep-sea habitats*". EBSAs are designated by the CBD, and although they boast no legal protection, the classification flags them as areas that serve important purposes to support the healthy functioning of the ocean. Although the CBD has no framework for designating MPAs in ABNJ, EBSAs are not limited to EEZs and can therefore be designated in ABNJ. In 2008, the Contracting Parties of the CBD established the guidelines for defining EBSAs: (1) uniqueness or rarity; (2) special importance for life-history stages; (3) importance for threatened, endangered or declining species and/or habitats; (4) vulnerability, fragility, sensitivity, or slow recovery; (5) biological productivity; (6) biological diversity; and (7) naturalness (CBD, 2009). Two workshops in Brazil and Namibia in 2012 and 2013 resulted in the identification of 22 EBSAs that cover areas in the South Atlantic, five of them being in the west and 17 in the east (Figure 1.6). The majority of EBSAs are within EEZs, although there are six transboundary EBSAs; the Walvis Ridge designation is the only EBSA solely covering ABNJ.

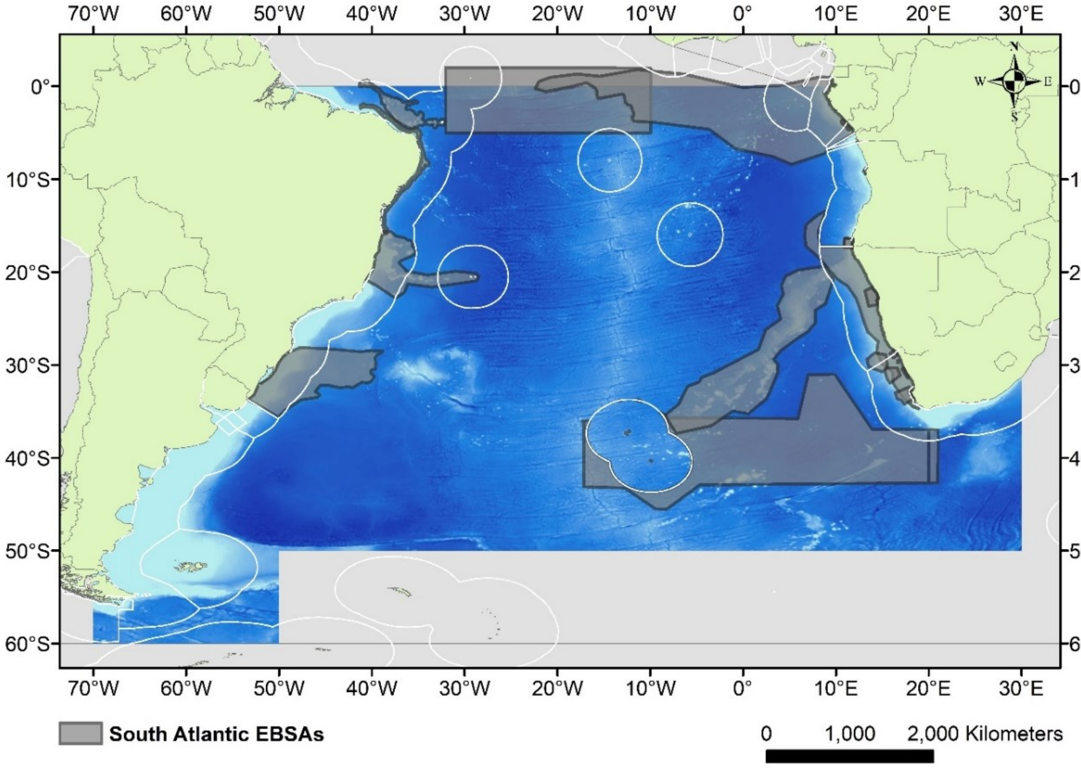

Figure 1.6: South Atlantic EBSAs identified by CBD Contracting Parties in 2012 and 2013. In the southwest Atlantic, there are five EBSAs; in the southeast Atlantic there are 17. EEZs denoted by the white lines. Underlying bathymetry provided by GEBCO 2020 Grid. Map drawn in WGS84.

1.4.1.2 Fisheries closures

RFMOs are the bodies established by the UN that regulate fisheries in ABNJ. In 2006, UNGA Resolution 61/105 called "*upon States to take action immediately, individually and through regional fisheries management organisations and arrangements, and consistent with the precautionary approach and ecosystem approaches, to sustainably* *manage fish stocks and protect vulnerable marine ecosystems (VMEs), including seamounts, hydrothermal vents and cold-water corals, from destructive fishing practices*". RFMOs were tasked with identifying where VMEs (Section 1.2.2) occur/are likely to occur in their Convention Areas, and then acting to prevent significant adverse impacts (SAIs) within their jurisdiction. This legislation gives RFMOs the capacity to close certain areas to fishing activities to prevent damage to VMEs.

The southeast Atlantic is a poorly studied region; although bathymetry data are available, resolution is typically coarse, thus forcing SEAFO to adopt a precautionary approach to its conservation measures in the form of a set of VME closures "*constituting a biogeographically representative selection of subareas likely to have VMEs*" (Figure 1.3). These closures were focused towards seamounts and seamount complexes with summit depths of less than 2,000 m. A suggested list of 13 closures was compiled in October 2006 in response to UNGA Resolution 61/105 using the criteria of a high chance of VMEs and known history of fishing exploitation. The SEAFO Scientific Commission agreed to close 10 of the 13 seamounts to all forms of bottom fishing during 2007 – 2010 through the adoption of Conservation Measure 06/06 (CM 06/06, 2006). In 2010, Discovery seamount complex was reopened, boundaries were changed to create larger closures and five new areas were closed along the MAR. In 2007, along with the suggestion of more closures, SEAFO recommended that for trawling to resume in any closed areas, VMEs should be mapped, and proposals for mapping, exploratory fishing and resumption of commercial fishing should be submitted to the SEAFO Scientific Committee for consideration. This means that areas outside of the current fishing footprint are subject to increased regulations. In 2016, the first VME closure was installed based on data from a scientific research cruise on Valdivia Bank (FAO, 2016) and consequently, only longlines and pots are permitted. SEAFO currently has

12 VME areas closed to bottom fishing or selected gear types summing to 3.2% of the Convention Area (Figure 1.3).

Although the International Guidelines for the Management of Deep-Sea Fisheries in the High Seas (FAO, 2009) provides examples of taxa indicative of VMEs, there are no universal technical definitions in terms of metrics, or thresholds for abundance/density (Auster *et al.*, 2011). This proves problematic when RFMOs are tasked with closing areas to avoid SAIs to VMEs; hence, the main solution to reducing SAIs is the 'move-on' rule. This protocol states that vessels using bottom fishing gears are required to move at least 2 nm away from the end point of the trawl/tow in the direction least likely to result in more encounters when they encounter a VME-indicator species above 'threshold levels' (defined individually by each RFMO). The incident is reported to the corresponding RFMO Executive Secretary who informs all Contracting Parties and archives the location information. If the encounter took place outside an existing fishing area, a temporary closure is implemented pending examination by the RFMO Scientific Committee. This strategy relies solely on the reporting of encounters to SEAFO by fisheries observers, and it is therefore imperative that observers are permitted to work freely and safely aboard vessels (Bell *et al.*, 2019).

The International Commission for the Conservation of Atlantic Tunas (ICCAT) is an Atlantic-wide RFMO that manages highly migratory species and can implement closures in the South Atlantic down to 60 ˚S, although these would be not adhered to by demersal fisheries, as the focus species within ICCAT are pelagic. Although there is no RFMO in the southwest Atlantic to which bottom fishing vessels report, the European Commission states that all vessels working in the southwest Atlantic fishing under European Union (EU) member state flags are subject to monitoring including onboard observers, and the Argentinian fishing fleet operating within the High Seas of the southwest Atlantic is reported to use VMS.

1.4.1.3 Deep seabed mining-related closures

The International Seabed Authority (ISA) was established in 1994 and is the global body, created by the UN, responsible for the sustainable management of seabed mining activities in ABNJ, acting on behalf of all humankind. Through the designation of Areas of Particular Environmental Interest (APEIs) and Preservation Reference Zones (PRZs), the ISA has the capacity to close areas to seabed mining activities in order to protect different habitat types and ensure representative areas are left to compare with mined areas. At present, the only APEIs and PRZs that exist are all located in the Clarion-Clipperton Fracture Zone (CCZ) in the northeastern Pacific. Although these areas are already designated, they are currently under review by the ISA as more information is published questioning the efficacy of the network (Taboada *et al.*, 2018; McQuaid *et al.*, 2020).

1.4.2 National waters management framework

The 1981 Convention for Cooperation in the Protection, Management and Development of the Marine and Coastal Environment of the Atlantic Coast of the West, Central and Southern Africa Region (henceforth referred to as the Abidjan Convention) was adopted under the UN Environment Programme (UNEP) Regional Seas Programme; Contracting Parties from the South Atlantic are: Angola, Democratic Republic of Congo, Republic of Congo, Gabon, Namibia and South Africa. The Abidjan Convention extends only to the ocean areas of its Contracting Parties within national jurisdiction, and extended continental shelf claims. To date, the regulatory framework within the

Convention has been developed solely to prevent and address issues of marine pollution. However, in 2014, a Memorandum of Understanding (MoU) was signed within which the Contracting Parties of the Abidjan Convention "*aimed to give support to the development of a Marine Protected Areas Protocol*". Additionally, an MoU was signed in 2013 between the Convention for the Protection of the Marine Environment of the North-East Atlantic (the 'OSPAR Convention') and the Abidjan Convention, acknowledging the importance of cooperation between the Atlantic-bordering-States in both hemispheres in the protection of the marine environment. Therefore, although the Abidjan Convention is not directly responsible for the designation of any MPAs in national waters or ABNJ, the Convention demonstrates an openness by Contracting Parties towards the conservation and sustainable use of marine resources (Ribeiro, 2017).

In 2004, the CBD formed the Programme of Work on Protected Areas, which, for marine biodiversity, aims to identify and preserve high-quality representative selections of marine habitats through the establishment of a coherent network of MPAs (Secretariat of the Convention on Biological Diversity, 2004). This requirement has since been ratified into national law across many nations, for example, the Marine and Coastal Access Act (2009) in the UK. This Act, and synonymous Acts in other countries, allows for the creation of MPAs to conserve biodiversity within EEZs. This said, unlike other collections of states with bordering seas, such as Europe, there is no combined management plan for bordering EEZs in the South Atlantic. However, there are some examples of inter-governmental initiatives such as the Benguela Current Commission that involves Angola, Namibia and South Africa to promote human and ecosystem wellbeing. Additionally, transboundary agreements for fisheries do exist such as the joint management of the Namibian and South African hake (*Merluccius* spp.) fishery. With regards to MPAs, some bordering states have protected larger amounts of their EEZ than others, with South Africa currently leading the way having designated an additional 20 MPAs in 2019, increasing protection from 0.4% to 5% of their waters.

The UK's Blue Belt Programme was a four-year project that ran from 2016 and aimed to provide long-term protection to over 4million km^2 of marine environment within UKOT EEZs, delivered by CEFAS and the Marine Management Organisation (MMO). In the South Atlantic, the UKOT of Saint Helena, Ascension and Tristan da Cunha protected 1.2 million km^2 of ocean under the project, with bottom trawling banned across the entire extent of the marine protection network.

1.4.3 The future of South Atlantic management

Approximately 50% of the planet is in ABNJ, representing a great reservoir of biodiversity, and arguably one of the earth's last great wildernesses (Ramirez-Llodra *et al.*, 2011), but, as outlined above, there is currently no single mechanism by which to designate MPAs that prohibit activities by multiple sectors. In 2018, the ISA announced the development of a Regional Environmental Management Plan (REMP) for South Atlantic seamounts, the purpose of which is to provide pro-active management tools to support informed decision-making. Workshops to develop the South Atlantic REMP are expected to be held in 2021 or 2022.

Faced with the prospect of seabed mining (among other industries) extending its footprint into the deep sea within the next decade, in 2015, UNCLOS member states agreed to UNGA Resolution 69/262 which outlines the need for an amendment to

UNCLOS in the form of a new international legally binding instrument (ILBI). This ILBI will outline the legal framework to facilitate the conservation and sustainable use of marine biodiversity beyond national jurisdiction (BBNJ). The most recent draft text was released in November 2019, with Part III titled "*measures such as area-based management tools, including marine protected areas*". The structure of the legal framework that will support these designations in ABNJ is still unclear, as is how the new framework will interact with existing management in ABNJ (e.g. with RFMOs and the ISA). Nevertheless, provision for area-based management tools in the draft text suggests that cross-sectoral MPAs in ABNJ will become a reality in the coming years. The BBNJ negotiations have been ongoing since 2015 and are now in their latter stages. However, the process is likely to continue for some time due to both the slow progress made during the COVID-19 pandemic, and the lack of existing frameworks for governance in this field.

Owing to major blue growth programmes in countries surrounding the South Atlantic (namely Brazil and South Africa), a number of bordering states have developed an interest in deep-sea research. When combined with the fact that one of the key items to be addressed in the proposed BBNJ legal instrument is capacity building and technology transfer, and that the ISA has issued its first exploratory mining licence in the basin, it is no wonder that the South Atlantic has become a focal region of late. With negotiations on the adoption of an ILBI to protect BBNJ under way, the emphasis on scientists to suggest areas that may require protection is growing. At present, the primary problem within the field of deep-sea science is lack of data leading to poorly informed management decisions. However, if applied appropriately, novel modelling approaches may allow us to create more accurate maps of ecosystems in the vast expanses of deep sea that represent ABNJ.

1.5 Tools for marine spatial planning

Marine spatial planning (MSP) refers to the organisation of human activities on the oceans so as to manage the interactions between human users and the marine environment (Ehler *et al.*, 2019). MSP processes often seek to balance ecological, social, economic and political objectives and involve the collation of evidence on which to base decisions. Access to a wide range of evidence to shape decision-making processes is therefore important and evidence may come from many sources including indigenous and local knowledge, ecosystem service models and other mapping products (Lombard *et al.*, 2019).

Many countries have devised MSP frameworks from which to manage shallow areas within their EEZs, often evidenced by high-resolution data on species' and habitat distribution, and user activities. However, the technical and logistical challenges associated with collecting data from greater depths generally means that marine spatial plans for nations' deep sea are significantly less developed than those for shallow water ecosystems. This is even more so the case for ABNJ where lack of data and absence of a regulatory framework to facilitate cross-sectoral management combine to impede holistic MSP (Wright *et al.*, 2019).

The following sections outline two methods that could potentially be employed to help fill vast data gaps for the deep sea, consequently providing information to aid management decision-making. These are habitat suitability modelling (HSM) and broad-scale benthic habitat classification.

1.5.1 An introduction to habitat suitability modelling

A major challenge facing the implementation of UNGA Resolution 61/105 by RFMOs is the lack of distribution data for VMEs (Weaver *et al.*, 2011) due to the logistical difficulties and expense associated with surveying the deep sea. Lack of data, not only in deep-sea biology, has led to the use of predictive species modelling techniques to create maps of potential distribution of vulnerable species and ecosystems over a multitude of scales (Davies *et al.*, 2008; Embling *et al.*, 2010; Davies & Guinotte, 2011; Howell *et al.*, 2011, 2016; Yesson *et al.*, 2012; Ross & Howell, 2013; Ashford *et al.*, 2014; Anderson *et al.*, 2016; Lauria *et al.*, 2017). Habitat suitability modelling (HSM; also known as species distribution modelling/predictive habitat/species modelling) refers to the use of computer algorithms to predict the possible distribution of a species/habitat based on a mathematical model of the relationship between species/habitat occurrence and environmental drivers of their distribution.

1.5.1.1 Uses of habitat suitability modelling

Understanding the spatial distribution of species' and habitats is becoming increasingly important as humans begin to exploit environments that were previously inaccessible, such as the deep sea. A large benefit of HSM is that it allows the use of pre-existing global biogeographic databases, such as the Ocean Biodiversity Information System (OBIS) to create the presence-only data required for some HSM software and methods. The generation of presence/absence models of species and habitat distribution can provide baseline knowledge for regions that have not been recently visited. This can then serve to inform subsequent surveys, thus increasing the efficacy of data collection. HSMs can also predict over scales that cannot be easily surveyed due to logistics (e.g.

basin-wide/global), an advantage that is particularly relevant to management of deep-sea taxa as many fauna display cosmopolitan distributions.

The use of HSM to inform MSP is becoming more prevalent in the marine sector, although there are still relatively few examples in comparison with terrestrial applications (Marshall *et al.*, 2014). HSM can be used by managers to inform conservation strategies of both sessile and migratory organisms, and also to locate candidate areas for protection (Cañadas *et al.*, 2005; Embling *et al.*, 2010; Lambert *et al.*, 2017). HSM can also be used to assess pre-existing MPA networks to test ecological coherence; for example, Sundblad *et al.* (2011) used HSM to assess the efficacy of the *Natura 2000* MPA network in the Baltic Sea for juvenile fish, designated under the EU Habitats Directive. Similarly, models can be used to see what proportion of a species'/habitat's potential distribution is protected in order to determine progress towards area-based conservation goals; for example, Ross & Howell (2013) used HSM to assess the extent of current protection of listed deep-sea habitats (CWC reefs, deep-sea sponge aggregations and xenophyophore aggregations) in northeast Atlantic MPAs.

Within the literature there are few examples of HSM being used in environmental impact assessments (EIAs), with all examples so far terrestrial (Angelieri *et al.*, 2016; Carneiro *et al.*, 2016). However, some marine environmental consultancy firms do list HSM as a marine consultancy service (APEM, 2017). HSM can also be used to evaluate the risk associated with invasive species, and therefore can be valuable in helping produce management strategies to reduce the risk of biological invasions (Townsend Peterson, 2003; Thuiller *et al.*, 2005; Jiménez-Valverde *et al.*, 2011). Other fields in which HSM is being used include; evolutionary biology to study speciation (Kozak *et al.*, 2008); epidemiology to predict the spread of diseases (Townsend Peterson *et al.*, 2002), and climate change science to help understand how it may affect species and ecosystems in the near and far future using the characterization of species' bioclimatic envelope to inform the model (Pearson & Dawson, 2003). In the literature, there are few examples of HSM being used for marine species/ecosystems under climate change scenarios (Cheung *et al.*, 2009; Gormley *et al.*, 2013; Morato *et al.*, 2020).

1.5.1.2 Habitat suitability modelling methods

When modelling the distribution of species, there is a vast range in both the model choice, and the parameters selected, that can drastically alter the model outputs (Elith & Graham, 2009). Presence-only or presence-absence modelling does not require density/abundance data and methods can be classified based on the statistical approach that they take and their data requirements.

Popular methods of HSM include generalized additive models (GAMs, Hastie & Tibshirani, 1990) and generalized linear models (GLMs, McCullagh & Nelder, 1989), both of which are well-established in the HSM literature, and often outperform other methods of modelling (Guisan & Zimmermann, 2000; Anderson *et al.*, 2006; Wisz *et al.*, 2008). They work by allowing non-linear relationships between response and explanatory variables to be modelled by relaxing the linearity assumptions associated with general linear models (Wood, 2006). GLMs and GAMs can be used in HSM because they allow different response variable distributions to be modelled, including binomial, which is applicable to presence-absence data. However, another choice of model is MaxEnt (Phillips *et al.*, 2006), proving popular with scientists having performed well compared to more traditional environmental niche models (Pearson *et al.*, 2007; Wisz *et al.*, 2008; Elith & Graham, 2009; Tittensor *et al.*, 2009).

1.5.1.3 Maximum Entropy modelling (Phillips et al., 2006)

Maximum Entropy Modelling (MaxEnt) is a popular machine-learning niche model that requires presence-only data. This type of data, as opposed to presence-absence, is more readily available, partially due to the high costs attached to collecting presence-absence data, but also because of the vast stores of presence-only data that exist in biogeographic databases around the world (e.g. natural history museums). However, the spatial and temporal accuracy of historical presence data should be considered, as well as the potential impact that varying environmental conditions throughout time would have on the distribution of modelled species. MaxEnt works by finding the most uniform distribution (i.e. the distribution of maximum entropy) across the grid cells provided in the study area, whilst adhering to all of the constraints dictated by the environmental and occurrence data.

MaxEnt runs using presence-only data but pseudo-absence data can be used instead of background data to build the model, and to create the mean values on which maximum entropy is based; the decision between using MaxEnt's background data or pseudo-absence data depends on the nature of the occurrence data. There is an inherent bias within surveys, especially within deep-sea science, due to survey design limitations and the expense associated with surveying this ecosystem. A cell (commonly 30-arc second - the size of the global bathymetry 2014 dataset GEBCO) may represent a presence for one modelled species, but if unobserved, can represent a pseudo-absence for another target species. Pseudo-absence is often used instead of true absence data because it is virtually impossible to rule out the presence of a species in large grid cells in the deep sea due to equipment often having small fields of view and transects being single lines through grid cells. We can however say that presence is very unlikely, hence the use of pseudo-absence. The benefit of using pseudo-absence in this example would be that any bias in the sample dataset is accounted for in the model. It is imperative to note that the decision between using MaxEnt's assigned background data, or contributing pseudo-absence data into the model is immensely dependent upon the dataset in question, and no definite rules can be applied.

MaxEnt uses training and test data sets to run and validate the models respectively. Training data (usually 75% of the dataset) is fed into the algorithm in order for the model to predict possible occurrence locations. The test data (usually the remaining 25% of the data set) is used to validate the model by looking at whether the model has correctly predicted the presences of the real data. This process is repeated numerous times in order to determine confidence intervals, creating many values of model performance. The mean and standard deviations are extracted from these values, providing an insight into the consistency and accuracy of the model. There are many different ways of assessing model performance, with different metrics being more suited for different reasons. The most commonly used metric for evaluating performance of a HSM is the 'area under curve' (AUC). This is used when the model is non-binary, and therefore predicts likelihood rather than using a threshold. For threshold-dependent models, the most commonly used metrics are percent correctly classified (PCC), sensitivity and specificity (explained in detail in Chapter 4).

Global MaxEnt models

Examples of global models built in MaxEnt can be found readily in the literature, with some including predicted distributions of deep-sea fauna, namely large sessile protozoans called xenophyophores (Ashford *et al.*, 2014) and CWCs (Davies & Guinotte, 2011; Yesson *et al.*, 2012), both of which are VME-indicator taxa (FAO, 2009).

Davies & Guinotte (2011) and Yesson *et al.* (2012) modelled the predicted global distribution of framework-forming CWCs and octocorals respectively. The latter is cited in multiple papers due to its novel method of categorizing environmental variables. Selection of environmental variables is critical in modelling, as many techniques are adversely affected by incorporating too many variables, thus potentially causing overfitting of the model (Townsend Peterson *et al.*, 2007). Yesson *et al.* (2012) identified 32 original variables deemed potentially important in determining octocoral distribution. Based on the results of correlative analysis, the 32 variables were categorised in seven groups of similar nature: bathymetry, carbonate chemistry, hydrodynamics, productivity, oxygen, chemistry and temperature. A single variable from each of the groups was then selected based on correlative tests at coral presence localities for each model in order to represent a wide range of potentially important biological parameters but to reduce the potential for model overfitting. The practice of grouping environmental parameters is now well reported within the literature (e.g. Ashford *et al.*, 2014). For these global models, both studies used 30 arc-second grid cells (roughly 1 km at the equator).

Ashford *et al.* (2014) modelled the taxonomic superfamily, Xenophyophoroidea (Tendal, 1972) as well as two taxonomically stable xenophyophore species. The results showed a difference in the environmental requirements of the species *versus* class hierarchies.

Basin-wide models

Howell *et al.* (2016) used MaxEnt to model the distribution of two deep-sea sponge aggregation types: *Pheronema carpenteri* (Thomson, 1869) and ostur aggregations, in the North Atlantic. The study used the model to answer questions regarding the environmental drivers of sponge grounds, and their distribution between MPAs in EEZs and in ABNJ. As the presence data for *P. carpenteri* were derived from video data collected for Ross & Howell (2013) this is an example where the authors used pseudo-absence data to build the model to account for sample bias. Data layers in this study were also regridded to 30 arc-second grid cells.

Sub-basin-wide models

Models focusing on scales smaller than whole ocean basins include Ross *et al.* (2015) and Anderson *et al.* (2016). The former focused on three VMEs in the North East Atlantic: CWC reefs*, P. carpenteri* aggregations and *Syringammina fragilissima* Brady, 1883 aggregations. The model was used to assess the extent of the current protection of the chosen VMEs; an example of a direct link between modelling and management. Anderson *et al.* (2016) built models for four reef-forming CWC species on the Louisville seamount chain in the South Pacific and independently validated them, a practice that is not common because of the limited number of data points available for most deep-sea taxa. The study focused on the distribution of VME taxa and outlines the limitations of the use of broad-scale models in fisheries management.

1.5.1.4 Limitations of habitat suitability modelling

Despite the widespread use of HSMs in the literature, there is a far smaller portion dedicated to the limitations of these models. There are some examples of limitations being outlined when the available data are insufficient to build a model, thus model outputs are not representative of true species distributions (Stockwell & Townsend Peterson, 2002; Kadmon *et al.*, 2003; Wisz *et al.*, 2008), and when predictions based on the model are not scientifically robust (Elith & Leathwick, 2009; Saupe *et al.*, 2012).

HSM has the capacity to support MPA network design and site designation, specifically in the deep-sea where the high cost of data collection acts as a barrier to marine planning. Previously, VME distribution data has mainly been compiled from interactions with the fishing industry, resulting in a bias in the data towards popular fishing grounds. This is also the case with seamount complexes/prominent topographic features as scientific exploration tends to occur here due to cost limitations. Again, this creates another bias in the data towards these features compared to less topographically heterogeneous areas. These also tend to be areas where VMEs are already known to occur (Clark *et al.*, 2006), or where models have predicted them to be (e.g. Ross & Howell, 2013).

The number of presence records used to build the model is very important in terms of model reliability; the higher the number of presences, often the higher the accuracy of the model (Wisz *et al.*, 2008). Ashford *et al.* (2014) found that the individual species of xenophyophores modelled had more specific habitat requirements than the Xenophyophoroidea model also created in the same study. The authors hypothesized that this was partially due to the small number and clustered nature of the presence records for the individual species, meaning that the environmental conditions at the presence localities were over weighted, causing model overfitting. Another explanation for the low performance model outputs in this study is that an individual species would have more specific habitat requirements than a group of species due to its occupation of a smaller niche.

Anderson *et al.* (2016) tested their CWC habitat suitability model using a photo-identification field-validation technique, and found that the patterns of observed and predicted coral distribution were not highly correlated. The poor performance of the model in this study was attributed to a lack of recorded species absence data to inform the model. Other factors thought to exacerbate the poor performance were the low precision of global bathymetric models, and a lack of data on the substrate type and geomorphology of the study area at scales relevant to the modeled taxa. This highlights an issue with deep-sea HSM in terms of the frequent mismatch between data availability and data requirements. The deep sea has not been well mapped using multibeam, and many quantitative descriptors extrapolated from high-resolution multibeam bathymetry data are commonly used as environmental predictor variables for pre-existing VME models (Howell *et al.*, 2011; Yesson *et al.*, 2012; Ross *et al.*, 2015).

HSM can also be a useful tool when carrying out EIAs, however Carneiro *et al.* (2016) show that HSM can be inappropriate, dependent upon the data. Their study used data collected for an EIA in the Amazon Basin for frog populations. There is little known about these animals' distributions, and many are newly described; this is also true for many deep-sea animals. It showed how data on the distribution of the target frog species were insufficient to build a HSM, and concluded that in order for a model to be useful, a much greater sample area is required than was used (~200 km^2).

Although it is clear that HSM is potentially a very useful tool for future MSP, models predict fundamental niches due to their inability to predict biotic interactions (Pearson & Dawson, 2003); fundamental niches are the full geographic area that exhibit favourable environmental conditions for the target species. However, most species occupy the 'realised niche' which is narrower due to the forces acted upon it by inter-specific competition, thus meaning that models are likely to over-predict natural distributions (Davis *et al.*, 1998; Soberon & Townsend Peterson, 2005; Araújo & Guisan, 2006). This limitation plays a role when modelling VMEs as both CWCs and sponges have predators, for example sea spiders and starfish respectively. In addition to predatory pressures on taxa that form VMEs, the role of inter-specific competition for resources (e.g. space) is likely to play some role in the distribution of VMEs. This being said, in general, not enough is known regarding the biotic interactions to include them in a model, despite whether there is any capability to do so.

When used to investigate the impact of climate change on species distributions, a limitation of HSM is that they cannot predict evolutionary changes. Climate-induced range shifts involve relocation into newly suitable areas, but Davis & Shaw (2001) also demonstrated that it involves selection against phenotypes that may be poorly adapted to local conditions, thus causing rapid evolutionary change. This causes the fundamental niche of an organism to change over time meaning that the distribution predicted by the model may not be correct in the future.

1.5.2 An introduction to benthic habitat classifications

Where there are insufficient data to model species or assemblage distributions, an alternative approach can be employed to infer biological pattern from environmental variability. Benthic habitat classifications, henceforth referred to as habitat classifications unless otherwise stated, allow visualisation of the spatial variation in community structure. Habitat classifications, sometimes referred to as habitat maps, organise combinations of biological and/or environmental data into distinct classes (Strong *et al.*, 2019). These classes are assumed to support distinct biological assemblages and therefore the production of habitat classifications can support MSP (e.g. McQuaid *et al.*, 2020).

1.5.2.1 Habitat classification methods

Principally, there are two approaches to building habitat classifications: hierarchical and non-hierarchical. As the name suggests, hierarchical habitat classifications follow a decision tree structure where variables are ordered. Hierarchical classifications allow for the combined use of environmental and biological data, typically with decisions based on environmental data being nearer the top of a classification, and biological data being used to facilitate the latter tiers (*sensu* Howell, 2010). An example of this is the Marine Habitat Classification of Britain and Ireland. In the deep-sea section of the classification developed by Parry *et al.* (2015), there are five levels that allow users to hierarchically discriminate between different environments until 'biological community' is reached (Figure 1.7). Hierarchical classification systems are useful, although restricted to areas where there is a sufficient literature base so as to confidently assign ranks to variables.

Figure 1.7: Structure of the deep-sea section for the Marine Habitat Classification of Britain and Ireland. Figure and caption from Parry et al. (2015)*. Figure has been removed due to Copyright restrictions.*

In the absence of sufficient information to inform the ranking of variables, non-hierarchical methods can be used. There are numerous ways in which non-hierarchical classifications can be built that are either literature based where variables are selected through expert review (Evans *et al.*, 2015; McQuaid *et al.*, 2020), or purely statistical where all available environmental variables are offered (Verfaillie *et al.*, 2009). Both methods have been employed to characterise the benthic communities of deep-sea areas (Hogg *et al.*, 2016; McQuaid *et al.*, 2020).

Both hierarchical and non-hierarchical habitat classification methods require broad-scale environmental data to inform the models. Although certain drivers of spatial variation in benthic communities are likely to be somewhat regionally-specific (e.g. upwelling or oxygen-minimum zones), Howell (2010) outlined a hierarchical benthic classification system to aid in the implementation of MPAs in ABNJ in the northeast Atlantic. Key variables identified were: biogeography, depth, substrate and biology.

1.5.2.2 Uses of habitat classifications

Robinson & Levings (1995) summarise the primary uses of habitat classifications as: (1) describe habitats that have similar physical and biophysical attributes; (2) creates inventories and maps of biodiversity; (3) provide structure; (4) standardize concepts and terminology used to describe habitats; (5) provide linkages between environmental maps and biophysical survey data; (6) aid in decisions about resource management and conservation; (7) assess influence of human disturbance of natural systems, and; (8) describe the distributions and extent of habitats, communities and species.

The sixth reason refers to the use of habitat classifications in MSP. Depending on the input data layers, habitat classifications can provide continuous habitat maps that aid in the creation of marine spatial plans by providing the baseline ecological data (e.g. Dove *et al.*, 2020; Zajac *et al.*, 2020). In the deep sea, habitat classifications have been used to inform MSP in EEZs, for example, the South African National Biodiversity Assessment Habitat Classification developed by Sink *et al*. (2019) was used to inform the latest update to South Africa's MPA network. Whilst holistic, cross-sectoral MSP in ABNJ is yet to become a reality, habitat classifications can be used to inform management plans for individual sectors. An example is a study by McQuaid *et al.* (2020) in which a habitat classification for the CCZ in was developed and used to test the habitat representativity of the ISA's APEI network in the region. Habitat classifications can also be retrospectively applied to underpin the conservation designations. This is particularly true for deep-sea and/or very large MPAs where continuous, biologically-derived habitat maps are unrealistic (Hogg *et al.*, 2018).

1.5.2.3 Limitations of habitat classifications

Although clearly a potentially useful tool in MSP for deep-sea areas in the future, habitat classifications do have some limitations, particularly associated with the input data. As with all models, the output is only as accurate as the data used to build it. To obtain continuous layers of environmental variables such as depth, some level of interpolation is required. In areas that have undergone little scientific exploration in the past (e.g. the South Atlantic), the interpolation required is stronger due to fewer true observations. Therefore, in data-poor areas, the data that are available as continuous layers are often of poorer quality than equivalent datasets in better explored regions. Continuous data layers are also typically only available at much coarser resolution than data used in, for example, fine-scale HSM. Again, this is linked to the fact that data are often interpolated from remote-sensing (e.g. GEBCO bathymetric grids). The resolution of the input data is the true resolution of the output; therefore resolution of habitat classifications is often in the scale tens of kilometres as opposed to metres. However, this may not be an issue if the habitat classification is to be used in MSP because management, particularly over large areas of the deep sea, is unlikely to be implemented in smaller spatial units than 10 km regardless.

Depending on the method used, there is often an element of subjectivity to habitat classifications. This is arguably truest for hierarchical classification where authors have to decide the rank of particular variables. In non-statistical, non-hierarchical classification systems, variable selection is still based on literature reviews and thus again is open to scrutiny. This means that the habitat maps produced by classifications can change substantially based on the certain human-selected properties (Strong *et al.*, 2019).

Finally, a limitation common to all modelling techniques when applied to deep-water ecosystems is the lack of validation data. This is a crucial step when determining whether modelled outputs, either from HSM or habitat classifications, are biologically relevant.

1.6 Thesis aims and outline

Within the limited literature available on the subject, there is strong evidence to suggest that VMEs and VME-indicator taxa are widespread in the South Atlantic (e.g. Pires, 2007; Bergstad *et al.*, 2019a). Although multiple areas of likely VME presence have been closed to bottom fishing in the southeast Atlantic by SEAFO, the southwest Atlantic remains a loosely regulated area, therefore likely putting areas where VMEs are present at risk.

The designation of MPAs in ABNJ is not yet possible, but processes identifying areas for protection have been undertaken though initiatives such as the CBD's EBSA process. In order for protected area networks to be fit for purpose and appropriately positioned, the decision-making processes behind such allocations need to be scientifically-robust and based on the best available data. Historic biases in sampling of the deep ocean mean that whilst the current baseline data in certain ocean areas is sufficient, there are vast data gaps for many areas of the world's oceans including the South Atlantic (Ho*well et al*., 2020b).

HSMs are increasingly becoming more important in multiple disciplines within marine ecology and conservation, including within the deep sea. HSM does have its limitations, and acknowledging them is important when considering their application in management strategies. Nevertheless, HSM has vastly improved since its establishment, and its application is now expanding into marine ecosystems. Here, HSMs have the potential to fill vast data gaps and so support environmental management efforts. If applied in novel ways, HSM could stand to help us gain a better insight into the ecology of deep-sea organisms by offering 'prior knowledge' on which to better direct field survey.

The overall aims of this thesis are to improve our understanding of the spatial distribution of benthic communities of the South Atlantic, particularly those found on seamounts and oceanic islands, and to develop tools to inform marine spatial planning in data-poor areas. Aims specific to each chapter are outlined in the introductions.

The first two data chapters of this thesis aim to characterise the diversity and community structure of seamount benthic communities in the South Atlantic. This is carried out using data collected during five separate cruises to the UK Overseas Territory of Saint Helena, Ascension and Tristan da Cunha, spanning 32 degrees of latitude. Chapter 2 seeks to determine whether seamount benthic communities adhere to previously described diversity gradients relating to depth and latitude, as well as identifying key environmental drivers of diversity at the ocean-basin scale. Using the same data plus additional transects, Chapter 3 describes the benthic communities (including VMEs) and how their structure changes across the latitudinal gradient of the basin, also identifying environmental parameters driving this.

The latter two data chapters are more experimental in their nature, both seeking to develop and test new tools to inform marine spatial planning at the basin scale. Chapter 4 tests whether a model calibrated in a data-rich region can be successfully transferred to a data-poor region to provide high-resolution maps for *D. pertusum* reef. The distribution data for this VME from Chapter 3 is used to independently validate the transferred model. This chapter explores how the current SEAFO fisheries closures aid in the protection of this VME and informs discussions on marine spatial planning at very fine scales. Chapter 5 uses low-resolution, broad-scale environmental data layers to build a top-down, global benthic habitat classification, which is compared with the fine-scale outputs from Chapter 4. This is then used to test the habitat representativity of the recently established UKOT MPA network in the South Atlantic. The advantages of this methodology are discussed in the context of basin scale marine spatial planning in data-poor areas where too few biological data exist to build reliable habitat classifications.

For all chapters, findings are individually discussed is the discussion sections. Chapter 6, the general discussion, summarises the key results of each chapter. The ecological findings of chapters 2 and 3 are contextualised using other studies. The findings of all chapters are discussed in the context of advancing baseline knowledge of South Atlantic ecology, and contribution to sustainable use of the oceans. General limitations and areas identified as requiring further research are recommended.

CHAPTER 2: DEPTH AND LATITUDINAL GRADIENTS OF DIVERSITY IN SEAMOUNT BENTHIC COMMUNITIES

2.1 Abstract

Latitudinal and bathymetric species diversity gradients in the deep sea have been identified, but studies have rarely considered these gradients across hard substrate habitats, such as seamount and oceanic island margins. This study aims to identify whether the current understanding of latitudinal and bathymetric gradients in α-diversity (species richness) apply to seamount ecosystems, as well as ascertaining whether identifiable trends were present in seamount β-diversity along a bathymetric gradient. Images from 39 transects, collected between 250 m and 950 m, were used to characterise species richness from within the Exclusive Economic Zones of Ascension Island, Saint Helena, and Tristan da Cunha, spanning 8°S to 40°S in the South Atlantic. A general linear model was subsequently applied to test possible environmental drivers of α-diversity across latitudinal and bathymetric ranges. Regression models were employed to investigate the β-diversity gradient, and species turnover with depth. Surface primary productivity and substrate hardness both had significant positive effects on species richness, and there was significantly higher species richness at temperate latitudes. No significant relationship between species richness and depth was detected, but there was a significant species turnover with depth. These results suggest seamounts and oceanic islands do not conform to established depth-diversity relationships within the depth range studied. However, despite their isolation and small sizes, seamounts and oceanic islands in the South Atlantic do appear to follow latitudinal patterns of deep-sea species richness established for specific taxonomic groups in different ecosystems.

2.2 Introduction

Latitudinal Diversity Gradients (LDGs) are one of the most well-researched natural patterns in the world but, despite this, the driving mechanisms are still unclear (Pianka, 1966; Rohde, 1992; Gaston & Spicer, 2004). In terrestrial systems, most taxa including trees, mammals and reptiles display a parabolic relationship whereby species richness is greatest in the tropics, and decreases poleward (Begon *et al.*, 2006). Similarly, in coastal marine ecosystems, LDGs are often parabolic for taxa such as molluscs and fish (Rohde, 1992; Clarke & Crame, 1997; Roy *et al.*, 1998), although some studies have shown that not all taxa adhere to this relationship (Kendall & Aschan, 1993).

The deep sea represents a third system where LDGs have been considered, but at present, there is no single consensus on the patterns and drivers of LDGs in the deep sea. Some studies show a poleward decline in diversity/richness that is comparable with terrestrial and shallow water ecosystems (Rex *et al.*, 1993, 2000; Culver & Buzas, 2000; Hillebrand, 2004), some show a poleward increase (Tietjen, 1984; Lambshead *et al.*, 2000), and some show a unimodal relationship per hemisphere with highest diversity/richness falling somewhere in the temperate latitudes (Rosa *et al.*, 2008; Woolley *et al.*, 2016). Explanation of these trends considers both evolutionary scale processes and present ecological conditions. The former refers to patterns driven by environmental and physical parameters over geological timescales. For example, the Norwegian Basin has been shown to have a depressed modern-day diversity in multiple taxa (Rex *et al.*, 1993; Culver & Buzas, 2000). Explanations for this include glaciation during the late Quaternary Period meaning there has been insufficient time for replenishment; and sediment flows into the basin 6,000-8,000 years ago causing local extinctions (Rex *et al.*, 1997). Historical ecology is often merged with biogeography to explain inter-regional differences in diversity and richness. For example, the South Atlantic is hypothesised as being more speciose than the North Atlantic (Culver & Buzas, 2000; Gage, 2004) due to its continuity with two other oceans (the Indian and Pacific), as well as the fact that it was less impacted by glaciation during the Quaternary Period (Wilson, 1998).

Modern ecological explanations of LDGs refer to how the environmental parameters of the present attempt to explain observed patterns. The most notable environmental parameter mentioned in almost all deep-sea LDG studies is productivity, or a linked parameter such as particulate organic carbon (POC) flux (Rex *et al.*, 1993, 2000; Culver & Buzas, 2000; Lambshead *et al.*, 2000, 2002; Gage, 2004; Smith *et al.*, 2008; Rosa *et al.*, 2008; Corliss *et al.*, 2009; Yasuhara *et al.*, 2009; Bodil *et al.*, 2011; Tittensor *et al.*, 2011; McClain *et al.*, 2012). Net primary production, occurring in the surface waters, is driven by the photosynthesis of phytoplankton, made possible by the input of nutrients and solar energy. Organic matter, in the form of decaying phytoplankton and faecal pellets, sinks through the water column and, although large amounts are remineralised by bacteria, a small proportion (ca. 0.5-2%) reaches abyssal depths (Smith *et al.*, 2008). The POC flux that reaches the deep seafloor acts as the main or only food source for many deep-sea ecosystems and has been modelled for the world's oceans, often showing peaks in temperate latitudes (Lutz *et al.*, 2007). Diversity driven by food supply is consistent with the species-energy hypothesis (Hutchinson, 1959), which suggests that the amount of available energy sets limits to the richness of the system.

Within the deep sea, bathymetric diversity gradients (BDGs) have also attracted significant research attention (Levin *et al.*, 2001; Howell *et al.*, 2002; Olabarria, 2005, 2006; Rex *et al.*, 2005; Danovaro *et al.*, 2008). The deep sea, here defined as occurring below 200 m, cannot be considered a uniform environment due to the vast changes in abiotic characteristics, such as pressure and temperature, which occur over the depth gradient. This change in the physical environment with depth is reflected in observed changes in diversity, with many studies across various taxa reporting peak diversity between 200 m and 4,000 m attributed to comparatively higher energy availability (than deeper waters) and greater environmental stability (than shallower waters) generating more ecological and evolutionary opportunities (Rex, 1973; Gage *et al.*, 2000; Brandt *et al.*, 2004; Rex *et al.*, 2006). However, similar to investigations into LDGs, results can be mixed, with a number of studies not recognising any bathymetric diversity gradient (Bodil *et al.*, 2011), or a multimodal gradient. Allen & Sanders (1996) and later Olabarria (2005) both reported that bivalve diversity increased with depth in the northeast Atlantic. Contrary to this, other studies have identified decreasing diversity with depth in taxa such as foraminiferans (Lagoe, 1976) and isopods (Svavarsson *et al.*, 1990). There can also be variability in BDGs within individual taxa, between ocean basins such as in gastropods where positive, negative and unimodal relationships between diversity and depth have been observed across 10 basins (Stuart & Rex, 2009).

Much less is known about deep-sea β-diversity, the variation in species diversity between two habitats or regions comprising one or a combination of species loss/gain (nestedness); or species replacement (turnover). Along bathymetric gradients, β-diversity trends have largely been interpreted as attributable to turnover (Carney, 2005; McClain & Hardy, 2010; Victorero *et al.*, 2018), possibly driven by environmental parameters correlated with depth (e.g. temperature). An example of where nestedness may dominate the β-diversity trend is in regions where diversity is depressed due to food scarcity e.g. in the abyss (Wagstaff *et al.*, 2014). In these areas, Rex *et al.* (2005) showed that abyssal communities of macrofaunal molluscs were actually nested subsets of lower bathyal communities because the abyssal populations were present in such low densities that they are not reproductively viable, and therefore act purely as a sink for bathyal populations. In regions where food supply is not limited in the abyss, turnover dominates, and is reflected in the presence of abyssal endemics (Brault *et al.*, 2013).

The vast majority of studies looking at both latitudinal and bathymetric diversity gradients in the deep sea have focused on sampling infaunal communities in soft-sediment areas such as abyssal plains or continental slopes using equipment not suitable for collecting data on hard substrates (Rex *et al.*, 1993, 2000; Culver & Buzas, 2000; Lambshead *et al.*, 2002). Multi-taxon studies of both diversity gradients from hard-bottom or more complex habitat types, such as seamounts, are rare (McClain *et al.*, 2010; McClain & Lundsten, 2015; Victorero *et al.*, 2018).

Seamounts are commonly defined as large topographic features that rise at least 1,000 m above the surrounding seafloor and are distributed throughout all the world's ocean basins (Rogers, 1994). They are associated with higher levels of production due to the entrapment of zooplankton over the summit during diurnal migration, and the upwelling of nutrient-rich, deeper water facilitating primary production (Clark *et al.*, 2010). The effects of increased primary production are also reflected further up the trophic chain with seamounts often being active foraging grounds for pelagic taxa, sometimes referred to as 'hotspots' when surrounded by comparatively oligotrophic open ocean (Hosegood *et al.*, 2019). Some seamounts break the surface forming oceanic islands.

Although not fully understood, the hydrodynamic regimes encircling both seamounts and oceanic islands are thought to be complex and energetic (Levin & Thomas, 1989; Roden, 1991; Chivers *et al.*, 2013; Turnewitsch *et al.*, 2013; Vlasenko *et al.*, 2018; Bell *et al.*, 2021), with enhanced currents that are associated with increased food supply and exposed hard substrate. Seamounts are topographically complex and can have high variability in substrate types, including rocky walls and ledges, and biogenic reef communities comprising sponges and corals (Rogers, 1994; Auster *et al.*, 2005; Clark *et al.*, 2010; Davies *et al.*, 2015), contrasting with the soft-sediment habitats that often surround their base. Although not heavily documented, changes in assemblage structure along bathymetric gradients on individual seamounts have been described (McClain *et al.*, 2010; Davies *et al.*, 2015; Morgan *et al.*, 2019). McClain *et al.* (2010) did not observe a gradient in α-diversity along a bathymetric gradient on a seamount in the northeast Pacific Ocean. However, they did record substantial change in assemblage structure with depth, suggesting that high β-diversity can ultimately be responsible for the increased total biodiversity of seamounts. Also focusing on a single seamount, Morgan *et al.* (2019) recorded increasing β-diversity with depth between 200 and 700 m, again attributing this to high species turnover with depth. However, due to the small number of studies focusing on the diversity patterns on seamounts, it is difficult to substantiate any broad generalisations of their diversity-depth relationship (Clark *et al.*, 2010; McClain *et al.*, 2010; Davies *et al.*, 2015). The limited sampling of seamounts, combined with the fact that they provide hard substrate in an otherwise relatively soft substrate dominated deep ocean, means these features may subvert our current understanding of bathymetric or latitudinal diversity gradients. Knowledge on whether seamount ecosystems conform to the current understanding of bathymetric and latitudinal diversity gradients will facilitate more targeted protection in the future, as well as contribute to our understanding of regional and global deep-sea diversity patterns.

The aims of this chapter are to investigate changes in seamount diversity across depth and latitude, specifically to answer the following questions: (1) are latitudinal and bathymetric gradients in α-diversity present in ecosystems on South Atlantic seamounts? and; (2) are identifiable trends present in seamount β-diversity along a bathymetric gradient?

2.3 Methods

2.3.1 Study area

Saint Helena, Ascension and Tristan da Cunha (henceforth referred to as St Helena, Ascension and Tristan) are governed as a single UK Overseas Territory (UKOT) in the South Atlantic Ocean (Figure 2.1). These oceanic islands have steep sides, descending into deep water very close to shore. Ascension forms part of the mid-Atlantic Ridge, St Helena forms part of the Guinea seamount chain, and both are located within the tropics, whereas Tristan is temperate and found at the most south westerly point of the Walvis Ridge. Over 90% of each of their exclusive economic zones (EEZs) comprise waters deeper than 1,000 m.

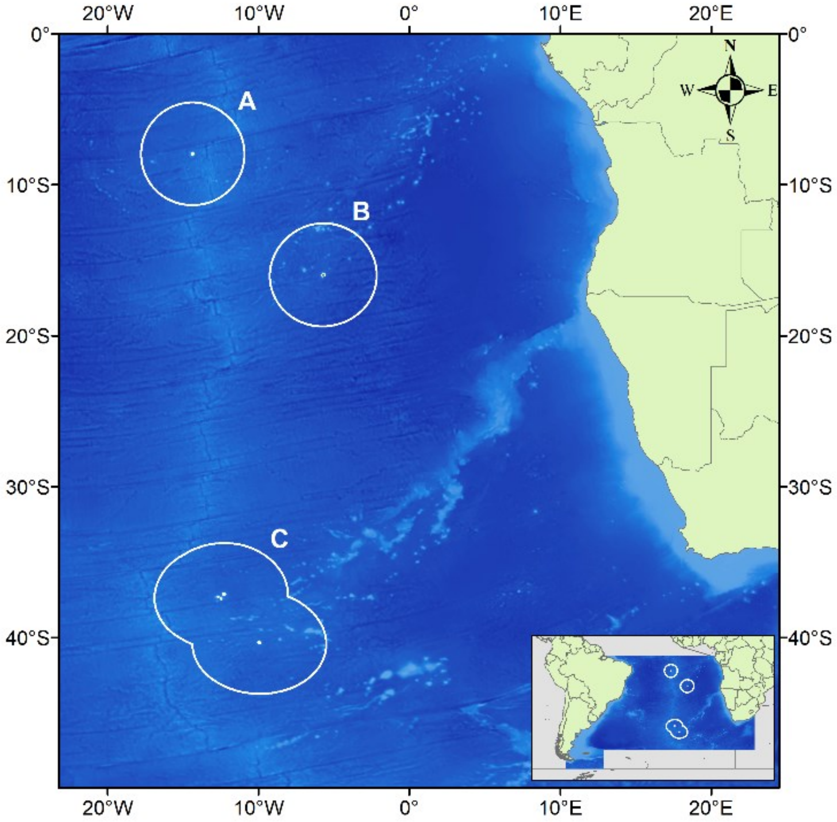

Figure 2.1: The Southeast Atlantic Ocean. The Exclusive Economic Zones of Ascension Island (A), Saint Helena (B) and Tristan da Cunha (C) are drawn in white and correspond to Figure 2.2A-C. Underlying bathymetry is from the General Bathymetric Chart of the Oceans (GEBCO_2014 Grid, version 20150318). Map drawn in WGS84.

2.3.2 Sampling methods

A bespoke camera lander (Shallow Underwater Camera System, SUCS, Appendix A.1) was used to collect image data in cluster transects (n = 39; Figure 2.2A-C) during the 2015 (Barnes *et al.*, 2015), 2017 (Barnes *et al.*, 2019) and 2018 (Morley *et al.*, 2018) cruises of the RRS *James Clark Ross*, and a 2019 cruise on the RRS *Discovery* (Whomersley *et al.*, 2019). The SUCS tripod design allows the lander to settle perpendicular to the seafloor and captures high-resolution images (approximately 20 in each cluster transect) of 0.14 m^2 area. An Ultra Short Base Line beacon mounted on the camera lander allowed for accurate Global Positioning System positions to be obtained. There are 13 transects from each UKOT EEZ (henceforth referred to as territories), within which three seamounts/islands (henceforth referred to as sites) were sampled per territory. A breakdown of the sampling structure is presented in Table 2.1 along with sampled depth ranges.

Table 2.1: Sampling structure indicating the number sites per territory and the depth range sampled at each.

Territory	Site	Depth range sampled (m)
Ascension Island	Ascension island	299 – 824
	Grattan seamount	487 – 854
	Harris-Stewart seamount	590 – 793
Saint Helena	Bonaparte seamount	433 – 734
	Cardno/Southern Cross seamount complex	278 – 950
	Saint Helena island	597 – 860
Tristan da Cunha	Crawford seamount	434 – 624
	Yakhont seamount	303 – 836
	RSA seamount	374 – 703

Multibeam seabed mapping using Kongsberg EM122 and EM710 multibeam echosounders allowed for characterisation of the sites prior to equipment deployments to ensure suitability for the SUCS. Temperature, salinity and other environmental profiles were recorded using a CTD at each transect.

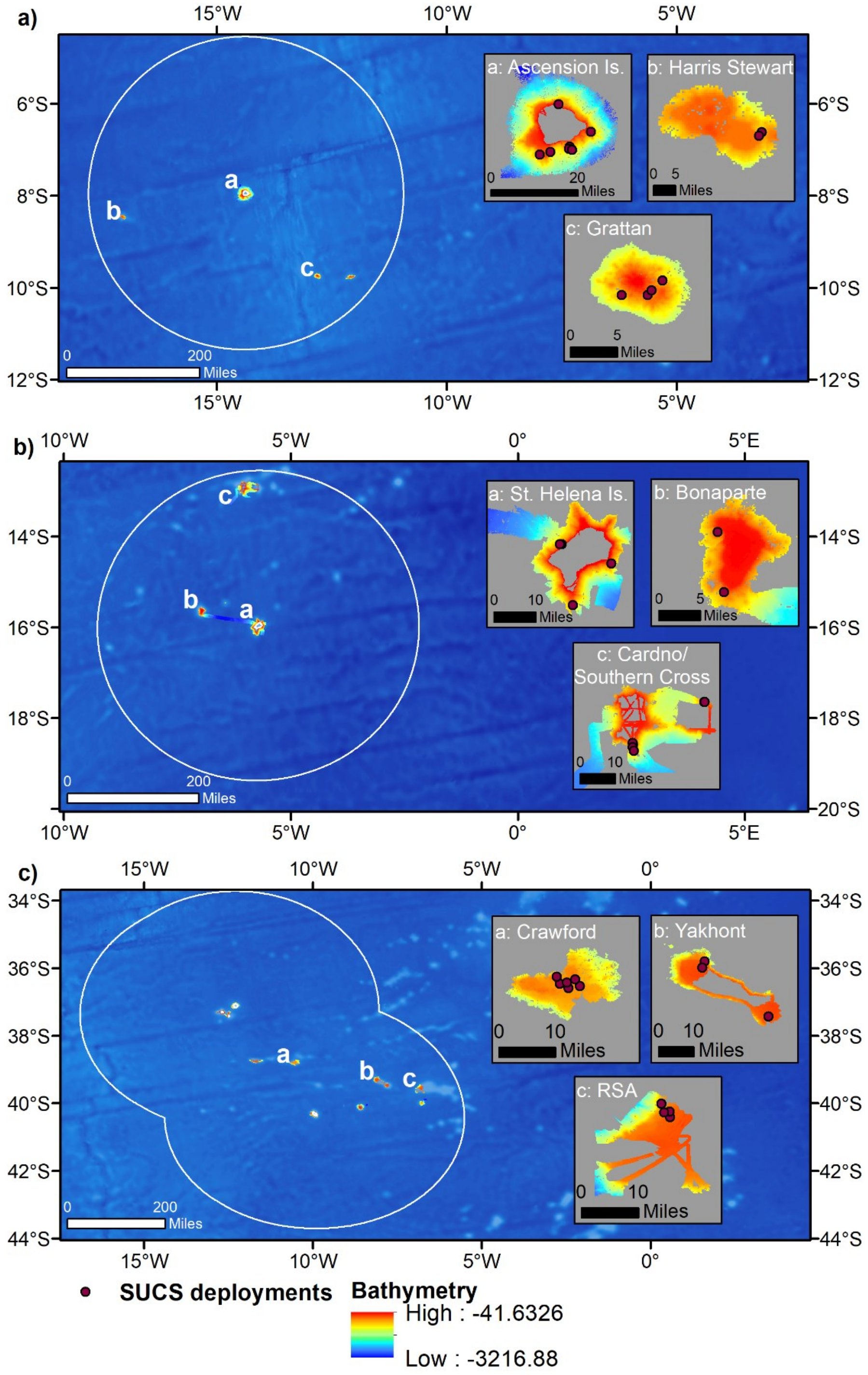

Figure 2.2A-C: Shallow Underwater Camera Systems (SUCS) deployments plotted on high-resolution (25 m) multibeam bathymetry across three sites within the A - Ascension Island EEZ, B – St Helena EEZ, C – Tristan da Cunha EEZ. Underlying bathymetry from General Bathymetric Chart of the Oceans (GEBCO_2014 Grid, version 20150318).

2.3.3 Image analysis

741 images were quantitatively analysed using ImageJ (Schneider *et al.*, 2012) or subsequently BIIGLE 2.0 (Langenkämper *et al.*, 2017) which facilitated comparable annotations but was found to be more efficient and fit for purpose. All organisms identified as distinct morphotaxa were assigned an Operational Taxonomic Unit (OTU). OTUs were identified to the highest taxonomic resolution possible. All individuals were counted, with encrusting and reef-forming species recorded only as percentage cover. For these OTUs values used were either 1% (as most were only present in very small abundances), or between 10% and 100% in 10% increments.

Primary and secondary substrate types were recorded using the following categories based on Wentworth (1922): bedrock, reef framework, live reef, cobbles, coral rubble, pebbles, coral gravel, gravel and sand (Appendix A.2). Images were also assigned a substrate hardness score based on the types and proportions of each substrate observed on a six point scale where 1 would equate to 100% sand and 6 to 100% bedrock. For example, if 50% of the image comprised sand and 50% comprised rock, the hardness score would be 3 to weight each appropriately.

2.3.4 Environmental data preparation

Multibeam files were gridded at 25 m cell size in QPS Qimera and projected into Goode Homolosine Ocean (an equal-area projection) in ArcGIS v10.7. The Benthic Terrain Modeller plugin (Walbridge *et al.*, 2018) was used to derive rugosity, slope, fine-scale bathymetry position index (FBPI), broad-scale bathymetry position index (BBPI) and curvature from the bathymetry. Inner and outer radii for BBPI and FBPI were 8 and 40 and 1 and 8, respectively, facilitating identification of megahabitats >1 km (e.g. banks and plateaus) and mesohabitats 200 m - 1 km (e.g. gulleys and reefs *sensu* Greene *et al.*, 1999). Using the 'mgcv' package (Wood, 2011) in R (R Core Team, 2019) a Generalised Additive Model (GAM) was used to create a bottom temperature layer for each territory from CTD casts undertaken during the same cruises, together with archived CTD casts in the British Oceanographic Data Centre database, containing data supplied by Natural Environment Research Council. Details of the GAMs for each territory are supplied in Appendix A.3. Depth, latitude and longitude were tested individually and in all possible combinations as predictors of temperature. Temperature records were partitioned for each territory at an 80/20% training/test split, and the test dataset used to validate the modelled predictions. For all three territories, depth was selected as the only predictor of temperature, and the Pearson's correlation coefficient between the *in-situ* test observations and the predictions was 0.99 (2 d.p.), suggesting predictions were strongly in line with recorded temperatures.

POC flux to depth values at a 5 arcmin resolution (approximately 9.2 km at the equator) derived from (Lutz *et al.*, 2007) were resampled and re-projected to 25 m resolution in Goode Homolosine Ocean. Mean surface primary productivity data were downloaded from Bio-Oracle (Assis *et al.*, 2018), and also resampled and re-projected from 5 arcmin to 25 m. Resampling does not alter the resolution of the underlying data, it only splits cells into a gradient of smaller cells to allow for raster stacking when mapping.

2.3.5 Statistical analysis

To confirm whether depth and substrate had been sampled evenly across territories, parametric statistics were employed using the 'car' package (Fox & Weisberg, 2019) in

R. Both variables were normally distributed and homogenous in terms of variance, and therefore a one-way Analysis of Variance (ANOVA) was calculated for each variable to determine if there were significant differences in transect depths and substrate hardness between territories. A Pearson's correlation test was used to determine if there was a significant relationship between depth and substrate hardness. There was no significant difference in the substrate hardness ($F_{(2, 36)} = 2.52$, $p > 0.05$) nor depths sampled ($F_{Tu} = 0.84$, $p > 0.05$) within each territory and no correlation (-0.16, $p > 0.05$) between depth and substrate hardness (Appendix B.1). This confirmed that the data from each territory were comparable, allowing for investigations into the effects of depth and latitude on α-diversity. A one-way ANOVA and a Tukey's Honest Significant Difference (HSD) post-hoc test were run on species richness to assess significant differences between territories and identify the strength of the differences, respectively.

To further explore possible drivers of α-diversity trends, a general linear model was constructed in R. Prior to building, all variables were investigated for correlation. Correlates with coefficients $\geq \pm 0.7$ were subject to further testing with GAMs, resulting in only one correlate being used (Appendix B.2). Consequently, the general linear model tested the following variables: surface primary productivity, temperature, POC flux to depth, substrate hardness, BBPI, FBPI, slope, curvature and rugosity. Hereafter, surface primary productivity and temperature are considered as proxies for latitude and depth, respectively. The choice to undertake the analysis using surface primary productivity and temperature is based on the understanding that these are more ecologically and biologically relevant than latitude and depth, and also allow for better contextualisation in the wider literature.

β-diversity across the bathymetric range was investigated using mantel tests and beta regression models from the ‘betareg’ package (Cribari-Neto & Zeileis, 2010) in R . The data were subset to create three separate datasets, one for each territory. Using the ‘vegan’ package (Oksanen *et al.*, 2019), pairwise Jaccard dissimilarity (d_{ij}) matrices (on species abundance data) and Euclidean distance dissimilarity matrices (i.e. absolute difference in depth) were constructed for each territory. Species turnover along the depth gradient for each territory was measured by plotting pairwise Jaccard similarity ($s_{ij} = 1 - d_{ij}$) against pairwise absolute difference in depth. For each of these, a distance-decay model was fitted to the points using a beta regression model. Although beta regression models are intended for use when the response variable, y, is $0 < y < 1$, when using the ‘betareg’ package, a minor transformation is required. This was following Smithson & Verkuilen (2006),

$$\tilde{y} = \frac{y \times (n-1) + 0.5}{n}$$

where n = sample size. One pairwise comparison at St Helena was removed as two transects that were spaced close together and so were not considered to be independent. Although exponential models are often employed to describe distance-decay (Millar *et al.*, 2011), in this case, beta regression models were more appropriate due to the small sample sizes within this dataset. The y-axis intercept (x100) of each model is interpretable as the expected percentage similarity between two transects at the same depth. Mantel tests were carried out on the Jaccard dissimilarity and Euclidean distance dissimilarity matrices to further characterise the relationship between depth and biological dissimilarity. The y-axis intercepts, slope values and mantel correlations were then compared across the territories as per Anderson *et al.* (2013).

2.4 Results

Mean species richness was significantly different between territories (ANOVA: $F_{(2, 36)} = 31.95$, $p < 0.01$; Figure 2.3). There were significant differences between Tristan and Ascension, and Tristan and St Helena (Tukey's HSD, both $p < 0.01$) but Ascension and St Helena had similar species richness (Tukey's HSD, $p > 0.05$).

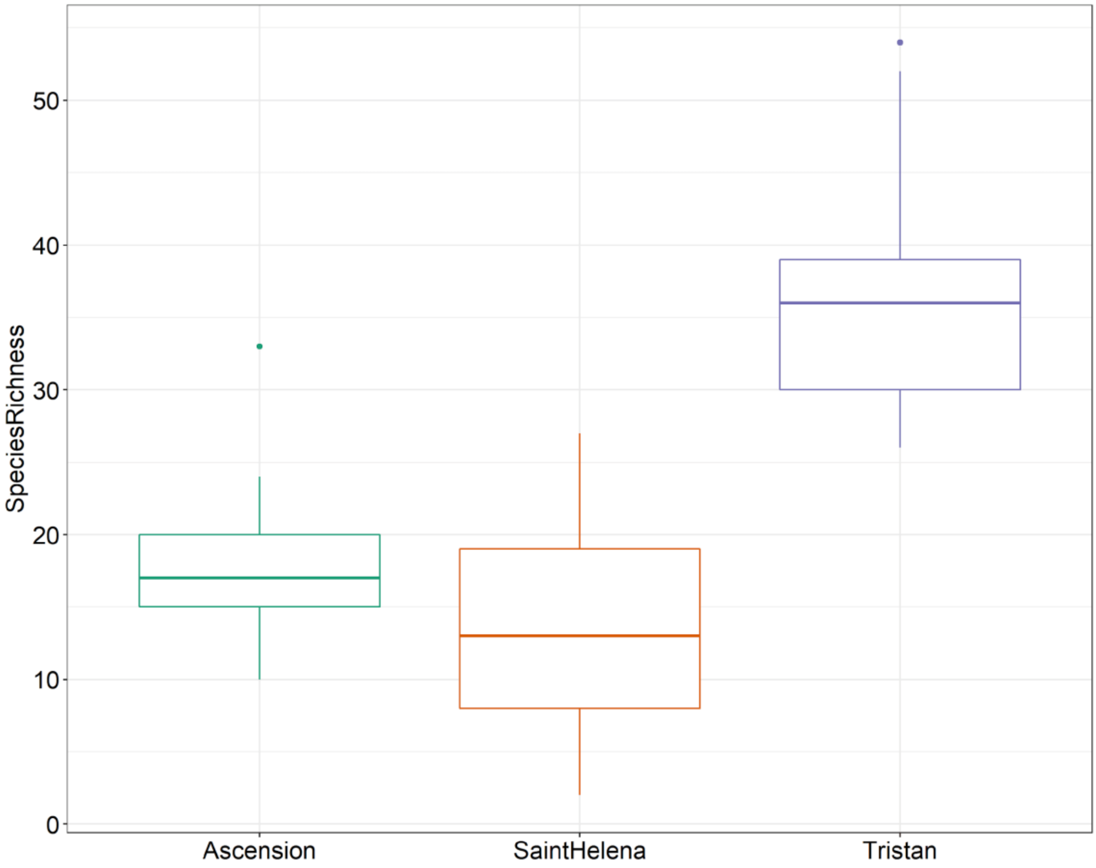

Figure 2.3: Mean species richness for each South Atlantic UK Overseas Territory. An ANOVA revealed significant differences (p < 0.01) between Tristan and the other two territories. Dots above the boxplots for Ascension and Tristan indicate an outlier transect.

Only surface primary productivity (a proxy for latitude) and substrate hardness were identified as significant predictors of species richness, both having positive effects (Table 2.2). However, as hardness did not vary significantly between territories, primary productivity seems the most likely driver of the higher species richness at Tristan. Temperature (a proxy for depth), was non-significant, suggesting neither play an important role in shaping species richness in this dataset; replacing temperature with depth in the linear model yielded the same non-significant results. Data are also presented three-dimensionally in Figure 2.4, supporting the lack of a significant relationship between depth and species richness for all territories.

Table 2.2: Metrics for the linear model run (with species richness as the response variable) for seamounts in the South Atlantic. Values for significant predictors of species richness are displayed in bold.

	Estimate	Std. Error	t value	p-value
Intercept	-11.543	8.333	-1.385	0.177
Surface primary productivity	**4.449×10^{3}**	**6.519×10^{2}**	**6.824**	**<0.001**
Substrate hardness	**3.680**	**1.107**	**3.324**	**<0.01**
Temperature	1.530	0.894	1.711	0.098
POC flux to depth	-5.856×10^{-1}	3.351×10^{-1}	-1.748	0.0911
Rugosity	1.740	2.347	0.741	0.46447
Slope	1.282×10^{-1}	1.079×10^{-1}	1.188	0.24429
BBPI	-2.929×10^{-2}	2.435×10^{-2}	-1.203	0.33127
FBPI	1.711×10^{-1}	1.723×10^{-1}	0.993	0.23888
Curvature	6.507×10^{-1}	1.302	0.500	0.62110

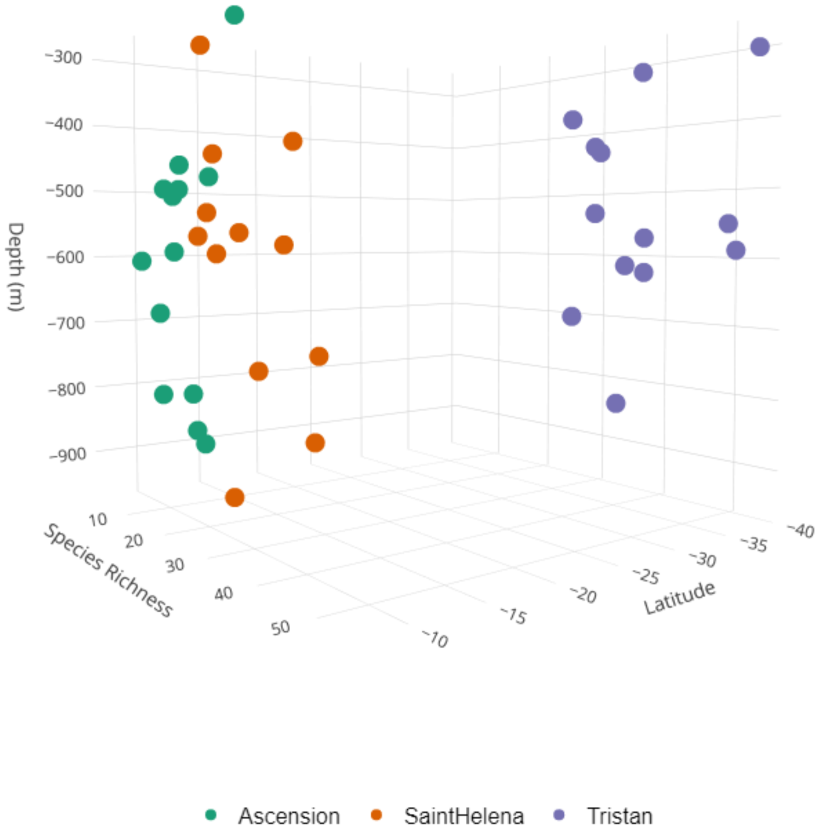

Figure 2.4: Three-dimensional plot of depth, species richness and latitude colour coded by UK Overseas Territory.

Fitted beta regression models for all three territories are shown in Figure 2.5 with details in Table 2.3. All three models identified absolute difference in depth as a significant predictor of similarity, concurring with the significant correlations identified by the Mantel tests (Table 2.3).

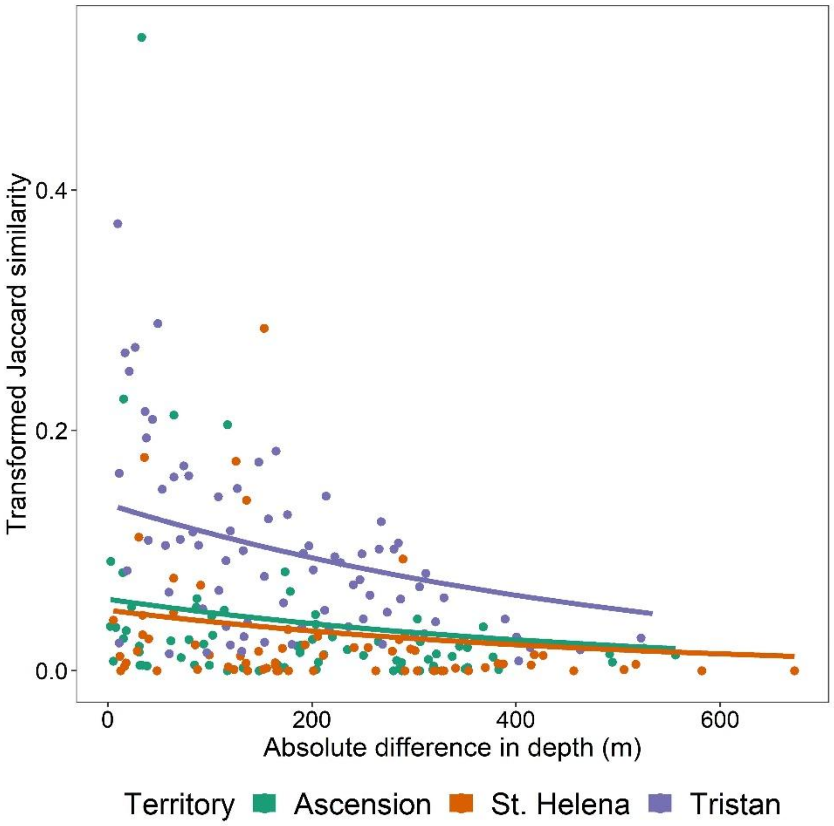

Figure 2.5: Fitted beta regression models showing the decay in similarity of benthic communities with increasing absolute differences in depth for each territory along with the underlying pairwise comparisons. All three models are significant ($p < 0.05$).

The degree of turnover in benthic communities with depth is measured by the slope of the models (Table 2.3). The slope of the Tristan model is significantly steeper than those for Ascension and St Helena, suggesting the rate of turnover is higher in temperate latitudes than tropical. Tristan has the highest modelled similarity between transects at the same depth (15.2%), with equivalents for Ascension (5.3%) and St Helena (3.4%) being much lower (Table 2.3), demonstrating that there was more within-depth-stratum variation in communities at Ascension and St Helena than at Tristan. Correlations between the biological and depth dissimilarity matrices were all significant ($p < 0.05$), but varied in strength with Tristan being highest and Ascension and St Helena being similar Table 2.3.

Table 2.3: Results from the beta regression model fits of beta diversity as turnover along a depth gradient, and for the mantel correlations for each territory.

Territory	**Slope (turnover with depth) ± SE**	**y-axis intercept (3 d.p.)**	**Mantel Rho (3 d.p.)**
Ascension	$1.85 \times 10^{-3} \pm 6.9 \times 10^{-4}$	0.053	0.390
St Helena	$1.35 \times 10^{-3} \pm 6.3 \times 10^{-4}$	0.034	0.318
Tristan	$3.08 \times 10^{-3} \pm 6.05 \times 10^{-4}$	0.152	0.539

2.5 Discussion

Our observations suggest that productivity represents a key driver of differences in species richness between ecosystems on temperate and tropical South Atlantic seamounts, while depth related gradients are only apparent in β-diversity, with no change in species richness across the depth range studied.

Increased surface primary productivity is the most likely driver of the higher species richness found at Tristan. This echoes the link between productivity and richness described in other studies investigating LDGs across different deep-sea habitats (e.g. Culver & Buzas, 2000; Lambshead *et al.*, 2000; Rex *et al.*, 2000; Tittensor *et al.*, 2011). The notable difference in our results is the significant relationship between species richness and surface primary productivity, but not modelled POC flux to depth. Tittensor *et al.* (2011) and McClain *et al.* (2012) argue for the importance of energy in explaining LDGs in the deep sea. Energy in the deep sea can be broadly categorised into two types: thermal and chemical. Thermal energy (i.e., temperature) can drive LDGs in the deep sea, particularly over geological timescales of ~100,000 years (Hunt *et al.*, 2005). Chemical energy is largely composed of POC inputs from overlying waters. Increasing depth leads to decreasing POC flux as organic matter is remineralised and sinks through the water column (Lutz *et al.*, 2007). This study focussed upon upper bathyal depths (<1,000 m; full data available in Appendix B.3) and therefore is likely to be more influenced by surface productivity than modelled POC flux to depth (e.g. >2,000 m) where bacterial remineralisation has had the chance to act, representing a disconnect between surface and seafloor. Furthermore, a model at the resolution of Lutz *et al.* (2007) (5 arcmin, roughly equivalent to 9.2 km at the equator) is unlikely to accurately represent the more complex topography and oceanography around seamounts and oceanic islands. This, combined with the relatively shallow depths of transects, may therefore provide reasons as to why surface primary productivity strongly influences species richness, but POC flux to depth does not. Rosa *et al.* (2008) investigated the drivers of diversity in pelagic cephalopods in the Atlantic Ocean, finding higher diversities at temperate latitudes. Following Rutherford *et al.* (1999), these diversity patterns were attributed to differences in the upper-ocean thermal structure allowing for weaker stratification at temperate latitudes. The more gradual temperature change in a thermocline with a deep base, as seen in temperate latitudes, may facilitate more niches per unit area than a sharp thermocline with a shallow base, as often seen in tropical latitudes, resulting in higher diversity. The surrounding pelagic environment is critical in shaping benthic substrate, so seamount benthic communities and diversity patterns could therefore also be affected by stratification regimes in the upper ocean, particularly on features with shallow summits. Consequently, differing stratification regimes may explain why observed species richness is higher at temperate latitudes than tropical.

If the species richness of seamounts and oceanic islands in the South Atlantic is driven by surface primary productivity, then the lack of significant difference in species richness between Ascension and St Helena is perhaps unsurprising as both territories are characterised by similarly low levels of surface primary productivity (full data available in Appendix B.3). Additionally, if productivity is the key driver of α-diversity, any underlying latitudinal diversity gradient is unlikely to be of uniform steepness from the equator, poleward towards temperate latitudes. This is because the majority of the South Atlantic ocean represents reasonably oligotrophic water, while the temperate latitudes facilitate comparatively high productivity due to the active frontal zones (Peterson & Stramma, 1991; Lutz *et al.*, 2007). This theory could lend some explanation as to why differences in α-diversity are identifiable over large latitudinal ranges/different productivity regimes (e.g. perhaps >10°), but not smaller ranges closer to the equator. Variable strength relationships between latitude and diversity were also described by Gage (2004) for the Atlantic. The existence of an LDG in the South Atlantic has previously been questioned. Rex *et al.* (1993) identified 'significant interregional variation' in the South Atlantic, but not a directional LDG, assigning a portion of the observed variation to patterns in the strength and variability of surface production. Similarly, Gage (2004) studied the large-scale biodiversity patterns of Cumacea (Peracarida: Crustacea), finding that when South Atlantic samples were separated out, linear regression relationships between diversity and latitude were not significant. However, the authors did highlight that sparse data from the South Atlantic would likely limit the ability to detect significant relationships if they were to exist.

The finding that α-diversity is significantly higher on features at Tristan than tropical sites is likely a result of Tristan's close proximity to the subtropical front (STF), where subtropical and subpolar waters converge (Smythe-Wright *et al.*, 1998). Frontal zones are known to increase surface primary productivity (Franks, 1992) and consequently support a diverse range of pelagic taxa (Bost *et al.*, 2009), perhaps explaining why species richness at Tristan is comparatively high. Not only does the enhanced productivity equate to an increased energy supply which would lead to higher species richness (Hutchinson, 1959), further ecological concepts such as resource partitioning, where multiple taxa use different parts of a resource, could be further driving species richness by reducing interspecific competition (Schoener, 1974).

The lack of an identifiable BDG agrees with the results of McClain *et al.* (2010) who also found no consistent bathymetric pattern in α-diversity on a seamount in the Northeast Pacific. Authors suggest a number of theories as to why this might be, including: (1) the seamount's proximity to productive coastal waters masking any bathymetric productivity gradient that would drive species richness; and, (2) the sampling of largely hard substrate. Although the former is not applicable to this dataset due to the isolated nature of all nine sites, the sampling of hard substrate could be shaping our results, particularly because the sampling restrictions of the SUCS under-represents steeper areas & cliffs, and thus potentially misses additional biodiversity. Unimodal BDGs are typically recorded in soft sediment areas where the communities largely comprise macrofaunal, deposit-feeding taxa (Rex *et al.*, 1997). For these types of organisms and communities, POC flux (that decreases with depth) may represent the only food delivery mechanism and therefore would be very important in regulating species richness. In contrast, hard substrate seamount communities tend to be dominated by suspension feeders (Lundsten *et al.*, 2009) that remove food from the surrounding water, using currents to maximise yield. Seamounts are hydrodynamically complex, so it is plausible that if taxa rely on currents as their food delivery mechanism, rather than passively sinking detritus, traditional bathymetric α-diversity gradients may not be observed. Another reason that there is no observed BDG could be a result of the size classification of taxa. Only megafaunal taxa were recorded in this study, and (Rex, 1981) reports that megafaunal taxa display weaker unimodal relationships with depth than macrofaunal taxa that are typically characterised by infaunal communities such as polychaetes, with some exceptions (Howell *et al.*, 2002). In our study, the lack of an observed BDG may be due to the narrow depth range sampled (200-1000 m), nevertheless, one would perhaps expect to see some increase in species richness from 200 m to 1,000 m if a unimodal relationship between depth and species richness with a peak in bathyal depths was present.

The identification of both temperature and depth as non-significant predictors of species richness strongly contrasts with the results of O'Hara & Tittensor (2010) who identified temperature as the *only* significant predictor of species richness of ophiuroids across 60 seamounts, based on data from 100 m to 3,000 m. Despite the identification of a different environmental parameter responsible for shaping species richness, they also found no evidence of a unimodal peak in diversity with depth.

Although there is no significant change in α-diversity with depth, the β-diversity analysis highlights significant bathymetric β-diversity gradients in the form of turnover (i.e. species replacement). These findings are similar to those of McClain *et al.* (2010) who also observed significant changes in β-diversity with depth, but a lack of a significant relationship between α-diversity and depth. McClain & Rex (2015) provide a review on β-diversity in the deep-sea benthos and surmise that latitudinal β-diversity gradients are more moderate than bathymetric β-diversity gradients, likely because the rates of environmental change are greater across depth than they are latitude. Statistically testing turnover along a latitudinal gradient was not possible due to the small size of the dataset prohibiting division into enough distinct depth bands; however, it is possible to discuss bathymetric β-diversity gradients in the context of latitude. The significantly higher slope value of the beta regression model for the Tristan data suggests that the rate of species turnover with depth may with location in the South Atlantic. Productivity hotspots are known to influence bathymetric species turnover, whereby increased productivity drives faster turnover (McClain & Rex, 2015), but the specific environmental drivers of community structure and species turnover require further research in the South Atlantic.

The relationship between dissimilarity and depth is considerably stronger for Tristan (Table 2.3). This may be a result of the stronger stratification of water mass structure at Tristan due to proximity to the STF as water mass structure is a known driver of community structure (Tyler & Zibrowius, 1992; Koslow, 1993; Bett, 2001; Howell *et al.*, 2002).

The lower expected similarities between transects at the same depth in the tropics (and therefore higher β-diversity) is perhaps counterintuitive when considering the significantly lower α-diversity compared to temperate latitudes (Figure 2.3). This is considered further in Chapter 3.

2.6 Conclusion

Species richness, a measure of α-diversity, of seamount ecosystems in the South Atlantic appears largely driven by surface primary productivity and is thus higher in temperate latitudes than the tropics. Although no polar transects were available, the comparatively lower surface primary productivity compared to temperate regions (Assis *et al.*, 2018) would suggest that seamounts and oceanic islands in the South Atlantic follow a parabolic LDG. There was no relationship between depth and α-diversity within the depth range sampled, although significant bathymetric β-diversity gradients were observed. There is a high level of variability in both the observed diversity patterns on seamounts and the environmental parameters that are deemed important in shaping said patterns across different seamount focused studies (McClain *et al.*, 2010; O'Hara & Tittensor, 2010; Victorero *et al.*, 2018; Morgan *et al.*, 2019). This inconsistency in the ability to identify the environmental parameters important for *all* seamount benthic communities again demonstrates the heterogeneity in seamount habitats. Our observations suggest that the current understanding of LDGs in deep-sea species richness does apply to seamount ecosystems in the South Atlantic, but as suggested in Clark *et al.* (2012), in order to be able to make any generic statements about seamount ecology, particularly at the global scale, environmental and biological characterisation of more seamounts is required, particularly those in data-poor areas and across different productivity regimes. The difference between the relationships of α-diversity and β-diversity with depth in this study demonstrates that both types of diversity should be taken into account when characterising seamounts.

CHAPTER 3: BENTHIC COMMUNITY COMPOSITION OF SOUTH ATLANTIC SEAMOUNTS

3.1 Abstract

Seamounts and oceanic islands rise from the seafloor and provide suitable habitat for a diverse range of biological assemblages including Vulnerable Marine Ecosystems (VMEs). While they have been the focus of some work globally, there has been little description of the biological and physical environments of seamounts in the South Atlantic Ocean. In this study, benthic community composition was characterised from 13 seamounts and oceanic islands spanning 8 °S to 40 °S within the Exclusive Economic Zones of Ascension Island, Saint Helena, and Tristan da Cunha. Drop camera imagery was collected between 170 m and 1,000 m. All fauna present in images was identified and quantified, and multivariate statistics were used to describe biological assemblages and identify environmental drivers. Benthic communities of the Tristan da Cunha were shown to be distinct from those found in Ascension and Saint Helena, with latitude and depth identified as key environmental drivers of community composition. Our results are consistent with the current understanding of the biogeography of the South Atlantic, both in terms of the distinction between tropical and temperate regions, and the influence of depth and water mass structure on assemblage distribution. Faunal assemblages are similar to those observed in the North Atlantic in terms of functional groups. VMEs are present within the EEZs of all three territories and are protected by large Marine Protected Areas (MPAs). Further characterisation of VME habitats in the South Atlantic is required to assess the conservation significance of these MPAs at basin scale.

3.2 Introduction

Seamounts are features generally defined as rising more than 1,000 m off the surrounding seabed and are found in all ocean basins (Clark *et al.*, 2010). Estimates of their number vary based on methods of identification and detection, but recent studies propose values between 25,000 and 35,000 (Kim & Wessel, 2011; Yesson *et al.*, 2011). If seamounts break the surface, they are referred to as oceanic islands, many of which are very isolated. In the South Atlantic, the United Kingdom Overseas Territory (UKOT) of Saint Helena, Ascension and Tristan da Cunha is made up of three geographically separated islands/island groups spanning ~8 to ~40 °S. These islands function similarly to seamounts in the sense that they provide a hard substrate habitat in an otherwise largely soft substrate deep sea (Rogers, 1994), as well as providing benthic habitat in areas that would otherwise be pelagic and thus are important in sustaining populations of benthic fauna, particularly when they are part of mid-ocean ridge systems (Priede *et al.*, 2013). Seamounts are also associated with increased production in surface waters due to the trapping of diurnally migrating zooplankton over the summit (Clark *et al.*, 2010). This attracts subsequent activity from organisms further up the trophic chain, all resulting in increased carbon flux to depth, which facilitates higher species richness and supports increased benthic biomass (Samadi *et al.*, 2006).

Seamount benthic macrofauna is typically dominated by sessile, filter feeding fauna (Samadi *et al.*, 2007; Rogers, 2018), with the flank regions often home to large, fragile cold-water coral (CWC) reefs (Roberts, 2002; Rogers *et al.*, 2007). Seamounts in the South Atlantic are understudied (Clark *et al.*, 2010), particularly with regards to the structure of benthic assemblages. The Vitória-Trindade seamount chain (VTC) found off the coast of Brazil in the southwest Atlantic has been the focus of a number of studies. However, most either study the shallower, mesophotic communities (e.g. Pereira-Filho *et al.*, 2012; Meirelles *et al.*, 2015), or only consider certain taxa (Leal & Bouchet, 1991; Santos *et al.*, 2020). O'Hara *et al.* (2010) investigated the environmental drivers of assemblages across the VTC, but data are based on presence-absence at the species level and therefore cannot be used to compare biological descriptions of assemblages. They do however provide a list of the six invertebrate phyla recorded, all of which are common to seamounts.

Caselle *et al.* (2018) carried out surveys to investigate the community structure at Tristan da Cunha in the southeast Atlantic. Although this largely focused on deep water vertebrates, they did list habitat forming organisms in deep water including gorgonians, antipatharians and sea pens in supplementary material. Seamounts on the Walvis Ridge in the southeast Atlantic are known to contain diverse assemblages of both fish and benthic invertebrates including CWC reefs (FAO, 2016). With a subset of the data used in this study, Barnes *et al.* (2019) described deep water assemblages around Ascension Island as often dominated by ophiuroids and corals, and assemblages on the surrounding seamounts as dominated by sessile suspension feeders.

There are many environmental factors that can influence both the composition and distribution of benthic assemblages on seamounts and oceanic islands, as well as their overall species richness. These include, but are not limited to, depth (Boschen *et al.*, 2015), biogeographic region (McClain *et al.*, 2009), local hydrodynamic regime (Levin & Thomas, 1989), surface productivity (Hernández-León *et al.*, 2020; Chapter 2), particulate organic carbon (POC) flux to depth (Morgan *et al.*, 2019), temperature

(O’Hara & Tittensor, 2010; Woolley *et al.*, 2016) and topography and substrate type (Lundsten *et al.*, 2009). In the South Atlantic, O’Hara *et al.* (2010) identified distance from shore, temperature, dissolved oxygen and particulate organic carbon as important environmental predictors of assemblage composition along the VTC. Depth, and/or covariate environmental parameters such as temperature, are known to play a significant role in structuring assemblages in the deep-sea (Howell *et al.*, 2002; McClain *et al.*, 2010; Long & Baco, 2014). However, the magnitude of the effect of depth and associated environmental variables vary, as does the effect when focusing on specific taxa *versus* full assemblages. Howell *et al.* (2002) investigated the depth-related distribution and abundance of seastars in the Porcupine Seabight area of the North Atlantic, and found that there was ~ 20% turnover every 1,000 m descended, although rate of turnover varied with depth. Focusing on broader megafaunal community structure, McClain *et al.* (2010) reported a 50% change in assemblage composition with every ~1,500 m descended on Davidson Seamount in the Northeast Pacific, whilst Long and Baco (2014) reported a 93% species turnover with a depth change of ~200 m in the Makapu'u coral bed off Hawaii.

Despite their importance as biodiverse ecosystems and as being essential feeding hotspots for pelagic predators and seabirds (Hosegood *et al.*, 2019; Requena *et al.*, 2020), seamounts face anthropogenic threats. Perhaps the most obvious human-induced pressure on seamounts comes in the form of fisheries, with Clark *et al.* (2007) reporting that in the late 1960s, at least 2 million metric tons of deep-sea species were trawled from seamounts globally. Their significance as fishing grounds is somewhat due to the presence of large coral and sponge gardens and reefs (Rogers *et al.*, 2007) which provide essential nursery habitat for many commercial fish species (Baillon *et al.*, 2012). Although particularly vulnerable to overexploitation (Watson *et al.*, 2007), some seamount fisheries have proven sustainable; typically for high-value species at low quantities (Clark, 2009). In addition to fishing pressure, many seamounts are also considered prospective deep-sea mining sites due to the high concentrations of desirable metals found within the crust that forms on seamounts (Hein *et al.*, 2000), and exposed to increasing pollution in the form of marine plastics (Barnes *et al.*, 2018).

The vulnerability of fragile ecosystems often found in high concentration on seamounts, combined with the observed negative impacts of bottom trawling (Clark *et al.*, 2016) prompted calls from the United Nations General Assembly (UNGA) to address issues surrounding the management of deep-sea fisheries, leading to the adoption of UN resolution 61/105, and subsequent resolutions, to protect Vulnerable Marine Ecosystems (VMEs) such as CWC reefs. This resolution requires that all Regional Fisheries Management Organisations (RFMOs) that manage fisheries in Areas Beyond National Jurisdiction (ABNJ) adopt a precautionary principle so as to mitigate any significant adverse impacts to VMEs (including those found on seamounts). Although measures implemented by some RFMOs have been effective, others require additional scientific and legal support to meet this objective (Bell *et al.*, 2019). This resolution, combined with the subsequent development of the International Guidelines for the Management of Deep-sea Fisheries in the High Seas (FAO, 2009), mean that in some scenarios, a level of protection is applied to seamounts in ABNJ.

Although the vast majority of seamounts fall in ABNJ, some states, particularly small-island nations and territories like the UKOTs, have multiple seamounts within their EEZs (Yesson *et al.*, 2011), and therefore a chance to significantly advance the conservation of seamounts. Those within the EEZs of Ascension, St Helena and Tristan da Cunha are now managed as part of large marine protected areas (MPAs) and/or a combination of fishing and no take zones in the South Atlantic.

In order to fully understand the conservation significance of these large MPAs and to support future management plans, it is important to characterise seamounts, and understand the ecology, distribution and environmental drivers of the species and habitats in the region (Ardron, 2008). This will allow managers to ensure the correct tools (e.g. areas based management tools such as MPAs) are employed in the optimal locations. For example, regional ecological and environmental characterisation is important to ensure population connectivity is maintained (Christie *et al.*, 2010; Sundblad *et al.*, 2011; Ross *et al.*, 2017; Balbar & Metaxas, 2019), and an understanding of species and/or habitat distribution is important in making sure representative areas are protected as opposed to atypical ones (Rice & Houston, 2011; Sundblad *et al.*, 2011). With this in mind, this chapter aims to; 1) identify the broad-scale environmental drivers of seamount benthic assemblage structure in the South Atlantic; 2) characterise the benthic assemblages of South Atlantic Seamounts, and; 3) identify VMEs protected by each large MPA to support future spatial management.

3.3 Methods

3.3.1 Study area

Saint Helena, Ascension Island and Tristan da Cunha (henceforth referred to as St Helena, Ascension and Tristan) make up a single UK Overseas Territory (UKOT) in the South Atlantic Ocean (Figure 3.1). These oceanic islands have steep, shelving sides and the seabed descends into deep water (200 m+) very close to shore. Ascension forms part of the mid-Atlantic Ridge (MAR), St Helena forms part of the Guinea seamount chain, and both are located within the tropics. Tristan is at the most westerly point of the Walvis Ridge and is therefore temperate. In all cases, over 90% of the exclusive economic zone (EEZ) comprises waters deeper than 1,000 m.

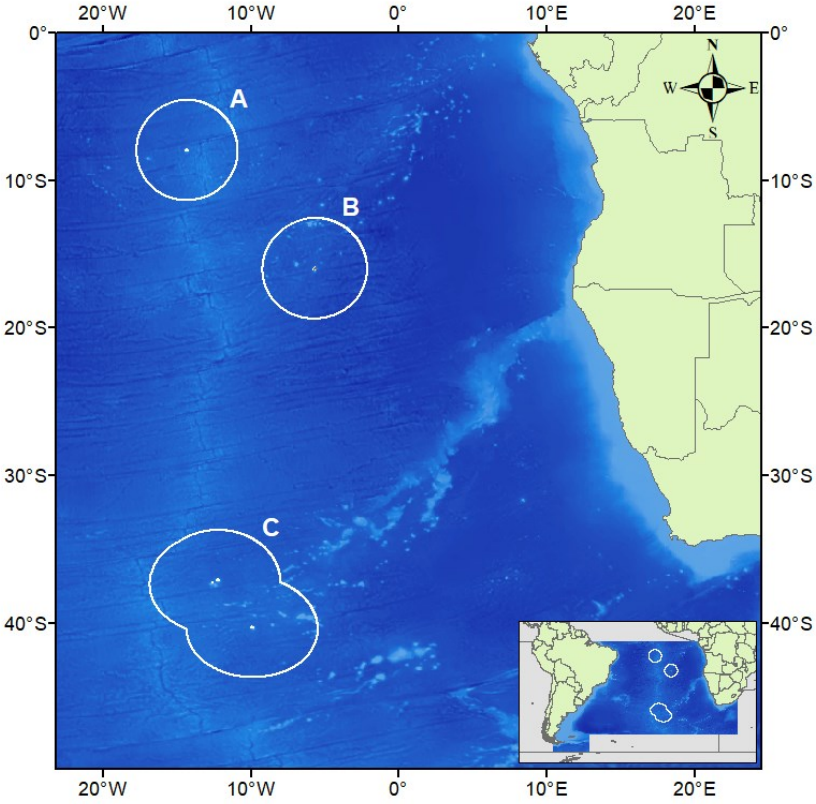

Figure 3.1: The South-east Atlantic Ocean with the Exclusive Economic Zones of Ascension Island (A), Saint Helena (B) and Tristan da Cunha (C) are drawn in white and correspond to Figure 3.2A-C. Underlying bathymetry is cropped for the region from General Bathymetric Chart of the Oceans (GEBCO_2014 Grid, version 20150318). Map drawn in WGS84.

3.3.2 Sampling methods

A bespoke camera lander (Shallow Underwater Camera System, SUCS, Appendix A) was used to collect image data in cluster transects (n = 74) during the 2013 (Barne*s et al.*, 2013), 2015 (Barnes *et al.*, 2015), 2017 (Barnes *et al.*, 2019) and 2018 (Morley *et al.*, 2018) cruises of the RRS *James Clark Ross*, and a 2019 cruise on the RRS *Discovery* (Whomersley *et al.*, 2019). Two cruises visited each of Ascension and Tristan, with sampling targeted towards the oceanic islands themselves in 2013 and 2015, and offshore seamounts in 2017 and 2018; (Figure 3.2A-C). Due to a mechanical fault with the SUCS, deployments were only made in the St Helena EEZ in 2019 but targeted both the main island itself and two offshore seamounts. Transects within each UKOT EEZ (henceforth referred to as territories) were collected from multiple seamounts/islands (henceforth referred to as sites), displayed in Table 3.1.

Table 3.1: Breakdown of the sampling structure showing transects (n=74) per site (n=13) and per territory.

Territory	**Site**	**Transects**
Ascension	Ascension Island	18
	Grattan Seamount	4
	Harris-Stewart Seamount	2
	Young (Unnamed) Seamount	1
St. Helena	Bonaparte Seamount	2
	Cardno/Southern Cross Seamount Complex	6
	St. Helena Island	5
Tristan	Crawford Seamount	12
	Yakhont Seamount	13
	RSA Seamount	4
	Gough Island	2
	McNish Seamount	4
	Tristan and Nightingale Island	1

The SUCS tripod design allows the lander to settle perpendicular to the sea floor using weights to steady itself, and captures high-resolution images (approximately 20 in each cluster transect) of 0.14 m^2 area using a 5 megapixel Allied Vision Prosilica GC2450 camera, a Fujinon HF12.5SA-1 lens and twin variable intensity lights, all controlled from a desktop computer on ship. An Ultra Short Base Line (USBL) beacon mounted on the camera lander allowed for an accurate Global Positioning System (GPS) position to be obtained.

Multibeam seabed mapping using Kongsberg EM122 and EM710 multibeam echosounders allowed for characterisation of the sites prior to equipment deployments to ensure suitability for the SUCS. Agassiz trawls were used to collect physical specimens for laboratory-based identification, and temperature and oxygen profiles were recorded using a CTD at each transect

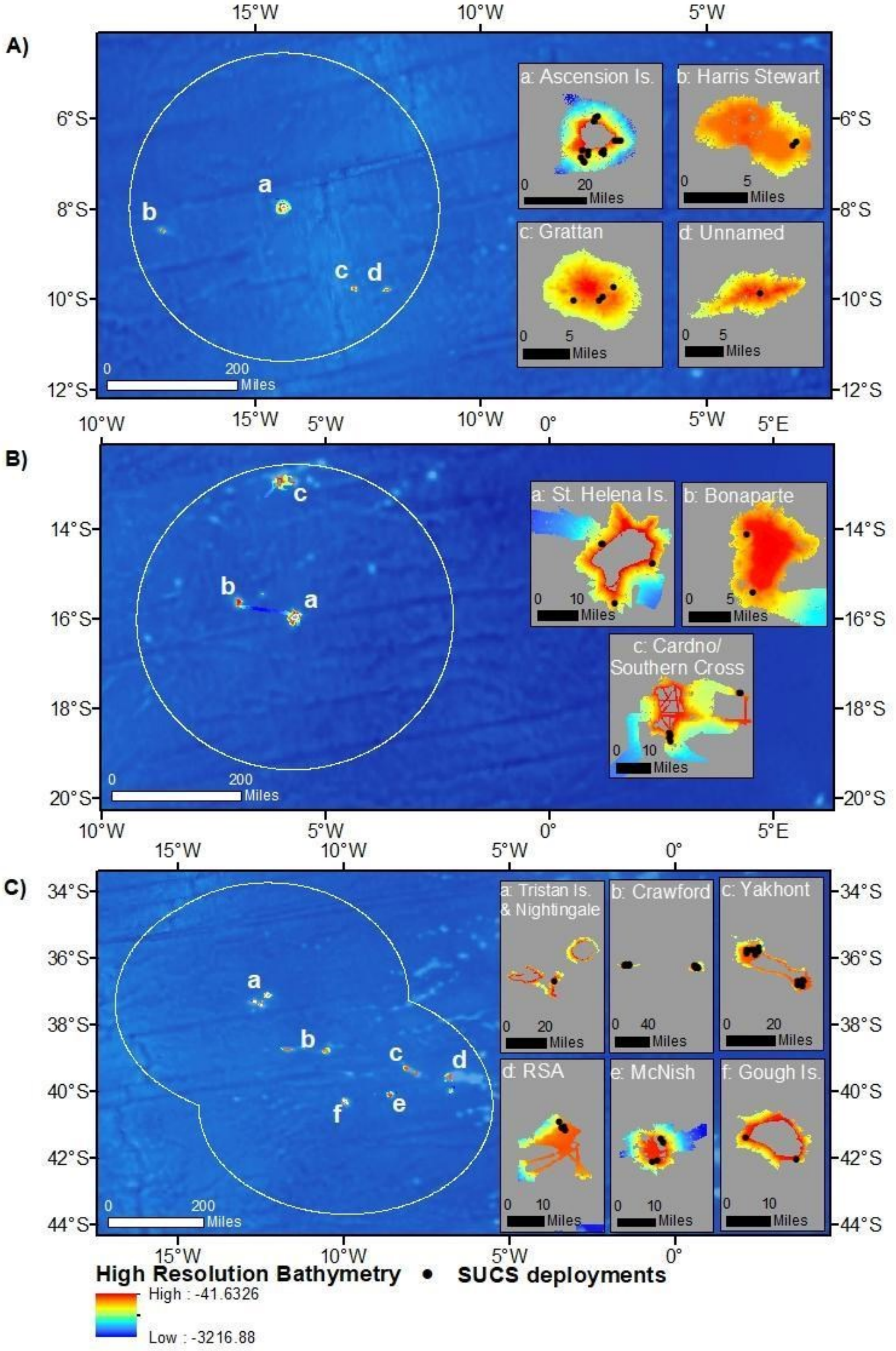

Figure 3.2A-C: Camera deployments plotted on high-resolution bathymetry across: (A) all four sites within the Ascension Island EEZ, (B) all three sites within the Saint Helena EEZ, and (C) all six sites within the Tristan da Cunha EEZ. Insets show each of the bathymetric features sampled in each territory. Underlying bathymetry from General Bathymetric Chart of the Oceans (GEBCO_2014 Grid, version 20150318).

3.3.3 Image analysis

1,293 images were quantitatively analysed using a combination of ImageJ (Schneider *et al.*, 2012) and BIIGLE, the latter being an online platform designed for the annotation of images (Langenkämper *et al.*, 2017) All organisms identified as distinct morphospecies were assigned an Operational Taxonomic Unit (OTU). OTUs were identified to the highest taxonomic resolution possible, facilitated through comparison of image data with physical specimens collected (by mini-Agassiz trawl), and the Howell *et al.* (2017) deep-sea species image catalogue. All individuals were counted up to 100, with some encrusting and reef-forming species recorded as percentage cover. For these OTUs values used were either 1% (as most were only present in very small abundances per image), or between 10% and 100% in 10% increments.

Primary and secondary substrate type(s) were recorded using the following categories based on Wentworth (1922): bedrock, reef framework, live reef, cobbles, coral rubble, pebbles, coral gravel, gravel and sand (Appendix A.2). Images were also assigned a substrate hardness score based on the types and proportions of each substrate observed in the image on a six point scale where 1 would equate to 100% sand and 6 to 100% bedrock. For example, if 50% of the image comprised sand and 50% comprised rock, the hardness score would be 3 to weight each substrate appropriately.

Transects were also assessed as to whether authors considered them Vulnerable Marine Ecosystems (VMEs), based on the list of VME-indicators and habitat types listed by ICES (2016).

3.3.4 Environmental data preparation

Raw multibeam files were cleaned, gridded at 25 m cell size in QPS Qimera v2.1.1 and projected from the native projection into Goode Homolosine Ocean in ArcGIS v10.7. The Benthic Terrain Modeller plugin (Walbridge *et al.*, 2018) was used to derive rugosity, slope, fine-scale bathymetry position index (FBPI), broad-scale bathymetric position index (BBPI) and curvature. The inner and outer radii for BBPI and FBPI were 8 and 40 and 1 and 8, respectively, facilitating identification of megahabitats >1km (e.g. banks and plateaus) and mesohabitats <1 km (e.g. gulley and reefs, Greene *et al.*, 1999). Using the 'mgcv' package (Wood, 2011) in R Studio (R Core Team, 2019), a Generalised Additive Model was used to create a bottom temperature layer for each territory from CTD casts undertaken during the aforementioned cruises, and archived CTD casts in the British Oceanographic Data Centre (BODC) database containing data supplied by Natural Environment Research Council (Appendix A.3). Temperature records were partitioned for each territory at an 80/20% training/test split, and the test dataset was used to validate the modelled predictions. For all three models, Pearson's correlation coefficient between the *in-situ* test observation and the predictions was 0.99, suggesting predictions were strongly in line with recorded temperatures.

Particulate organic carbon (POC) flux to depth values at a 5 arcmin resolution (approximately 9.2 km at the equator) taken from Lutz *et al.* (2007) were resampled and re-projected to a 25 m resolution in Goode Homolosine Ocean. Mean surface primary productivity data were downloaded from Bio-Oracle, an online database of environmental variables for ecologists, and also resampled and re-projected from 5 arcmin to 25 m (Assis *et al.*, 2018). It is important to note that this resampling does not alter the resolution of the underlying data, it simply splits grid cells into smaller cells to allow for raster stacking in mapping programmes.

3.3.5 Statistical analysis

To allow for single combined analysis of OTUs, abundance and percent cover datasets need to be brought onto the same scale by dividing one dataset by a selected value so as to equal the range of the other (as *per* Howell *et al.*, 2010a). The two datasets were checked and their distributions deemed similar enough to combine; both also ranged from 0 – 100, therefore no division was required, but data were square-rooted to account for high abundances of certain OTUs (namely reef-associated ophiuroids). A Bray-Curtis similarity matrix was created in Primer v.6 (Clarke & Gorley, 2006) for the 74 transects. Similarity/dissimilarity between samples was visualised using hierarchical cluster analysis (CLUSTER) with a Similarity Profile Analysis (SIMPROF) test (at $p = 0.05$) and non-metric multidimensional scaling (nMDS). Two Similarity Percentage Routines (SIMPER) were performed to determine: (1) the dominant taxa driving the distinction between SIMPROF clusters, and (2) the taxa that characterise each territory. These were run using a 50% cumulative cut-off.

Environmental data (latitude, longitude, surface primary productivity, depth, rugosity, curvature, slope, FBPI, BBPI, temperature, substrate hardness and POC flux to depth) were visualised using Draftsman's Plots and rugosity was log-transformed as the raw distribution was skewed. A distance-based linear model (DistLM) from the PERMANOVA+ software (Anderson *et al.*, 2008) was run in Primer v.6 with all 12 variables to ascertain whether they were individually significant predictors of community structure, requiring the analysis to also print a correlation matrix (Appendix C.1). Correlations >±0.7 were considered strong and therefore one of each correlated pair was removed from further analysis based on the ecological relevance of the correlate, and their individual performance in DistLM marginal tests. A DistLM using the final variables was then run on the community composition matrix. This determined which potential environmental drivers could best describe the relationship between community structure and the environmental data using Akaike information criterion (AIC) as the selection criterion and a step-wise selection procedure, with 999 permutations to test significance. Distance-based redundancy analysis (dbRDA) plots were used to visualise the DistLM results in two dimensions.

3.4 Results

3.4.1 Environmental drivers of assemblage structure

The correlation matrix with the 12 environmental variables revealed two correlation coefficients >±0.7 (temperature and depth, and surface primary productivity and latitude, Appendix C.1). Exploration of variable contribution and significance using DistLM marginal tests revealed all four correlates were individually significant. Depth was selected over temperature as it explained more variance and is a proxy for multiple environmental variables (including temperature) that are known to drive community structure. Latitude was selected over surface primary productivity for further analysis as similarly, it can be assumed a proxy for other variables. Therefore, the following 10 variables were taken forward for analysis in the DistLM: latitude, longitude, depth, rugosity, curvature, slope, FBPI, BBPI, substrate hardness and POC flux to depth. The best solution from the DistLM routine, selected based on AIC score, is detailed in Table 3.2. The five selected variables combined explain approximately 27% (R^2 0.268) of the variation in the community structure across the three territories. Latitude was the only variable that individually accounted for >5%. Substituting latitude and depth for surface primary productivity and temperature in the available variables list did not significantly change the proportion of variance explained by the five selected variables, although it did alter the order of longitude and FBPI (results available in Appendix C.2).

Table 3.2: DistLM metrics for the best model selected in Primer v.6.

Variable	**SS (trace)**	**Pseudo-F**	**p-value**	**% variance explained (2 d.p.)**
Latitude	45970	13.023	0.001	15.32
Depth	13276	3.9132	0.001	4.42
Longitude	7621.4	2.2871	0.001	2.54
FBPI	6947.5	2.1182	0.001	2.31
Slope	6760.3	2.0938	0.001	2.25

Distance-based redundancy analysis (dbRDA) plots allow visualisation of the DistLM results for each significant environmental variable (Figure 3.3). Decreased latitude (poleward movement) drives the separation between Ascension and St Helena transects and those from Tristan. Increased slope also appears important in separating the tropical from the temperate, although the variance in the biological data that it explains was relatively minor. Depth was important for structuring communities within all territories. The dbRDA plotted by SIMPROF clusters is available in Appendix C.3.

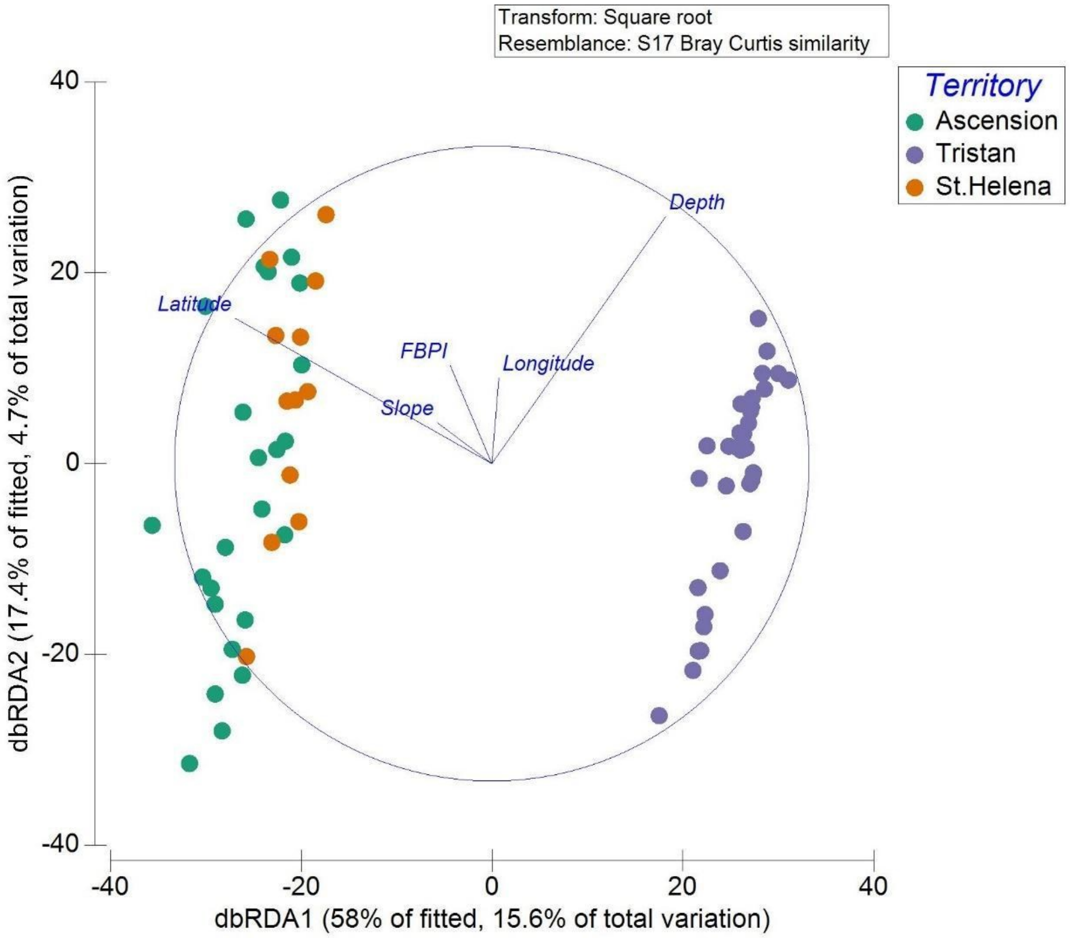

Figure 3.3: Transects displayed on the dbRDA plot allowing visualisation of the DistLM. Individual transects are plotted with colours denoting the territory in which they occur. Environmental gradients are overlaid depicting how each variable contributes to the structure within the biological dataset.

3.4.2 Biological assemblages

A SIMPROF routine identified 22 biologically distinct assemblages labelled alphabetically from a – v (Appendix C.4); environmental characteristics of these are presented in Table 3.3. Sixteen of the assemblages comprise transects exclusively from Tristan, whilst the remaining six clusters contain transects from Ascension and St Helena mixed together. A collapsed version of the dendrogram at 22% similarity is seen in Figure 3.4. After the latitudinally driven split at ~ 5% similarity, depth appears to become a driving factor (see Appendix C.5 for transect depth values). Alternative visualisation of the SIMPROF clustering is presented in Appendix C.6 on a non-metric multidimensional scaling plot. Nine clusters (a, b, d, e, f, l, o, p and r) contained only one transect. Some of these were deemed outliers due to emptiness; for example, the transect listed as assemblage ‘r’ contains very few live taxa and is unlike any other area imaged. Others represent the only transect from a specific site, for example, assemblage ‘b’ contains the only transect from around Nightingale Island in the Tristan EEZ but is ~45% similar to other temperate island transects (Figure 3.4). Full environmental characterisation for all clusters (including those containing only one transect) and example images can be found in Appendix C.7.

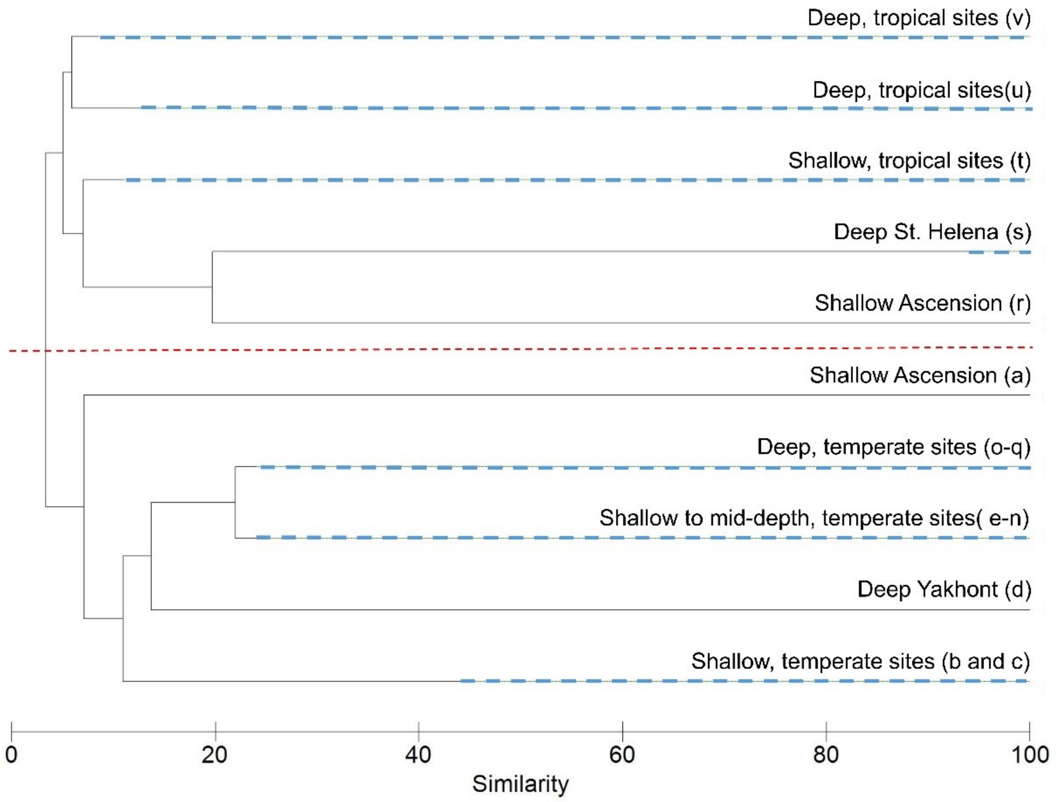

Figure 3.4: Cluster dendrogram from the Similarity Profile Analysis (SIMPROF) routine on the community composition of each transect revealed 22 statistically significant biological assemblages. These have been collapsed at 22% similarity into major groupings with descriptions and SIMPROF cluster labels in brackets (refer to Appendix C.5 for transect descriptions, or Table 3.3 for cluster descriptions). Nodes containing multiple, distinct clusters are denoted by dashed, blue lines. The dashed red line depicts the latitudinally driven split at ~5% with the tropical clusters positioned above the line, and the temperate below (excluding Shallow Ascension (a)). Appendix C.4 gives an alternative visualisation.

Transects from Ascension and St Helena split into three main clusters (t-v, Figure 3.4) with three smaller clusters also identified (a, r and s). Cluster t contains 14 shallower transects and is characterised by a range of substrates both hard and soft, reflected in an average substrate hardness of 3.7/6 (Table 3.3). The remaining two large clusters (u and v) have similar average depths (Table 3.3), but are much more homogenous in their substrate, with the first containing all soft substrate transects and the second largely hard substrate transects, again reflected in their average substrate hardness scores (Table 3.3). These tropical clusters contain transects from multiple seamounts across both territories suggesting similar assemblages across the EEZs of Ascension and St Helena.

Transects from Tristan cluster in smaller groupings (b – q), also appearing to cluster initially by depth (Figure 3.4), however this is followed by further splitting based largely on individual sites (Table 3.3), suggesting a larger diversity of communities between seamounts at this location.

Table 3.3: Overview of environmental data, suggested VME classification and taxon composition (determined by SIMPER) of individual SIMPROF clusters. The cut off for cumulative percentage (C. %) contribution to group similarity is 50%. 'SF' and 'EC' refer to structure-forming and encrusting sponge morphologies, respectively. Taxa considered VME-indicators in ICES (2016) *are denoted in bold. VME habitats identified from WGDEC 2015 report on VMEs (with the addition of hard-bottom cup coral fields (HBCCF); VMEs listed as partial where <50% of the cluster can be identified as VME.*

Cluster code	**No. of transects and sites in cluster**	**Mean substrate hardness (1 - 6)**	**Temp. range (°C)**	**Mean temp. (°C)**	**Depth range (m)**	**Mean depth (m)**	**SIMPER similarity level**	**C. %**	**Characterising taxa identified by SIMPER**	**VME habitat**
Temperate clusters										
b	1, 1	2.7	-	10.8	-	178	-	-	-	HBCCF and coral garden
c	2, 1	5.1	10.8 - 10.8	10.8	170 - 186	178	58.67	58.00	**Hard-bottom *Caryophyllia* spp**. (45.95), ***Thouarella* spp**. (12.05)	HBCCF and coral garden
d	1, 1	2.7	-	3.9	-	837	-	-	-	-
e	1, 1	5.8	-	8.7	-	376	-	-	-	-
f	1, 1	4.3	-	6.4	-	531	-	-	-	-
g	2, 1	4.1	8 - 8.38	8.4	374 - 423	399	54.78	55.91	**SF sponge 1** (16.3), **SF sponge 2** (9.04), *Ophiomusium* sp. (8.46), **Stylasteridae 1**	-

									(7.83), Hydroid 1 (7.15), Bryozoan 1 (7.15)	
h	4, 1	4.1	10.2 - 10.6	10.4	190 - 249	217	57.07	54.39	**Hard-bottom *Caryophyllia* spp**. (12.65), Bivalvia 1 (12.07), EC sponge 1 (8.71), **SF sponge 1** (7.18), EC sponge 2 (7.06), EC sponge 3 (6.71)	HBCCF and coral garden
i	3, 1	4.6	9.2 - 10	9.6	285 - 345	319	65.84	50.49	Hydroid 2 (12.38), **SF sponge 1** (11.81), Hydroid 3 (8.46), *Ophiomusium* sp. (7.24), EC sponge 1 (5.58), **SF sponge 3** (5.02)	-
j	4, 1	3.8	9.5 - 10	9.8	273 - 323	298	58.94	50.94	**Hard-bottom *Caryophyllia* spp**. (10.16), *Ophiomusium sp.* (6.94), **SF sponge 1** (6.09), **Actiniaria 1** (5.64), Zoantharia (5.62), Hydroid 1 (4.99), EC sponge 1 (4.96), Hydroid 2 (3.42), EC sponge 3 (3.12)	HBCCF and coral garden
k	5, 1	4.1	9.3 - 9.7	9.5	314 - 338	328	52.24	52.63	**Actiniaria 1** (17.93), *Ophiomusium sp.* (12.7), Hydroid 1 (8.06), **Hard-bottom *Caryophyllia* spp**. (7.04), **SF sponge 4** (6.9)	Partial CWC reef
l	1, 1	3.1	-	8.6	-	386	-	-	-	-
m	2, 1	2.5	9.7 - 9.8	9.8	297 - 307	302	67.70	50.04	**SF sponge 1** (13.67), **Hard-bottom *Caryophyllia* spp**. (12.83), Gastropoda 1 (9.07), Hydroid 1 (7.24), **Hormathiidae** (7.24)	-

n	2, 1	3.5	9.6 - 9.9	9.7	295 - 318	307	67.56	52.47	**Hard-bottom *Caryophyllia* spp.** (22.61), **SF sponge 1** (8.37), Bryozoan 1 (5.0), Gastropoda 1 (4.48), Hydroid 1 (4.48), EC sponge 1 (3.88), **SF sponge 5** (3.66)	HBCCF and coral garden
o	1, 1	4.3	-	4.7	-	703	-	-	-	Hard bottom coral garden
p	1, 1	3.7	-	7.7	-	434	-	-	-	-
q	5, 1	5.1	5.5 - 6.2	5.8	550 - 624	590	47.53	52.19	**SF sponge 1** (9.73), Brachiopoda (8.22), **Stylasteridae 1** (8.07), EC sponge 4 (6.60), Hydroid 3 (5.69), Galatheoidea (5.48), EC sponge 1 (4.58), Bivalvia 2 (3.82)	CWC reef and coral garden
Tropical clusters										
a	1, 1	4.0	-	13.1	-	190	-	-	-	-
r	1, 1	2.0	-	11.5	-	218	-	-	-	-
s	2, 1	2.0	6.1 - 6.1	6.1	597 - 597	597	94.25	71.01	**Actiniaria 3** (71.01)	-
t	14, 6	3.7	6.2 - 11	8.1	232 - 581	434	15.67	60.07	Reef-associated Ophiuroidea (27.12), Cidaroida (18.35), **Soft-bottom Caryophyllidae** (14.6)	Partial CWC reef and sea pen field
u	7, 3	2.9	4.9 - 10.8	6.1	278 - 875	712	19.86	64.45	Gastropoda 2 (25.65), **Soft-bottom Caryophyllidae** (22.27), **Actiniaria 4** (16.53)	-

v	13, 6	4.4	4.2 - 7.8	5.5	487 - 1011	758	12.11	52.02	Serpulidae (17.49), Reef-associated Ophiuroidea (10.44), Decapoda (9.19), Brachiopoda (8.52), Bryozoan 2 (6.38)	Partial CWC reef

3.4.2.1 Faunal comparisons at the territory level

Faunal similarity between the territories is variable. Tristan is the most distinct with 3.17% and 4.13% similarity with Ascension and St Helena, respectively, and is characterised by encrusting sponges, hard-bottom *Caryophyllia* Lamarck, 1801 spp. cup corals, massive structure-forming sponges, hydroids and non-reef-associated ophiuroids (*Ophiomusium* Lyman, 1869 sp.). Tristan transects also share the highest within-group similarity at 27.48% (Table 3.4).

The within-group similarities for Ascension and St Helena transects are substantially lower at 8.68% and 9.33%, respectively. Ascension is characterised by CWC reef-associated ophiuroids, soft-bottom cup corals from the Caryophyllidae family and decapod crustaceans; St Helena is characterised largely by cidarid urchins and CWC reef-associated ophiuroids (Table 3.4). A reef-building scleractinian coral (*Desmophyllum pertusum*, formerly *Lophelia pertusa*) is also present throughout numerous transects but in very low abundances.

Table 3.4: Taxon composition (determined by SIMPER) of territories. The cut off for cumulative percentage contribution to group similarity is 50%. 'SF' = structure-forming; and 'EC' = encrusting sponge morphologies. Cumu. (%) = Cumulative percentage. Taxa considered VME-indicators in ICES (2016) *are denoted in bold.*

Territory: within-group similarity (%)	**Taxa (contributing %)**	**Cumu. (%)**
Ascension: 8.68	Reef-associated Ophiuroidea (14.53), **Soft-bottom Caryophyllidae** (13.45), Decapoda (12.24), Gastropoda 2 (7.84), Cidaroida (3.12)	51.18
St Helena: 9.33	Cidaroida (22.25), Reef-associated Ophiuroidea (11.56), **Actiniaria 3** (10.36), **Soft-bottom Caryophyllidae** (7.26)	51.43
Tristan: 27.48	**SF sponge 1** (11.62), **Hard-bottom *Caryophyllia* spp**. (11.38), EC sponge 1 (7.12), *Ophiomusium* sp. (6.26), **Hydroid 3** (4.43), **SF sponge 3** (4.02), Gastropoda 1 (3.73), EC sponge 3 (3.64)	52.21

Of the 36 transects from the Tristan EEZ, 53% were determined as VMEs based on the habitat types listed in ICES (2016) and assessment against the FAO criteria (FAO, 2009). This was significantly higher than the 24 and 23% from Ascension and St Helena, respectively (Table 3.5). There was also a higher number of different VME types observed at Tristan compared to the other two territories.

*Table 3.5: Number of transects per territory deemed Vulnerable Marine Ecosystems, some of which present as a mosaic of >1 type. * Hard-bottom cup coral fields have been since added, but are not listed in the 2015 report (ICES, 2016).*

Territory	**VME habitat type (ICES, 2016)**	**No. transects identified as each VME habitat type**	**Total no. VME transects per territory (%)**
Ascension	Sea pen field	1	6 (24%)
	Cold-water coral reef	5	
St Helena	Cold-water coral reef	3	3 (23%)
Tristan	Hard-bottom coral garden	4	19 (53%)
	Hard-bottom coral garden/hard-bottom cup coral field*	8	
	Cold-water coral reef	4	
	Hard-bottom cup coral field*	3	

3.4.2.2 Faunal comparisons between clusters

In the tropics mid-depth transects (cluster t) were characterised by CWC reef-associated ophiuroids, cidarid urchins and soft-bottom cup corals (Table 3.3). *Desmophyllum pertusum* reef is a VME habitat and was observed in six of the 14 transects within this cluster, a sea pen field was also recorded. The remaining two deeper tropical clusters (u and v) appear to split based on their substrate, with the hard-bottom cluster being characterised by serpulid worms, decapods and brachiopods, and the soft-bottom counterpart characterised by soft-bottom cup corals and gastropods (Table 3.3). *Solenosmilia variabilis* reef (a VME habitat type) was present in two of the 13 transects in cluster v; cluster u contains no VME habitat types. All three tropical clusters have comparatively fewer characterising taxa than temperate clusters, with a higher dominance of some taxa leading to decreased diversity (Chapter 2).

The nodes at which clusters split into distinct communities for the Tristan groups are located at much higher values along the similarity axis, suggesting differences between the assemblages in temperate latitudes are more subtle. Shallower (ca. 170 – 300 m) communities (clusters c, h, j, m and n) are characterised by structure-forming and encrusting sponges and hard-bottom *Caryophyllia* spp., with four of the five assemblages considered coral garden VMEs, with antipatharians, stylasterids and gorgonians present. Mid-depth (ca. 330 – 500 m) communities (clusters g and k) are characterised by small hydroids, structure-forming sponges and often *Ophiomusium* sp., and of the five transects that constitute cluster k, one of these contains *D. pertusum* reef. For many of the Tristan clusters, the environmental conditions are similar, except for the fact they are on different seamounts/different sides of the same seamount. In these clusters, the characterising taxa are often the same/similar, but the relative abundances are different, resulting in separate clustering. The deeper temperate assemblage (cluster q) is characterised more by sponges and brachiopods that represent the associated fauna of coral gardens and *S. variabilis* reef.

3.5 Discussion

3.5.1 Environmental drivers

Our observations suggest that the large-scale drivers of benthic assemblage structure in the South Atlantic include latitude, depth, longitude, FBPI and slope (Table 3.2). Previous studies have found that community composition is strongly driven by factors that correlate with latitude and depth across multiple systems (seamount, canyon, slope, etc.) and locations (Rowe & Menzies, 1969; Rex, 1981; L*evin et al.*, 1991; Billett *et al.*, 2001; Ruhl & Smith, 2004); therefore our results concur with the literature on key environmental drivers of community structure in the deep sea.

Latitude in itself is not ecologically relevant, but it acts as a proxy for other variables. Surface primary productivity was strongly correlated with latitude (-0.99), and when used in the DistLM, yields the same results of ~15% variation explained. Food availability has been found to strongly influence community structure in deep-sea ecosystems (Billett *et al.*, 2001; Ruhl & Smith, 2004; Smith *et al.*, 2008; Leduc *et al.*, 2014). Varying levels of resource (food) availability impacts the abundance of most groups of taxa, leading to differences in assemblage structure (this is further explored in relation to specific biological assemblages observed in Section 3.5.2).

The orientation of depth in Figure 3.3, as well as the clustering patterns in Figure 3.4, show that depth is heavily involved in structuring the communities within each region. Depth is commonly assessed as a key driver of faunal composition in the deep sea (Rex *et al.*, 1997; Levin *et al.*, 2001; Howell *et al.*, 2002; Stuart & Rex, 2009; Rex & Etter, 2010), but it is the correlated variables that are more ecologically relevant, including temperature and water mass structure among others. Temperature is key in driving species distributions because it is an important regulator of metabolism. It is therefore likely that some of the importance attributed to depth in shaping benthic assemblages actually reflects the importance of temperature, particularly because the two variables are so strongly correlated (0.94).

Water mass structure has been found to be a key determinant of faunal composition in the deep sea (Tyler & Zibrowius, 1992; Koslow, 1993; Bett, 2001; Howell *et al.*, 2002). In this study the effect of water mass structure on driving the distinction and distribution of biological communities is particularly evident when focusing on the clustering patterns of the Tristan transects. Tristan da Cunha comprises four oceanic islands; three (Tristan, Nightingale and Inaccessible) are in the northern section of the EEZ around 37 °S and the fourth, Gough Island, at ~40 °S. The Subtropical Convergence Front (STCF) lies between the two island groups and refers to where the warmer, temperate waters of the South Atlantic Gyre (SAG) meet the colder waters of the Subtropical Convergence Zone (Smythe-Wright *et al.*, 1998). The exact location of the STCF fluctuates temporally, shifting north in the austral summer and south in the austral winter. The island group in the north always falls within the SAG meaning it receives warmer, temperate waters all year round, and Gough Island always sits in the Subtropical Convergence Zone meaning it is always surrounded by cooler water. Gough used to be subject to colder fronts that travelled further north than present day, hence the presence of sub-Antarctic bryozoans (Barnes & Griffiths, 2007). In contrast, the seamounts between the island groups are subject to large variations in temperature and salinity (and therefore water mass structure) depending on the time of year. This dynamic oceanographic regime means that dependent on where a feature is within the Tristan EEZ, it could be in one of three separate oceanographic systems (because the far south of the EEZ falls within the subantarctic frontal region), and thus support different faunal communities. In order to further explore this, temporal monitoring of water properties at the Tristan sites would be beneficial to map water mass movement.

Topographic variables including slope and bathymetric position index (BPI) are, as our results support, often identified as key drivers of benthic assemblages in the deep sea, both at the inter- and intra-seamount level (Boschen *et al.*, 2015; Morgan *et al.*, 2019). Slope and BPI can be used to infer the geomorphology of a region (Greene *et al.*, 1999), which in turn can provide insight into the hydrodynamics, and thus substrate types observed within an area (Stephens & Diesing, 2015).

Steeply sloping areas such as those sampled at Ascension (and to a lesser extent St Helena) are typically characterised by fast flowing bottom currents that can scour the seabed, in some cases revealing the bedrock (Stephens & Diesing, 2015). CWC reef built of species such as *D. pertusum* (examples of which were recorded in all territories) favours these locations due to the increased food supply available to filter from the faster bottom currents. In much of our imagery from the tropical transects, the CWC reef was dead resulting in assemblages strongly dominated by reef-associated ophiuroids (cluster t). This link between the distinct ophiuroid-dominated assemblages and high slope areas that were once home to much live CWC reef may somewhat explain the identification of slope as a significant driver of benthic assemblage structure in the South Atlantic. The wide range of FBPI values at Ascension and St Helena suggest the seabed is relatively ‘bumpy’, with parts that sit above or below surrounding areas such as gulleys and reefs. These seabed depressions allow for the accumulation of sediments within them, hence the identification of some soft substrate assemblages within the tropical data (e.g. cluster u), providing a link between geomorphology and substrate type.

More gently sloping areas can also be found on seamounts, typically around the summit region. The areas are generally subject to slower currents that allow for the build-up of sediment to create soft substrate environments, or allow for the accumulation of cobbles that are not swept away (as frequently observed often at Tristan). These rocks increase substrate heterogeneity that has been shown to increase the macrofaunal diversity of an area due to required adaptations (Taylor & Wilson, 2003; Bergmann *et al.*, 2011; Roy *et al.*, 2014), and slower currents may also mean a wider range of filter feeding taxa can survive here without the risk of delicate feeding appendages being damaged by fast flows. This is evidenced by the wide range of small, filter-feeding taxa observed in many communities at Tristan (e.g. cluster h, Table 3.3, Table 3.4).

While average substrate hardness was not identified as a significant driver in the final DistLM, it was identified as individually significant in the preliminary marginal tests. It is possible that the importance of substrate type in driving assemblage structure within this dataset is represented in the identification of slope (steeper areas lead to more exposed hard substrate and CWC reef communities) and FBPI (depressions become filled with soft substrate) as significant drivers. This would concur with studies such as Serrano *et al.* (2017) who identified depth and substrate type as a primary driver of soft substrate benthic assemblage distribution, and slope as a key determinant in the distribution of hard substrate assemblages. Our results report the significance of variables that Serrano *et al.* (2017) used to predict the distribution of both hard and soft substrate assemblages, thus suggesting our results capture the variability in drivers between substrates across the basin.

The majority of previous studies focusing on benthic assemblages on seamounts investigate individual seamounts (McClain & Lundsten, 2015; Victorero *et al.*, 2018; Morgan *et al.*, 2019). Those that have investigated assemblage structure and/or its drivers over multiple seamounts (Howell, 2010; O'Hara *et al.*, 2010; Boschen *et al.*, 2015; Clark & Bowden, 2015) have done so from the same geological feature/ridge system, and therefore often only present data from a single biogeographic region. This study compares a total of 13 seamounts/oceanic islands across 32 degrees of latitude, from different biogeographic regions (Zezina, 1973, 1997; Sutton *et al.*, 2017). Despite this, as previously detailed, the five variables identified as significant drivers of assemblage structure are similar to the results yielded in studies focusing on smaller regions or individual seamounts. This similarity suggests that results obtained in this study are representative of reality and are not an artefact of data structure. The five variables identified here as significant are so over the entire dataset, and therefore site-specific drivers, such as small-scale local hydrographic features, have likely been overlooked. This is because they are not representative of the whole dataset. In this sense, this analysis has identified common variables across the basin, and therefore those that are likely to influence many seamounts (at least in tropical and temperate areas). Whilst this represents significant progress in the understanding of seamounts in the South Atlantic, it is important to continue to assume a precautionary stance when generalising these ecosystems.

3.5.2 Biological communities

The SIMPROF test identifies a large number of assemblages present at Tristan (16 out of 22) compared with the six clusters containing all transects from Ascension and St Helena (Figure 3.4), suggesting that assemblage diversity (i.e. β-diversity) is higher at Tristan than the other territories. Spatial and seasonal differences in water mass structure, as outlined above, across the Tristan EEZ likely explain why the biological data from Tristan splits into many distinct assemblages; there will be taxa acclimated to the warmer waters around the northern island group, some to the cooler waters around

Gough Island and a number of assemblages on the seamounts that can tolerate fluctuations in temperature and salinity throughout the seasons. Although increased productivity due to frontal proximity may explain high numbers of assemblages in temperate latitudes, it is important to note that six sites (i.e. seamounts and oceanic islands) were sampled at Tristan in comparison to the three at St Helena and four at Ascension. The disparity in the number of different sites sampled per EEZ is likely somewhat responsible for the higher numbers of assemblages observed at Tristan.

Tristan's benthic assemblages are characterised largely by filter-feeding taxa such as sponges (both structure-forming and encrusting) and hard-bottom *Caryophyllia* cup coral species. Contrastingly, tropical benthic assemblages found at Ascension and St Helena are frequently dominated by scavenging and/or detritivorous taxa including CWC reef-associated Ophiuroidea (brittle stars) and cidarid sea urchins (Table 3.3). Surface primary productivity is thought to drive diversity patterns in the deep sea (e.g. Sun *et al.*, 2006; Woolley *et al.*, 2016; Chapter 2), but less work has focused on the effect it may have on community structure. Benthic taxa inhabiting the seafloor below oligotrophic, low productivity surface waters such as those in the tropics are likely to have developed strategies to help cope with the sporadic food (energy) supply, and/or are less likely to have feeding strategies that heavily/solely depend on sinking organic matter. Due to the specialist strategies employed by successful species in these low productivity regions, communities may be more likely to display high levels of dominance by fewer, more specialist taxa that are able to thrive. This would explain the high within-depth-stratum variation but low α-diversity in tropical regions (Chapter 2). Opposingly, Tristan is surrounded by high-productivity waters and the deep-sea benthic taxa here are likely accustomed to relatively plentiful sinking organic matter upon which filter-feeding taxa heavily rely. The greater food supply may support more ecological niches leading to communities at Tristan that: (a) comprise of different taxa to those found in lower productivity areas resulting in separate SIMPROF clusters, and (b) have a higher species richness, with less dominance by few, specialist taxa. This is evidenced by the higher number of characterising taxa (and thus more even communities) counted in the 16 Tristan assemblages (Table 3.3), as well as the dominance of filter-feeding taxa (sponges, hydroids, corals etc.). Similar results linking high variability in community structure to surface chlorophyll-α concentration are described by Clark and Bowden (2015) for a seamount chain in the Ross Sea, Antarctica. Although their surface productivity metric is slightly different to the surface primary productivity data used in this study, both relate to the photosynthetic activity, and induced productivity in surface waters above deep-sea benthic assemblages. Given this explanation, it is surprising that POC flux to depth is not considered a significant driver of assemblage structure. This is likely because of the relatively shallow bathymetric range from which the data are collected for this study (170 – 1010 m). Both Chapter 2, using a subset of the data presented here, and Woolley *et al.* (2016) found that in the upper ocean (down to 1,000 m and 2,000 m, respectively), variables linked to solar energy input were better predictors of diversity. The data extracted for each transect for POC flux to depth comes from Lutz *et al.*'s (2007) model that uses depth as a function. Using satellite-derived, surface primary productivity data for these shallower ranges, represents better productivity data than Lutz *et al.* (2007) and therefore explains why it is not a selected variable in the DistLM best solution.

3.5.2.1 Vulnerable Marine Ecosystems

Seamounts contain VMEs, and the seamounts of the South Atlantic are no exception, with VMEs being recorded in all three territories. Significantly more, both in terms of abundance and richness, were observed at Tristan, where 53% of transects were considered VMEs. Whilst the epifaunal communities of the CWC reef in the South Atlantic are likely characterised by different species to those on reefs in the North Atlantic, there does seem to be a strong crossover in the functional similarity and overall ecology of assemblages found in each basin on both *D. pertusum* and *S. variabilis*. However, there is less similarity between the coral garden and sea pen field assemblages. Descriptions of each VME type are found below.

Cold-water coral reef

In our study, both *D. pertusum* and *S. variabilis* reef were recorded, but only the former was found in all three territories. *Desmophyllum pertusum* is a reef-building Scleractinian known to have a ubiquitous distribution and has been recorded in reef structure across the South Atlantic previously, in both the Namibian and Brazilian EEZs (Hanz *et al.*, 2019; Kitahara *et al.*, 2020).

At Tristan, *D. pertusum* reef is recorded in one transect within cluster k that shows dense, living reef with a few attached, epifaunal taxa present (namely CWC reef-associated ophiuroids and some decapods), and multiple serranid fish (*Lepidoperca coatsii* (Regan, 1913)). Live reef is thought to support few attached epifauna because the coral itself is successful in preventing biofouling (Freiwald *et al.*, 2004). This transect may therefore correspond to the living summit region of the reef system (Mortensen *et al.*, 1995). When focusing on the mobile epifaunal community, this assemblage bears similarity to a *D. pertusum* reef described in Howell *et al.* (2010a) in the North Atlantic that also had decapods and ophiuroids among the key epifaunal taxa.

However, due to the limited images of this reef within the transect, more data are required to fully interrogate this comparison.

Cluster q contains deeper *S. variabilis* reef from Tristan, although much of the reef is dead with very few small patches of live coral, suggesting it forms part of the dead framework slopes. There is less literature describing assemblages associated with *S. variabilis*, but its presence is known in the South Atlantic (see Raddatz *et al*. (2020) for compiled presences). Frequently observed epifaunal framework taxa in our images consist of CWC reef-associated ophiuroids, encrusting sponges, squat lobsters and hydroids. Davies *et al.* (2014) describe an '*ophiuroids and Munida sarsi associated with coral rubble'* biotope to which cluster q is similar in some respects. Parallels can be drawn between the strong presence of ophiuroids and squat lobsters, but their study describes this assemblage as corresponding to the '*Lophelia* rubble zone' (*sensu* Mortensen *et al.*, 1995). However, if the ophiuroids and squat lobsters simply require dead framework as opposed to live reef, it may not be significant as to whether the reef is intact or in rubble form. Mortensen *et al.* (1995) and Roberts *et al.* (2009) describe dead framework as being characterised by sponges, gorgonians and hydroids. This is similar to the epifaunal community observed here, although it is on a different species of reef-building scleractinian coral.

For Ascension and St Helena, all the *D. pertusum* reef clusters together in t, where six of the 14 transects within the cluster were deemed to be this VME, although again much of the reef framework is dead with only small, infrequent patches of live coral. Coral framework is thought to facilitate higher diversity than areas of the living reef (Jensen & Frederiksen, 1992), often supporting suspension feeders and other coral species

(Mortensen *et al.*, 1995). The notion of higher diversity associated with coral framework appears to hold true for the *D. pertusum* reef in cluster t. Frequently observed epifaunal taxa on the reef framework consist of a bright orange anemone, multiple species of the sponge genus *Aphrocallistes* Gray, 1858, dense mats of ophiuroids, and small patches of live *Madrepora oculata* Linnaeus, 1758, another species of reef-building scleractinian. Reef is interspersed with soft sediment areas providing habitat for the same soft-bottom dwelling taxa (typically *Cidaris* Leske, 1778 sp., soft-bottom Caryophyllidae cup corals and often the large anemone, *Actinauge richardi* (Marion, 1882)) as the wider expanses on soft sediment found within the same cluster; this is likely why *D. pertusum* reef does not cluster individually. Frequent patches of soft sediment within reef framework are also described in the '*predominantly dead low-lying coral framework'* biotope from Davies *et al.* (2014), as are live patches of *M. oculata*.

Cluster v comprised transects found significantly deeper than the above clusters, and is the only assemblage containing *S. variabilis* reef. Images show a mixture of dead framework and coral rubble, suggesting this transect may represent the transition zone between the dead framework slope and rubble apron (Mortensen *et al.*, 1995). Much of the dead reef and surrounding rubble in cluster v provides habitat for brachiopods, encrusting sponges or small ophiuroids. In areas where the framework is more intact, there are aggregations of brisingids and antipatharians. This description seems to reflect parts of the description of the epifaunal communities on dead framework in Freiwald *et al.* (2004). The cluster also contains large areas of exposed bedrock that support the same/similar taxa as those found on the framework. The exposed bedrock suggests the presence of reasonable currents in the area which may explain the higher diversity of filter feeding epifauna in cluster v.

Hard-bottom cup coral fields and/or coral gardens

Hard-bottom cup coral fields and coral gardens are only observed within the Tristan EEZ. The substrate in these areas typically consisted of cobbles and boulders, on which the corals were growing. Clusters b, c, h and n were all identified as being mosaic assemblages representing both cup coral fields and coral gardens dominated by gorgonians (often *Thouarella*, Gray, 1870 spp.), multiple stylasterid taxa and occasionally antipatharians. Despite their protected habitat status, there are few descriptions of the assemblages that often form coral gardens with which to compare our findings. Davies *et al.* (2015) describe multiple types of coral garden in the North Atlantic and identify high numbers of *Caryophyllia* spp. cup corals and sponges in their coral gardens; both are true for Tristan coral gardens also. However, the North Atlantic coral gardens also appear to be dominated by larger corals such as *Keratoisis* Wright, 1869 spp. or patches of reef-building scleractinian (this is similar to coral gardens in the Mediterranean that harbour large individuals, Bo *et al.*, 2012). Although they were not classed as coral gardens because they were too sparse, Bullimore *et al.* (2013) do describe coral-dominated assemblages but similarly to Davies *et al.* (2015), stylasterids are not listed as typical taxa; at Tristan, stylasterids are present in most of the coral garden clusters. The distinct lack of large individuals and the presence of numerous small stylasterids in the coral gardens at Tristan is perhaps driven by the substrate in the coral gardens at Tristan being unfixed, and therefore unable to support larger (heavier) corals. Multiple sponge species are acknowledged as being associated with coral gardens in both the similar coral garden assemblages from Davies *et al.* (2015), and are considered characterising taxa of the Tristan coral gardens (Table 3.3). The disparities in the morphologies of key taxa when comparing Tristan's coral gardens to those found elsewhere suggest those found at Tristan may not be widespread in the North Atlantic.

Sea pen fields

Only one sea pen field was recorded in the data, located in cluster t (alongside the *D. pertusum* reef). The field comprised two morphospecies of sea pen and appeared to be located around the edges of the *D. pertusum* reef in soft sediment alongside cidarid urchins. Unfortunately, there has been no confirmed identification of the sea pens beyond the rank of order (Pennatulacea), although one appears similar to species in the *Protoptilum* Kölliker, 1872 genus. Despite the habitat being suitable for other taxa such as cerinathids and other soft-bottom fauna, the area appears to only support sea pens and urchins. This is unlike the sea pen fields described by Davies *et al.* (2014) and Howell *et al.* (2010a) that both describe populations of cerinathids within sea pen fields. Sea pens are known to enhance the biodiversity of an area by increasing habitat heterogeneity (Buhl-Mortensen *et al.*, 2010) however, it is not possible to record epifaunal communities on the sea pens from this dataset due to the downward facing angle of the camera. Due to the single occurrence of this VME, and the clustering with other VMEs, it is difficult to distinguish the characterising taxa of the sea pen field itself, although visual inspection suggests the sea pens themselves dominate and potentially outcompete other taxa.

3.5.3 Management implications

Some suggested management strategies for a number of deep-sea industries such as fishing and seabed mining propose areas to be set aside and excluded from exploitation activities to facilitate the conservation of biodiversity in a specific region, as well as to provide a baseline against which to interpret data on the environmental impacts of industry activities (e.g. Areas of Particular Environmental Interest designated by the International Seabed Authority). Results show high β-diversity at Tristan, possibly linked to the high environmental variability as a result of temporal and spatial changes in water mass structure associated with the STCF. When designing management strategies, it is therefore not wise to assume that close geographical proximity infers similarity in the biological assemblages of features. Our results suggest it is important to consider the environmental variability of the region, particularly in terms of the water mass structure and oceanographic conditions. In this respect, a bioregionalisation approach (*sensu* Howell, 2010) could be important in helping to identify areas of high environmental variability, and ultimately to support effective management decisions. However, it is important to note that further investigation should be undertaken of bioregionalisation approaches to ensure they adequately capture variability, and that this environmental variability is linked to different assemblages.

The governments of each UKOT island from which our data were collected have all developed marine management plans and offered varying levels of protection within their EEZ. Bottom trawling is a method of fishing for demersal species by towing nets and other mobile gear along the seabed. Evidence suggests that bottom trawling significantly reduces the benthic biomass of seamounts (Koslow *et al.*, 2001), and that benthic megafaunal communities have little resilience against this practice (Clark *et al.*, 2019). All three territories have prohibited bottom trawling within the EEZs, a measure that will undoubtedly strengthen the protection of VMEs. This dataset provides important information on the distribution of VMEs within the UKOT of Saint Helena, Ascension and Tristan da Cunha, but it is now important to understand the wider distribution of VMEs across the Atlantic. Few biological surveys have been undertaken in ABNJ in the South Atlantic, although seamounts within the Convention Area of the South East Atlantic Fisheries Organisation (SEAFO) were the target of two surveys in 2015 and 2019. Data collected contributed towards the closure of bottom fisheries on a number of features along the Walvis Ridge (CM 30/15, 2015) to protect VMEs (FAO, 2016). The prevailing current in this region flows in an easterly direction as the southern arm of the South Atlantic gyre (Peterson & Stramma, 1991; Smythe-Wright *et al.*, 1998). The protection afforded to seamounts within the Tristan EEZ may therefore have a positive knock-on effect on VMEs on seamounts in ABNJ (e.g. by way of increased larval recruitment, Ross *et al.*, 2017), but this is not substantiated as of yet. Ascension and St Helena are connected to other ridge systems (MAR and Guinea seamount chain, respectively) and therefore similar effects may be felt should MPAs/fisheries closures be designated in the northern southeast Atlantic. Investment in furthering our understanding on the health and connectivity of VME populations in the South Atlantic will facilitate incorporation of these principles into broad-scale sustainable management, and ultimately make management plans more robust. It will also allow insight into the conservation significance of the existing large MPAs in the South Atlantic and allow for assessment of the ecological coherence of the South Atlantic MPA network as a whole (Foster *et al.*, 2017; Ross *et al.*, 2017).

3.6 Conclusion

Our data highlight variability in the megafaunal benthic communities of seamounts and oceanic islands across the South Atlantic Ocean basin. This is true for seamounts that are separated by large distances (i.e. in different biogeographic regions), but in the case of temperate latitudes, features in relatively close proximity also appear to harbour distinct communities, possibly linked to varying levels of environmental variability. Multiple biological communities observed within this dataset constitute VMEs under UNGA 61/105. Some of these, namely CWC reef, bear similarities to assemblages identified in the North Atlantic, while the coral garden VMEs identified within the

Tristan EEZ are more distinct. Our results evidence the importance of accounting for environmental variability of the region when designing management plans, as well as highlighting the need for further research into the distribution of VMEs across the South Atlantic, and the effects that current protection measures are having.

CHAPTER 4: FILLING THE DATA GAPS: TRANSFERRING MODELS FROM DATA-RICH TO DATA-POOR DEEP-SEA AREAS TO SUPPORT SPATIAL MANAGEMENT

4.1 Abstract

Spatial management of the deep sea including areas beyond national jurisdiction (ABNJ) is challenging due to limited available data on the distribution of species and habitats to support decision-making. In the well-studied North Atlantic, predictive models of species distribution and habitat suitability have been used to fill data gaps. In the South Atlantic and other poorly studied regions, this is not possible due to a lack of data. In this study, authors ask whether models constructed in data-rich areas can be used to inform data-poor regions. Aa model transfer approach was used to identify whether a habitat suitability model for *Desmophyllum pertusum* cold-water coral reef, built in a data-rich deep-sea basin (North Atlantic), can be transferred to a data-poor basin (South Atlantic). The transferred model was built using the Maximum Entropy (MaxEnt) algorithm and constructed with 227 presence and 3,064 pseudo-absence points, and 200 m resolution environmental grids. Performance in the new area was validated using an independent dataset of *D. pertusum* presences and absences, with assessments made using both threshold-dependent and -independent metrics. Results suggest that a model for *D. pertusum* reef fitted to North Atlantic data transfers well to the South Atlantic basin, with an area under the curve of 0.72. Suitable habitat for *D. pertusum* reef is predicted on 21 of the assessed 27 features including seamounts. In ABNJ, four seamounts that provide suitable habitat for *D. pertusum* reef are at least partially protected from bottom trawling, while three do not fall within closures. Marine Protected Areas/Zones designated by Saint Helena, Ascension Island and Tristan da Cunha provide significant protection for *D. pertusum* reef habitat. In conclusion, model transfer approaches can provide significant contributions to spatial planning processes, particularly in ABNJ and areas that have previously undergone little scientific exploration.

4.2 Introduction

As the global human population increases, so does the demand for a variety of natural resources, including some from the deep ocean (Ramirez-Llodra *et al.*, 2011; Halpern *et al.*, 2015; Van Dover *et al.*, 2017; Kroodsma *et al.*, 2018). Increased anthropogenic pressure on the deep sea, in the form of mining, fishing, and climate change, mean that effective, integrated management, including marine spatial planning, is becoming ever more critical (Mengerink *et al.*, 2014; Wright *et al.*, 2019). In order to allow for cross-sectoral protection of ocean in Areas Beyond National Jurisdiction (ABNJ), the United Nations are leading negotiations on an international, legally-binding instrument on the conservation and sustainable use of marine biological diversity in ABNJ (commonly referred to as the Biodiversity Beyond National Jurisdiction (BBNJ) negotiations). This legal instrument aims to use a multidisciplinary approach to allow for the sustainable use of ocean resources in an equitable manner, while allowing for the conservation of species and habitats via implementation of area-based management tools (ABMTs). The drive for area-based management is also apparent in national waters, evidenced by in-country programmes designed to facilitate both conservation and sustainable use of ocean resources in Exclusive Economic Zones (EEZs). An example of this is the South African Marine Protected Area (MPA) network designated in 2019 that protects 5% of the South African EEZ. In-country initiatives should be considered within broader regional scale projects that work across neighbouring countries along continental margins in the interest of developing ocean governance structures and management plans that reflect the spatial extent of, and boundaries between, different marine ecosystems, rather than national boundaries (e.g. the Benguela Current Commission). This transboundary principle can also be applied to the management of specific resources, for example, the management of the South African and Namibian hake fishery.

MPAs are defined by the International Union for Conservation of Nature (IUCN) as "*parts of intertidal or subtidal environments, together with their overlying waters, flora and fauna and other features, that have been reserved and protected by law or other effective means*" (IUCN-WCPA, 2008), and are one of several ABMTs that can be employed. Over the last few decades, scientists and conservationists have engaged in a number of political processes led by international conventions and statutory bodies, designed to identify key geographic areas to put forward for varying levels of protection in the High Seas. Many of the existing ABMTs apply only to specific sectors, for example, fisheries closures led by Regional Fisheries Management Organisations (RFMOs), and the Areas of Particular Environmental Interest (APEI) selection process led by the International Seabed Authority in relation to seabed mining. Other processes have taken a more cross-sectoral approach, focusing on identifying areas that could be candidates for protection from multiple industries if the appropriate legislation were in place. An example of this approach would be the process led by the Convention on Biological Diversity that facilitated the identification and designation of Ecologically or Biologically Significant Areas (EBSAs). These different types of MPAs are either not legally binding (e.g. EBSAs), or can only protect against adverse impacts from individual sectors (e.g. APEIs and RFMO fisheries closures). However, the commonality among them is that they are all based around the concept of area-based management.

Historically, most MPAs have been designated individually on an ad-hoc basis to meet a range of national-level conservation targets (UNEP-WCMC, 2008). However, the high connectivity between most marine ecosystems means that the concept of 'ecological coherence' within networks of MPAs is now considered an important aspect in numerous pieces of legislation (e.g. United Nations, 2002; CBD, 2004). An important aspect of ensuring the ecological coherence of any MPA network is to ensure decisions are evidence-based with regards to: (1) the location of areas identified for protection, (2) the species/habitats named as protected features, and (3) which/how activities are restricted to protect said areas. Having access to accurate biological maps is therefore integral to any spatial management process, something which becomes progressively more difficult with increasing area. Thus far, broad-scale management has frequently been based on few data and assumptions. For example, some RFMOs have shortlisted key features such as seamounts purely on the assumption that certain topographic features host habitats of conservation importance (*sensu* Watling and Auster, 2017). Resultantly, there are often few/no data to assess representativity or coherence of these closure networks. These closures work only in the sense that impacts are excluded, but there are no data on population trends within/without these areas to determine their effectiveness. Since there is a widespread impetus for basin scale networks of spatial management, the largely data-limited nature of the deep sea stands to pose a major challenge to evidence-based decision making.

Habitat suitability modelling (HSM) has the potential to be an important tool when it comes to building maps of the spatial distribution of species and habitats in the deep sea. There are a large number of different HSM techniques (García-Callejas & Araújo, 2016), but all are founded on the same basic principle: using knowledge of where species/habitats occur to predict where else they might occur based on environmental similarities. HSM has been used to successfully predict the distributions of a variety of deep-sea taxa including scleractinian corals across multiple basins (Davi*es et al*., 2008; Davies & Guinotte, 2011; Yesson *et al*., 2012; Ross & Howell, 2013; Ashford *et al*., 2014; Howell *et al*., 2016; Rowden *et al*., 2017).

The NE Atlantic has been described as "*the cradle of deep-sea biology*" (Gage, 2001) thanks to it being the focus of many scientific cruises to understand the biology and ecology of deep-sea habitats. These include, but are not limited to, studies of the continental slope (Howell *et al.*, 2010b), seamounts (Davies *et al.*, 2015) and abyssal plains (Durden *et al.*, 2015). Here, the concept of mapping and modelling the distribution of vulnerable habitats has been explored, particularly for those designated by the UN General Assembly (UNGA) as Vulnerable Marine Ecosystems (VMEs) under Resolution 61/105. These areas can be defined as those that may be vulnerable to the impacts of fishing (FAO, 2009), and include cold-water coral (CWC) reefs and deep-sea sponge aggregations. Ross and Howell (2013), used HSM to both assess the extent and distributions of VMEs in the NE Atlantic, and to quantify the efficacy of the existing UK and Ireland MPA network in relation to political conservation targets. Furthermore, in 2016, Howell *et al.*, used the same HSM methodology to predict the distribution of deep-sea sponge aggregations in the North Atlantic and suggest management strategies in ABNJ that would be beneficial to the conservation of the ecosystems.

The deep sea is a challenging environment to study both in terms of operational logistics and financial costs. Large datasets are achievable for ocean basins that have been the focus of scientific research for decades (e.g. the North Atlantic), but for less studied oceanic basins where few biological data have been collected, such as those in the southern hemisphere, this remains impossible (Menegotto and Rangel, 2018; Howell *et al.*, 2020a). This problem persists despite technological advances meaning that all areas of the oceans are accessible, because the capacity to deploy such technologies is restricted to a limited group of countries and/or organisations with sufficient infrastructure and funding (Howell *et al.*, 2020b). The strong spatial sampling effort bias in the deep sea towards the northern hemisphere means that for many deep-sea habitats and species, scientists lack the fundamental knowledge of their distribution elsewhere. Consequently, there are very few accurate biological maps that can be drawn upon to facilitate evidence-based marine spatial planning in the under-explored regions.

The South Atlantic Ocean lies between the African and South American continents and despite representing 11.1% of the global ocean area (Eakins & Sharman, 2010), is poorly-understood, particularly in relation to the distribution of species and habitats within it (Howell *et al.*, 2020b). It is therefore currently not possible to build reliable HSMs using data *from* the South Atlantic, *for* the South Atlantic. Although more commonly used as tools to predict across the same geographical areas that the data used to build and calibrate the model comes from, established HSMs can also be transferred into different regions (Torres *et al.*, 2015). Model transfer occurs when the model is used to predict into a different area/region from which the model is calibrated, an example of which would be across ocean basins. Yates *et al.* (2018) provided a thorough review of ecological model transferability and identified knowledge gaps that contribute to the fundamental challenges of successful model transfer. Among others, the authors addressed questions on how complexity may influence model transferability, suggesting that more simple models enable more successful transfer. Additionally, taxa that exhibit less adaptive and behavioural plasticity typically have a higher transfer potential. However, the highest priority knowledge gap identified features around the lack of standardised methods for evaluating model transferability.

Model transfer, although requiring further development, has the potential to become a particularly valuable tool, as it provides an opportunity to mediate historic geographic biases. Specifically, it allows models to be transferred from 'data-rich' areas where data are comparably plentiful (e.g. the North Atlantic), to 'data-poor' areas where historically there has been little scientific survey effort (e.g. the South Atlantic). Good performance across this data gradient could facilitate evidence-based marine management in areas that historically have not been the scientific focus.

This chapter seeks to answer the question: can models built in relatively data-rich regions can perform well when applied to data-poor regions? Specifically, a habitat suitability model for *D. pertusum* reef in the North Atlantic was constructed and transferred to the South Atlantic. Transfer performance was then evaluated using an independent dataset, and an example given of how the resulting modelled map might be used to inform the area-based management of the region.

4.3 Methods

4.3.1 The North Atlantic model

The data-rich, *Desmophyllum pertusum* reef HSM transferred in this study spans the NE Atlantic to the west of the United Kingdom and Ireland (Figure 4.1).

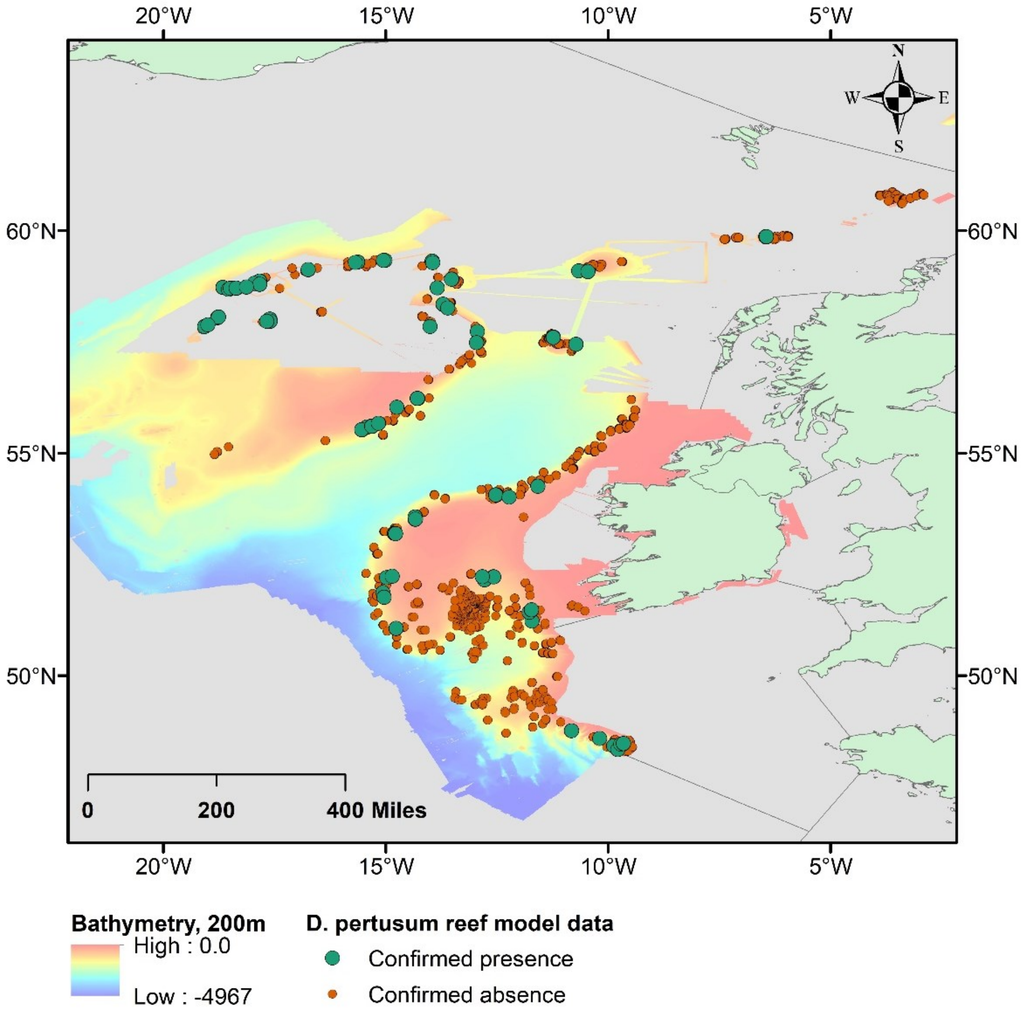

Figure 4.1: Desmophyllum pertusum reef habitat suitability model extent shown. Presence-absence data used to build the model are plotted on top of the high-resolution bathymetry and detailed in the text. Map drawn in Goode Homolosine Ocean.

4.3.1.1 Environmental data preparation

High-resolution multibeam bathymetry data were taken from Ross & Howell (2013) and Ross *et al.* (2015), and combined with newly collected data from five research cruises to the northeast Atlantic: i) Eurofleets2 funded DeepMap cruise CE15011 (2015), with ROV Holland I; ii) NERC funded Deep Links JC136 (2016), with ROV ISIS; iii, iv, v) Sea Rovers RH17001 (2017), RH18002 (2018) and CE19015 (2019), with ROV Holland I. These were jointly funded by the Irish Government and European Union. Data were gridded at 200 m resolution and re-projected from WGS84 into Goode Homolosine Ocean, an equal area projection (Figure 4.1). Raster grids for seven bathymetrically derived topographic variables were calculated using the Benthic Terrain Modeller plug-in (Walbridge *et al.*, 2018) in ArcMap v10.7, these were: rugosity (neighbourhood = 3), curvature, plan curvature, profile curvature, slope, broad-scale bathymetric positions index (BBPI, inner and outer radii = 5 and 50) and fine-scale bathymetric position index (FBPI, inner and outer radii = 1 and 5). Rationale for selecting these variables and their calculation can be found in the existing literature (Guinan *et al.*, 2009a; Yesson *et al.*, 2012; Ross & Howell, 2013). Radii values for both BBPI and FBPI were selected to facilitate identification of topographic features known to provide suitable habitat for *D. pertusum* reef such as canyons and gulleys.

Using *in-situ* CTD data associated with the ROV deployments and archived CTD casts from the British Oceanographic Data Centre (BODC), the relationships between depth, latitude and longitude, and temperature and salinity across the study area were characterised using generalised additive models (GAMs) built in the mgcv package (Wood, 2011) in R (R Core Team, 2019); see Appendix D.1 for full details. GAMs were used to predict temperature and salinity values across the extent of the bathymetry, resulting in continuous data layers for these variables.

4.3.1.2 Biological data preparation

Biological data (i.e. *D. pertusum* reef presences and absences) were extracted from Ross & Howell (2013) and Ross *et al.* (2015), and combined with newly collected data from the aforementioned five research cruises. Collectively these research cruises provide a dataset consisting of 188 high definition video transects spread across the study area (Figure 4.1).

Presence and absence data for *D. pertusum* reef were reduced to one point per cell to avoid overweighting of certain values. Cells containing any presence points were denoted as a presence, all other points were denoted as absence. The final biological data used to build the model therefore consisted of 227 presence points (at one point per cell) and 3,064 absence points for *D. pertusum* that all sit on high-resolution multibeam bathymetry (Appendix D.2).

4.3.1.3 Pre-selection of model variables

Environmental data underlying the biological data for all 3,291 points were extracted in ArcGIS v10.7 and exported to R. Significance and explanatory power of the individual variables were established using GAMs (Appendix D.3). Variables were then assessed for correlation, after which highly correlated (>±0.7) pairs were either removed or trialled as substitutes during forward and backward stepwise selection of variables using GAMs (Appendix D.4 and D.5). Depth was identified as the most significant environmental variable, but the regionally dependent relationship between depth and other environmental drivers such as temperature means that models with depth as a predictor are likely to be less transferable. Although significant, the loss in performance when temperature was substituted for depth was minimal (Appendix D.5) and therefore temperature was selected to promote transferability of the model. Selection of final variables was ascertained using GAMs, employing both forward and backward stepwise selection procedures (Appendix D.5). The final variables used in the model were temperature, rugosity, FBPI and plan curvature.

4.3.1.4 Final habitat suitability model

Maximum entropy modelling (MaxEnt, Phillips *et al.*, 2006), was used to build the final models. MaxEnt is a type of HSM that aims to find the distribution of predictions that provide maximum entropy (i.e. the most uniform order). As well as being a proven popular choice among ecologists (Elith *et al.*, 2011; Merow *et al.*, 2013), MaxEnt performs well when compared to other HSM techniques (Piechaud *et al.*, 2015; Kaky *et al.*, 2020), and Duque-Lazo *et al.* (2016) found it transferred best compared to other modelling techniques. The models were built using a regularisation parameter of one and allowing only for linear, quadratic and product features to be used for the variable response curves (i.e. removal of hinge and threshold feature options). The final MaxEnt models were constrained to sampled conditions using the MaxEnt novel climates output; a mask that removes predictions in areas where environmental conditions fall outside the ranges of the input data.

4.3.1.5 Internal model validation

Model evaluation was completed by partitioning the dataset into a 70/30 training/test dataset 10 times. Prevalence, the ratio of presence:absence, within each test and training dataset were checked manually to ensure consistency using the prevalence of the whole dataset as a guide. Any partitions identified as having >±1% change in the amount of presence data within the full dataset were discarded and another random partition made until all partitions satisfied this criteria. Using the partitioned data, 10 new models were built and evaluated using the ‘PresenceAbsence’ package (Freeman & Moisen, 2008) in R. Consideration was given to three different thresholding methods as suggested in Liu *et al.* (2009), these were sensitivity-specificity equality (Sens=Spec), sensitivity-specificity sum maximization (MaxSens+Spec) and minimum distance to the top left corner in the receiver operating characteristic curve plot (MinROCdist). Using the presence.absence.accuracy() function, the thresholding techniques and resulting model performances were assessed using three widely used indices: sensitivity, specificity and percent correctly classified (PCC). Sensitivity and specificity refer to the model’s ability to correctly predict whether known points are presences (sensitivity) or absences (specificity); PCC is similar but does not discriminate between presences and absences. True skills statistics (TSS) was also calculated from sensitivity and specificity and is used in place of Cohen’s kappa as it corrects the overall accuracy of the model predictions using the accuracy expected to occur by chance, and is particularly suited to presence-only modelling (Allouch*e et al.*, 2006). For both AUC and threshold-dependent metrics the mean and standard deviation for each metric was calculated for the 10 partitioned datasets and for the full model.

4.3.2 The South Atlantic transfer

The South Atlantic was deemed an appropriate basin for transfer due to the similarity in the predictor variable ranges (plan curvature, rugosity, temperature and FBPI) between the two regions (Appendix D.6), and similarity between ecosystems observed in the two basins (Chapter 3).

4.3.2.1 Environmental data preparation

To create a comparable dataset on which to transfer the North Atlantic model, high-resolution 200 m bathymetry from the South Atlantic basin was collated from multiple sources (Table 4.1) to obtain the largest geographical extent possible. This basin-wide bathymetry layer was cropped to a maximum depth of 1,500 m to reduce the computational power required to manipulate the data and to encompass the known depth niche of *D. pertusum* (Wisshak *et al.*, 2005; Davies *et al.*, 2008). It was then re-projected into Goode Homolosine Ocean after which plan curvature, rugosity and FBPI layers were made in the Benthic Terrain Modeller toolbox using the same flexible options as used in the North Atlantic.

Table 4.1: Sources of high-resolution 200 m multibeam bathymetry in the South Atlantic.

Data provider	**Description**	**Citation**
Global Multi-Resolution Topography (GMRT)	All available bathymetry in the database covering the region 0 °N, 30 °E, 70 °W, 60 °S.	(Ry*an et al.*, 2009)
UK Government Blue Belt Programme	Data collected during the 2018 and 2019 cruises aboard the *RRS James Clark Ross* (JR17004) and *RRS Discovery* (DY100) within the Exclusive Economic Zones (EEZs) of Tristan da Cunha and Saint Helena.	(Morley *et al.*, 2018; Whomersley *et al.*, 2019)
British Antarctic Survey	Data collected during the 2013 cruise aboard the *RRS James Clark Ross* (JR287) within the EEZ of Tristan da Cunha	(Barnes *et al.*, 2013)
British Antarctic Survey/National Geographic	Data collected from the 2015 and 2017 cruises aboard the *RRS James Clark Ross* (JR864 and JR16NG) within the EEZ of Ascension Island	(Barne*s et al.*, 2019)
Alfred Wegener Institute	Data collected from the 2012 cruise (MSM20/2) aboard the *R/V Maria S. Merian* from Namibia to Brazil	(Jegen *et al.*, 2015; Geissler *et al.*, 2020)
Southeast Atlantic Fisheries Organisations (SEAFO)/Food and Agriculture Organisation (FAO) EAF-Nansen Programme	Data collected during the 2015 and 2019 surveys in the SEAFO Convention Area aboard the *R/V Nansen*. This paper/report uses data collected through the scientific surveys with the R/V Dr Fridtjof Nansen as part of the collaboration between the FAO EAF-Nansen Programme and SEAFO. The programme supports the implementation of the ecosystem approach to fisheries management in the partner countries. The EAF-Nansen Programme is executed by the Food and Agriculture Organization of the United Nations (FAO), in close collaboration with the Norwegian Institute of Marine Research (IMR), and funded by the Norwegian Agency for Development Cooperation (Norad).	(Be*rgstad et al.*, 2019b; FAO, 2019)

In a similar manner to how the North Atlantic bottom temperature layer was built, CTD casts from the five cruises to UK Overseas Territories listed in Table 4.1 were combined with data available in the BODC archive to create a list of 3,494 casts (Appendix D.7). Due to computational power restrictions, the South Atlantic was split into six tiles and for each, the following was undertaken. Data were partitioned at an 80:20 ratio to create training and test datasets. For each explanatory variable (depth, latitude and longitude), an individual GAM was built to assess significance in predicting temperature values (Appendix D.7). In all models for all tiles, all explanatory variables were individually significant and therefore combinations of predictors were assessed to maximise temperature prediction accuracy. For five of the six tiles, the final GAM used depth, latitude and longitude to predict temperature, and for one tile latitude was not selected. Pearson's correlation analyses undertaken between predictions built using the training data and validated using the test data showed that all models performed well, with five of the six receiving coefficients of >0.95; the performance of one model was slightly lower at 0.82 (Appendix D.7).

Using the predict() function in the 'mgcv' package in R, predictions were made for bottom temperature based on the South Atlantic bathymetry layer down to 1,500 m. These prediction files were exported into ArcGIS and made into continuous bottom temperature layers using the 'Point to Raster' tool.

4.3.2.2 Biological data

Desmophyllum pertusum is ubiquitously found across the world's oceans and is therefore a good candidate for model transfer between basins. *Desmophyllum pertusum* reef presence locations were extracted from an image dataset spanning 7 °S to 40 °S as *per* Chapter 3. Presence and absence points were projected into Goode Homolosine Ocean and formatted in a one-point-per-cell structure against the high-resolution bathymetry layer, resulting in six presences and 88 absences.

4.3.2.3 Model transfer

Although Goode Homolosine Ocean keeps the vast majority of each ocean basin as one continuous section, the far southeast and southwest sections of the South Atlantic fall in a separate segments of the projection (Appendix D.8), and therefore rasters that expand the full area are very large. The four variable rasters (plan curvature, FBPI, rugosity and temperature) were consequently each split into seven corresponding tiles to reduce the size of the files. The original North Atlantic MaxEnt model was rerun seven times, changing the ASCII files in the projection directory to those containing South Atlantic data for each tile. Prediction rasters were imported into ArcGIS and masked by the MaxEnt novel climate outputs for each tile, removing areas where environmental variables fell outside the range on which the model was trained. The seven individual tiles were then stitched together to create a full basin prediction using the 'Mosaic to New Raster' tool in ArcGIS. Prediction values were extracted for each of the South Atlantic presence and absence points in the one-point-per-cell format and exported from ArcGIS for validation in R.

4.3.2.4 Independent model validation

Area-Under the Curve (AUC) was calculated as a threshold-independent metric. Performance was assessed using the threshold selected in the evaluation of the North Atlantic model, and three new thresholds using the same techniques (Sens=Spec, MaxSens+Spec and MinROCdist) were calculated based on the independent data using the optimal.threshold() function. Again, the presence.absence.accuracy() function was used to obtain validation metrics for each different thresholding method.

4.4 Results

4.4.1 North Atlantic model performance

Model predictions for the North Atlantic revealed much suitable habitat for *D. pertusum* reef in the northeast Atlantic (Figure 4.2).

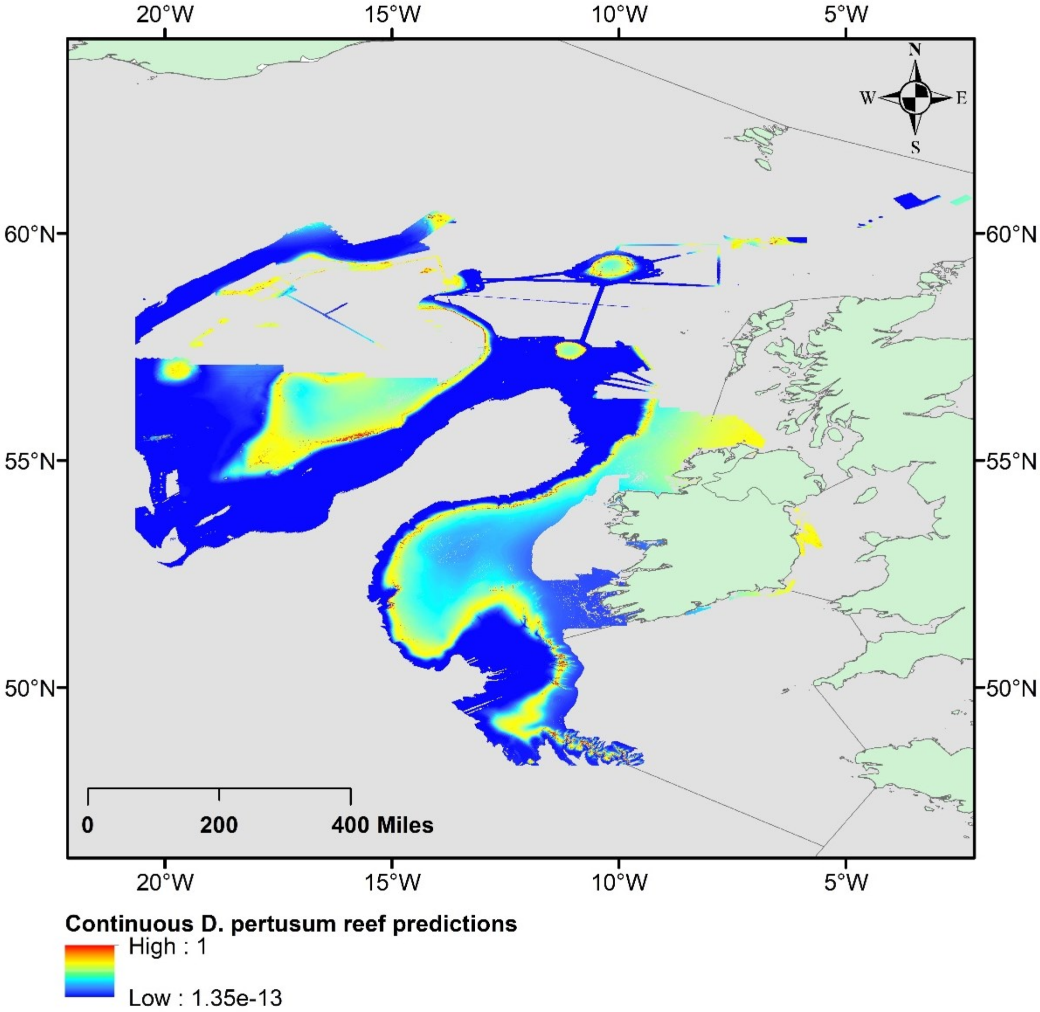

Figure 4.2: <u>Desmophyllum pertusum</u> reef habitat suitability model predictions for the northeast Atlantic. Map drawn in Goode Homolosine Ocean.

Consideration of common performance indices (Table 4.2) allowed for selection of final thresholding methods. Sens=Spec was chosen providing a threshold of 0.43. The AUC value for the full internally validated model and the averages for all internal validation models were deemed excellent (0.9+). The 0.43 threshold generated good (0.8-0.9) results for PCC, sensitivity and specificity for the full model and all cross validation (test/train) models.

When variables are considered in isolation, model gain (i.e. explanatory power) is highest for temperature, followed by rugosity, FBPI and plan curvature as depicted in the jackknife plot (Appendix D.9). Temperature also decreased the model gain the most when removed as a variable, further illustrating its importance as the major variable on which predictions are reliant.

Table 4.2: Threshold-dependent evaluation indices for the North Atlantic <u>*Desmophyllum pertusum*</u> *reef habitat suitability model. Data are presented for the training, test, and full models. PCC = Percent correctly classified; Sens = Sensitivity; Spec = Specificity; TH = Threshold; S=S = Sens=Spec; MaxS+S = MaxSens+Spec; MRD = MinROCdist.*

	Average Training			**Average Test**			**Full Model**			
TH approach	**PCC (SD)**	**Sens (SD)**	**Spec (SD)**	**PCC (SD)**	**Sens (SD)**	**Spec (SD)**	**PCC (SD)**	**Sens (SD)**	**Spec (SD)**	**TH**
S=S	0.83 (0.01)	0.83 (0.03)	0.83 (0.01)	0.82 (0.01)	0.82 (0.05)	0.82 (0.01)	0.83 (0.01)	0.82 (0.03)	0.83 (0.01)	0.43
MaxS+S	0.81 (0.01)	0.89 (0.02)	0.80 (0.01)	0.78 (0.01)	0.92 (0.03)	0.77 (0.01)	0.81 (0.01)	0.90 (0.02)	0.80 (0.01)	0.41
MRD	0.82 (0.01)	0.87 (0.03)	0.82 (0.01)	0.81 (0.01)	0.88 (0.04)	0.80 (0.01)	0.81 (0.01)	0.90 (0.02)	0.80 (0.01)	0.41

4.4.2 Transferred model performance

When presented with the independent dataset from the South Atlantic, the model built in the North Atlantic performs well (Table 4.3). When assessed using the previously selected threshold of 0.43, the AUC drops from 0.91 (excellent) to 0.72 (fair). Although the overall percent correctly classified (PCC) remains high at 83%, there is a large difference in prediction accuracy between presences (sensitivity) and absences (specificity) with absences being more likely to be correctly predicted.

The three new thresholds calculated using the South Atlantic data points are presented in Table 4.3. Although Sens=Spec was selected as the favourable thresholding method for the original model, the metrics when using this method with independent data report poorly. MaxSens+Spec and MinROCdist both use a higher threshold of 0.43 (the same as the North Atlantic threshold), and report higher scores for both PCC and specificity (ability to correctly predict absences), thus this threshold is used in further evaluation and discussion of the transferred model.

Table 4.3: Model transfer independent validation metrics calculated using the 'PresenceAbsence' package in R. PCC = Percent correctly classified; Sens = Sensitivity; Spec = Specificity; TH = Threshold; S=S = Sens=Spec; MaxS+S = MaxSens+Spec; MRD = MinROCdist.

	TH approach	**PCC (SD)**	**Sens (SD)**	**Spec (SD)**	**TSS** **(Sens + Spec -1)**	**AUC (SD)**	**TH**
TH-independent evaluation	-	-	-	-	-	0.72	-
TH-dependent evaluation	-	0.83 (0.04)	0.67 (0.21)	0.85 (0.04)	0.51	0.72 (0.14)	0.43
Re-TH	S=S	0.68 (0.05)	0.67 (0.21)	0.67 (0.06)	0.34	0.72 (0.14)	0.27
	MaxS+S	0.83 (0.04)	0.67 (0.21)	0.85 (0.04)	0.51	0.72 (0.14)	0.43
	MRD	0.83 (0.04)	0.67 (0.21)	0.85 (0.04)	0.51	0.72 (0.14)	0.43

4.4.3 Modelled distribution of habitat suitable for *D. pertusum* reef in the South Atlantic

There was very little environmental data available for the southwest Atlantic, and of the small coverage acquired, none was for geomorphological features appropriate for *D. pertusum* to form reef structures; therefore predictions are only presented in the context of the southeast Atlantic. Predictions were made across 27 main features in the southeast Atlantic (Figure 4.3). Of the 91.29 km^2 of seabed for which environmental data were suitable to predict on, 3.74 km^2 received predictions above the threshold of 0.43 (approximately 4.1%), and thus are classed as suitable habitat for *D. pertusum* reef.

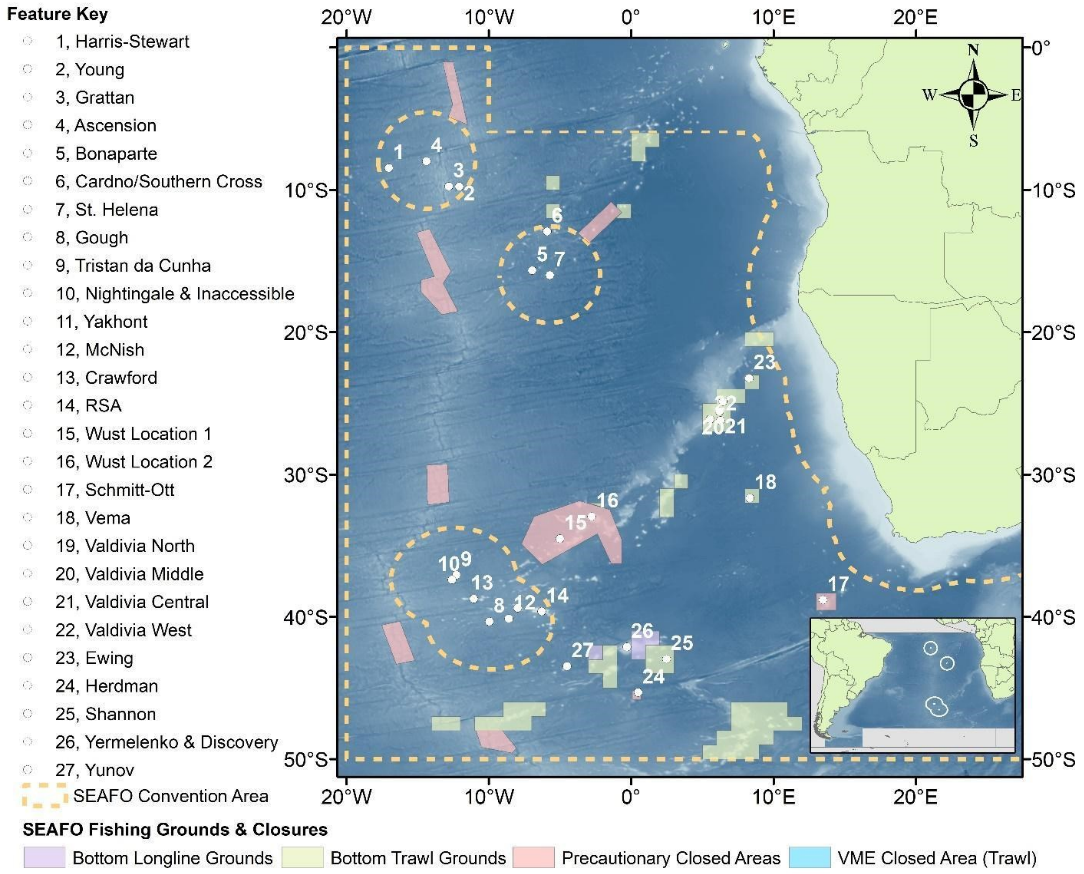

Figure 4.3: All features with suitable environmental data that allowed for the transfer of the Desmophyllum pertusum reef model. The dashed line depicts the South East Atlantic Fisheries Organisation (SEAFO) Convention Area. Designated fishing grounds and closures are also shown. Map drawn in WGS84.

Of the 27 features (seamounts, islands and banks) for which there was sufficient environmental data, 21 received at least one prediction >0.43 (Table 4.4). Fourteen of the features are within MPAs that legislate against bottom trawling (all within the EEZs of Saint Helena, Ascension Island and Tristan da Cunha). The Southeast Atlantic Fisheries Organisation (SEAFO) have designated precautionary full VME closures on five of the features within ABNJ, whilst Valdivia Central falls partially within their existing VME Closed Area. Eight of the features in ABNJ are undesignated (i.e. they are not identified as fishing grounds nor closed areas) or remain at least partially open to bottom trawling.

Table 4.4: Prediction area for each feature/complex with the percentage of which were above the selected threshold of 0.43. STSE = Subtropical southeast. TSE = Temperate southeast. Asc = Ascension Island. SH = St Helena. TdC = Tristan da Cunha. 'Open' fishing zones are still subject to their respective SEAFO conservation measures.

No. in Figure 4.3	**Feature/Complex**	**Broad Location**	**Prediction Area (m^2)**	**% of predictions above threshold (2 d.p.)**	**Bottom fishing status**
1	Harris-Stewart	Asc EEZ	292,800	45.36	Ban
2	Young	Asc EEZ	351,600	29.81	Ban
3	Grattan	Asc EEZ	562,600	24.78	Ban
4	Ascension	Asc EEZ	1,539,600	16.68	Ban
5	Bonaparte	SH EEZ	379,600	22.81	Ban
6	Cardno/Southern Cross	SH EEZ	876,200	20.63	Ban
7	Saint Helena	SH EEZ	1,205,800	20.07	Ban
8	Gough	TdC EEZ	369,400	25.39	Ban
9	Tristan da Cunha	TdC EEZ	368,000	23.04	Ban
10	Nightingale & Inaccessible	TdC EEZ	1,718,800	18.07	Ban
11	Yakhont	TdC EEZ	1,583,200	16.93	Ban
12	McNish	TdC EEZ	444,600	13.81	Ban
13	Crawford	TdC EEZ	2,188,800	7.75	Ban
14	RSA	TdC EEZ	2,082,000	6.06	Ban
15	Wust Seamount 1	STSE	938,400	0.23	Ban, VME precautionary closure
16	Wust Seamount 2	STSE	2,237,000	6.21	Ban, VME precautionary closure
17	Schmitt-Ott	TSE	332,400	0	Ban, VME precautionary closure
18	Vema	STSE	10,600	33.96	Ban, VME precautionary closure
19	Valdivia North	STSE	70,400	0.28	Open
20	Valdivia Middle	STSE	97,000	3.30	Open
21	Valdivia Central	STSE	470,200	2.76	Mostly open, partial VME closure
22	Valdivia West	STSE	93,200	3.65	Open

No. in Figure 4.3	Feature/Complex	Broad Location	Prediction Area (m^2)	% of predictions above threshold (2 d.p.)	Bottom fishing status
23	Ewing	Tropical southeast Atlantic	94,800	0	Open
24	Herdman	TSE	21,800	0	Ban, VME precautionary closure
25	Shannon	TSE	972,200	0	Open
26	Yermelenko & Discovery	TSE	8,450,400	0	Open and/or not designated
27	Yunov	TSE	207,400	0	Not designated

The mean depth of suitable habitat for *D. pertusum* reef was 654 m and generally occurred on feature flanks, creating a ring-like pattern, often tracing the summit-slope break (presence histograms for each variable are available in Appendix D.10). Predictions for Wust (seamount 2) and Valdivia Central have been mapped (Figure 4.4); these features were selected to provide examples of predictive patterns.

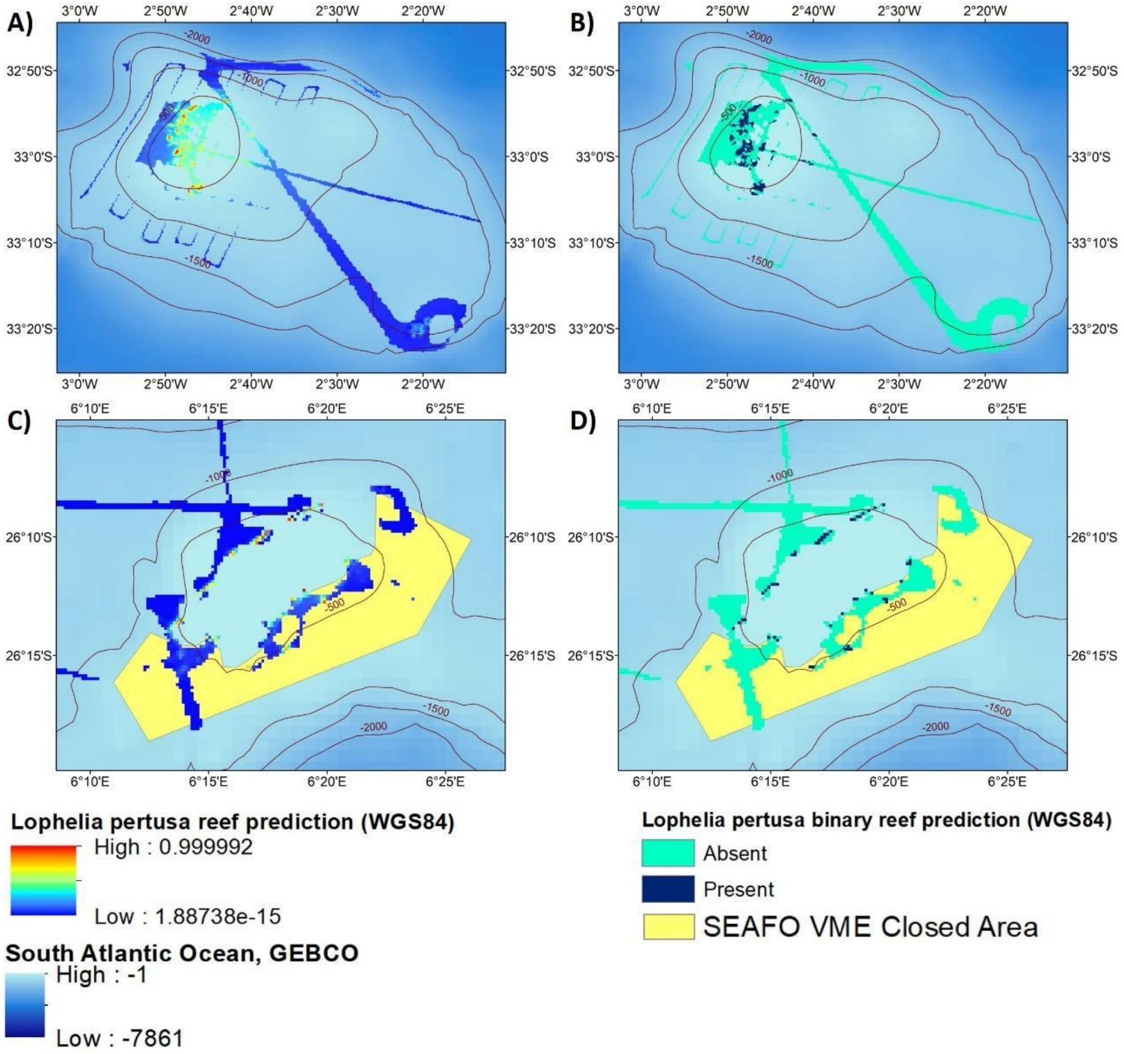

Figure 4.4: Both threshold-dependent (0.43) and continuous predictions for Wust seamount 2 (A, B) Valdivia Central (C, D).

4.5 Discussion

When the transferred model was evaluated using an independent dataset from the South Atlantic, the model performed well with an AUC score of 0.72, which is considered fair performance. Although the PCC and specificity remained high, the model's ability to correctly predict presences (sensitivity) did drop in comparison to its performance in the North Atlantic.

4.5.1 Is model transfer an option for data-poor regions of the deep sea?

There are a number of factors that may have contributed towards the successful transfer of this model, not least of all because of the unique environments it deals with. At a global scale, the deep sea is a more uniform environment than the terrestrial biome, with much greater similarity in environmental conditions between ocean basins than between, for example, terrestrial continents. Many previous studies have reported poor and/or variable model transferability across large regions, but these have largely targeted terrestrial habitats/species (Bamford *et al.*, 2009; Torres *et al.*, 2015; Roach *et al.*, 2017). The environmental similarity and long-term stability in deep ocean conditions between basins may mean that deep-sea habitats and species are particularly suited to model transfer (*sensu* Yates *et al.*, 2018).

This said, there are stark differences in the water mass structure between ocean basins which means predictor choice is key in designing a good-performing, transferrable model. Whilst depth is often the variable with the highest predictive power, a reliance upon depth, without acknowledgement of its correlates, in models designed for transfer across ocean basins may inhibit success. This is because high dissimilarity (e.g. water mass structure) between the reference and target systems will increase prediction error (Yates *et al.*, 2018). An example of the importance of this choice in practice can be drawn from this study. *D. pertusum* is known to have different depth ranges across ocean basins, because its distribution is mainly driven by temperature (Freiwald *et al.*, 2004; Roberts *et al.*, 2006). Should depth have been selected as a predictor instead of temperature, differences in water mass structure between basins would likely have meant that MaxEnt would have masked many predictions because the South Atlantic conditions would fall outside the data range on which the model was trained, resulting in a transferred model with little use due to the limited geographic extent of the relationship it is based on. Therefore, when building models for the purpose of transfer, it is important to consider the generality of the predictors and where possible, select the most appropriate without foregoing model performance.

In addition to its improved generality compared with depth, the selection of temperature as a predictor may also contribute to successful model transfer because it's a *direct* predictor. Direct and indirect gradients are initially described in Austin (1980, 1985) and Austin and Smith (1990). Direct predictors are variables that are required for physiological maintenance but are not consumed (e.g. temperature, pH). Indirect predictors are those that are not directly linked to physiological performance but are thought to be linked via other processes (e.g. bathymetrically derived variables such as rugosity and curvature). A number of studies and reviews focusing on both marine and terrestrial fauna have found that SDMs based on direct predictors are more transferable than those that use indirect predictors (Graf *et al.*, 2006; Randin *et al.*, 2006; Strauss & Biedermann, 2007; Gray *et al.*, 2009; Sundblad *et al.*, 2009). While there are four predictor variables used in the North Atlantic model, temperature is significantly more important than bathymetrically-derived (indirect) predictors. The strong reliance of the model on the only direct predictor may contribute to the success of the transfer.

When considering models of deep-sea habitat and/or species distribution for transfer, it is important to understand the importance of parsimony (i.e. model simplicity). Yates *et al.* (2018) discuss this, suggesting that less complex models with fewer predictors and smooth response curves would, in theory, facilitate greater transferability. In this study, the selection of only four predictor variables and the smooth response curves (as model parameters were constrained to exclude hinge and threshold features) has likely contributed to its successful transfer. Therefore, although complex models do have their uses (e.g. in very dynamic systems), model parsimony is a key consideration for effectively transferring models from data-rich to data-poor regions.

Yates *et al.* (2018) consider whether model transferability is trait- or taxon-specific, and this is another factor that would be helpful to consider prior to building models with the intent of transfer. *Desmophyllum pertusum* is a sessile coral with a relatively well-defined niche thanks to it being the focus of many deep-sea studies (Rogers, 1999; Roberts *et al.*, 2006; Dodds *et al.*, 2007; Howell *et al.*, 2011), and this has likely contributed to the successful transfer here. On the contrary, building transferrable models for taxa with high behavioural and/or adaptive plasticity is more challenging as the assumption that underpins distribution modelling, that the relationship between taxa and the environment is constant despite geographic location, is less rational (Yates *et al.*, 2018). Therefore, in order to build reliable models for transfer from data-rich to data-poor deep-sea regions, it is perhaps safer to focus on sessile taxa that often provide the habitat for other species.

Manzoo*r et al.* (2018) investigated the role of resolution (also known as grain-size) on the transferability of invasive plant models built in MaxEnt. The study found that although fine-scale (50 m) resolution models predicted best in the region in which they were calibrated, intermediate-scale (300 m) resolution models transferred better than both fine- and broad-scale (1 km) resolution models, a finding also reported by Marshall (2011). Similarly, Olivier and Wotherspoon (2008) address the issue of scale in transferability of HSMs. They investigated nest selection by snow petrels in Antarctica, and found that when transferred, models at the habitat-scale were more successful than those at the nest-scale, attributing this to high variability at smaller scales. The transferred model in this study has a resolution of 200 m, similar to the medium-scale resolution in Manzoor *et al.* (2018). Finer-scale models can be prone to over-fitting (Olivier & Wotherspoon, 2008), where predictions are too specific to the dataset on which the model was trained and thus the model is unable to predict in new areas. Conversely, a coarser model is more likely to overestimate distribution (Marshall, 2011), and depending on the size of the ecosystems/features that are targeted, may not be useful from a management perspective. Therefore, when building models for transfer in the deep sea, intermediate resolutions (e.g. 200 m in this study) will likely perform better because they are coarse enough to be transferrable, but fine enough to perform well. This is of course only if the variability of the predictors are relevant to that resolution – if the predictor variable varies considerably on smaller scales than the resolution, then the model will not appropriately capture this and the performance will suffer. Another benefit of building models of intermediate resolution are that they able to be incorporated into spatial management plans. This is particularly true in the High Seas where spatial management is likely to discussed in units of much larger than 200 m^2.

When assessed against threshold dependent metrics, the transferred model has the same PCC value as the North Atlantic model. Upon further inspection, it is clear that this is entirely reflective of an increase in specificity. The sensitivity score however drops from 0.82 to 0.67 when transferred. This means that the transferred model is not as successful at predicting presences correctly using the selected threshold. In this study, there were only six presences available to validate the model, acutely highlighting just how few data are available for the South Atlantic. As a result, it is difficult to ascertain whether this reduction in sensitivity is truly reflective of the model performance, or an artefact of the limited validation data, although the excellent validation performance of the model in the North Atlantic is important to consider. Four of the six validation points were above the 0.43 threshold calculated to determine *D. pertusum* reef presence, but two points received significantly lower predictions (0.20 and 0.08). These points were located on the summits of Crawford and Yakhont seamounts in the Tristan da Cunha EEZ in areas where the 200 m multibeam bathymetry showed flat seabed with low topographic complexity. Vertical walls and overhangs are known to provide important habitat for reef-building CWCs including *D. pertusum* (Huvenne *et al.*, 2011; Davies *et al.*, 2017), but features such as pinnacles that provide vertical habitat can have a small footprint. In both cases, it is plausible that multibeam bathymetry gridded at 200 m resolution is not capable of sufficiently identifying these features, and instead artificially smooths the seabed within cells where these features are present. This would explain the presence of *D. pertusum* reef, but the low prediction likelihood values for these cells. This result also raises the possibility of whether key predictors are missing. However, this is unlikely due to the good performance of the model in the North Atlantic (Table 4.2).

Depending on the intended use of the model outputs, one may wish to select a different thresholding method, for example in a cruise planning exercise, maximising the sensitivity may be more beneficial than the specificity due to the high costs of ship time. It is possible that the choice of threshold (MaxSens+Spec) in our model is driving the low performance to some degree by giving more power to the correct prediction of absences which is perhaps likely in a low prevalence dataset. However, this would not have changed the outcome in our evaluation as the two presences below the selected threshold of 0.43 were also below 0.27 (the threshold identified using the Sens=Spec approach).

4.5.2 How is *D. pertusum* reef distributed across the study area?

The transferred model provides best available scientific data on the likely occurrence of *D. pertusum* reef habitat in the modelled regions. Suitable habitat is predicted to occur on 21 of 27 modelled features, suggesting *D. pertusum* reef is widespread across (at least) the southeast Atlantic. All features where >5% of the modelled surface was suitable for *D. pertusum* reef have legislation in place that prohibits bottom trawling, although it is important to note that these closures were not necessarily designated based on the presence of *D. pertusum* reef.

Features within the EEZs of Ascension Island, Saint Helena and Tristan da Cunha provide large areas, highly suitable for *D. pertusum* reef as represented by their high percentages of presence predictions per feature (Table 4.4). Observations of *D. pertusum* reef (some of which were used to validate the model) also confirm the presence of this VME here. The governments of Ascension and Saint Helena have both approved large MPAs that prohibit bottom-trawling and therefore protect VMEs including CWC reef. While full habitat mapping of the South Atlantic is required in order to quantify the basin scale importance of these MPAs, it is likely they play an important role in conserving *D. pertusum* reef given the high number of features they cover and the high percentages of each feature that receive presence predictions. The Tristan da Cunha government has recently implemented a Marine Protection Zone, within which different activities are permitted. Whilst sub-sections of the seamounts remain open to longline fishing (around 86% of the area shallower than 1000 m) to support the island economy, bottom trawling, the most damaging practice, is prohibited in all 763,900 km^2 of the EEZ.

The model predicts presence of *D. pertusum* reef across seven acoustically mapped seamounts in ABNJ (Table 4.4), but finds no likely presence of reef on six features. These findings are important in the context of fisheries management of the region. The South East Atlantic Fisheries Organisation (SEAFO) is the RFMO for ABNJ east of 20 °W in the South Atlantic (Figure 4.3). Under the UNGA Resolution 61/105 and subsequent instruments, RFMOs are required to regulate bottom fisheries in ABNJ and to adopt the precautionary principle in order to avoid significant adverse impacts on VMEs. In reality, this is managed by bottom fishery closures, and through enforcing more reactive measures such as the move-on protocol which requires fishing vessels to move away at least 2 nautical miles if they come into contact with VME-indicator taxa when fishing. Up to this point, VME data for the region have largely been collected through the FAO EAF-Nansen programme (Bergst*ad et al.*, 2019a), or ad-hoc reporting from vessels whose encounters have triggered the move-on protocol. This approach has resulted in a number of spatial closures to bottom trawl fishing. Four of the seven features with above-threshold predictions for *D. pertusum* are already either entirely closed or have a portion closed to bottom trawling (Table 4.4).

Valdivia Bank is a seamount complex in the subtropical southeast Atlantic and has previously been bottom-trawled for orange roughy and/or alfonsino (FAO, 2011). In 2016 a small area of Valdivia Central, one of the seamounts in the complex, was closed to all fishing except for pots and set longlines (CM 30/15) to protect VMEs. The closure roughly tracks the 550 m bathymetric contour around the southern flank of the feature, and whilst it does encompass some areas with high prediction values, the northern flank of Valdivia Central appears to provide more (both spatially and environmentally) suitable area for *D. pertusum* reef (Figure 4.4C-D). This VME closure, although not providing maximum coverage for *D. pertusum* reef, will likely incorporate other VMEs such as *Solenosmilia variabilis* reef, or deep-sea sponge aggregations, and therefore predictive outputs for other taxa like those created in this study will be valuable to fisheries managers during reviews of existing and future VME closed areas. The modelled outputs presented here identify all four features within the wider Valdivia Bank complex as likely harbouring *D. pertusum* reef. They also represented the only features within ABNJ that have high predicted likelihood of *D. pertusum* reef habitat, whilst still being open to bottom trawling. Therefore, in the case of Valdivia Bank, our data suggest that additional closures could further prevent significant adverse impacts to *D. pertusum* reef in the subtropical southeast Atlantic.

Six features in ABNJ show no likely presence of *D. pertusum* reef in the modelled outputs, and this is based on their environmental profiles. Despite their varying latitudes, Herdman, Ewing and Schmitt-Ott all receive no presence prediction for *D. pertusum* reef, likely because they all have deep (>800 m) summit depths, although both Herman and Schmitt-Ott fall within VME precautionary closures. On the contrary, from the small amount of high-resolution bathymetry available, Shannon, Yunov, Yermelenko and Discovery all appear to have shallower summits (<500 m). However, they are all located below the South Subtropical Front at approximately 39 °S, and are therefore permanently surrounded by cooler subantarctic water (Deacon, 1937; Smythe-Wright *et al.*, 1998) below 6 °C. The lowest temperature record in the presence data from the North Atlantic is 6.2 °C and therefore the thermal profile of these features is too cold for *D. pertusum* reef to be predicted as present (Rogers, 1999). However, lower temperatures do not rule out the presence of other VMEs including *S. variabilis* reef that is also found in the South Atlantic (Chapter 3). This reef building coral inhabits similar topographic environments to *D. pertusum* (e.g. sloping sides of seamounts), but favours cooler waters. Shannon, Yermelenko and Discovery all harbour open fishing grounds, whilst Yunov remains undesignated to either closure or fishing. While the lack of *D. pertusum* reef suitable habitat on these features suggests that any fishing taking place may not adversely impact this particular VME, further exploration should be undertaken to ascertain whether other VMEs are present on these features and if so, act accordingly to protect these from significant adverse impacts.

4.5.3 Wider application of modelled maps

VMEs are offered protection in the Convention Areas of RFMOs through the enforcement of fisheries closures that are typically designated after vessels trigger the move-on protocol. Whilst this protocol can be effective if adequately monitored, it is reactive, not precautionary (Bell *et al.*, 2019). Knowing the distribution of VMEs in ocean basins before fishing grounds are adopted so as to avoid contact would be more in accord with the precautionary principle, and help facilitate robust environmental impact assessments prior to new fishing licences being granted.

Whilst VMEs are afforded protection in ABNJ from damage caused by fishing activity, they represent an anomaly in terms of protection in ABNJ. In general, conservation of biodiversity in the High Seas is either difficult to establish due to a lack of international legal framework, or is managed on an individual sector-by-sector basis (e.g. the

International Seabed Authority has the power to protect biodiversity only from mining activities). In order to allow for global sustainability and conservation goals to be achieved (e.g. SDG14), while continually enabling the equitable use of the oceans from a multitude of different sectors, the international community will need to enact protection through the BBNJ legal instrument.

This study is the first example of a geographically broad-scale, intermediate resolution deep-sea HSM being transferred from a data-rich to a data-poor ocean basin, and our results are promising. However, more research is urgently needed to understand when it is likely to work and when not; it is only after this that the full potential of this method will be realised. The South Atlantic is an example of a data-poor ocean basin, but as highlighted in Howell *et al.* (2020b), much of the deep ocean in the southern hemisphere is understudied, particularly in ABNJ. The issues arising from our lack of knowledge of species' and habitat distribution in ABNJ will become more prevalent because there is not enough time to conduct biological surveys of the vast amount of the ocean that remains unexplored before the process of proposing possible High Seas MPAs will likely begin post-ratification of the BBNJ legal instrument. It is therefore crucial that novel technologies and methods such as model transfer be investigated and if appropriate, utilised to ensure that management decisions are based on the best available scientific data.

4.6 Conclusion

Without accurate maps of where different habitats occur or are likely to occur, it will be difficult to implement an ecologically coherent, evidence-based High Seas MPA network to help achieve global sustainability targets. Whilst ensuring access to robust, independent validation data is important, particularly for model transfer studies, the biggest hurdle in creating transferable models at oceanographic basin scales is the lack of intermediate resolution (i.e. 200 to 300 m) environmental data. In this study, this is highlighted by the lack of predictions for the southwest Atlantic, despite the known presence of geomorphological structures suitable for reef-building scleractinians to inhabit (e.g. the Rio Grande Rise, a seamount chain in the subtropical southwest). Without an RFMO, management of the southwest Atlantic is particularly lacking and therefore if it facilitates spatial management, the BBNJ instrument may be all the more important here. Although collecting this type of data is considered 'easier' than physical samples, in 2018 less than 9% of the seafloor had been directly mapped using multibeam sonar data (Mayer *et al.*, 2018), although in June 2021, the figure surpassed 20%; the remainder is an approximation of seafloor shape derived from satellite altimeter data at varying scales between 1 km and 5 km. The remote nature, logistical challenges and high cost associated with open ocean research, alongside the encroaching need to consider areas for protection in the near future means that successful transfer of basin scale HSMs stands to provide significant contributions to the spatial planning process, particularly in ABNJ and areas that have previously undergone little scientific exploration. Initiatives such as the Nippon Foundation-GEBCO Seabed 2030 Project that advocate for 100% of the ocean floor to be mapped by 2030 could help significantly advance our understanding of model transfer techniques, ultimately facilitating more evidence-based decision making in spatial management processes.

CHAPTER 5: A GLOBAL, BROAD-SCALE BENTHIC HABITAT CLASSIFICATION: A TOOL FOR MARINE SPATIAL PLANNING

5.1 Abstract

Technological advancements are allowing humans to expand industry further into the deep sea, yet despite this, ocean management is hindered by lack of data, particularly in areas beyond national jurisdiction. To galvanise support and instigate progress, a number of legal instruments have set global protection targets of varying ambitions, stressing that the target percentages of protection should contain a representative selection of ecosystems. Broad-scale habitat classifications can facilitate marine spatial planning in data-poor regions by providing baseline data on the distribution of benthic assemblages, and by providing a tool with which to conduct efficacy assessments of existing area-based protection measures. This chapter presents a broad-scale, top-down, benthic habitat classification for the globe. Non-hierarchical, k-medoids clustering was employed to distinguish classes in ecologically-relevant input variables (water mass structure, topography, productivity) that were then combined with a biogeographic regionalisation to create the final habitat classification. An example of how habitat classifications can inform sustainable management is provided by assessing the representativity of the South Atlantic UK Overseas Territory protection network, and perform a quasi-groundtruthing of the classification through comparison with the predictive outputs from a high-resolution habitat suitability model for *Desmophyllum pertusum* reef. The final habitat classification contains 1,750 habitat classes across the world's ocean, each assumed to harbour a distinct community, and shows agreement with faunal zonation patterns in the literature. Several habitat classes were identified as having >10% of their area in the UKOT protection network, demonstrating that the habitat classification can assist in our understanding of the efficacy of existing protected areas/networks. Initial ground-truthing results suggest some level of alignment between fine- and broad-scale habitat maps is possible. Broad-scale habitat classifications, although typically lower resolution than in-country initiatives, are necessary for

informing basin scale marine spatial planning. Specifically, their use in transboundary marine management will likely serve to encourage ecosystem-based management at the ocean-basin scale.

5.2 Introduction

5.2.1 Policy drivers

There is a growing need to manage activities in the global oceans in response to increasing anthropogenic activities and climate change (Ramirez-Llodra *et al.*, 2011; Mengerink *et al.*, 2014; Halpern *et al.*, 2015; Levin *et al.*, 2020). As a result there are a number of international commitments to protect varying percentages of the world's habitats within certain time frames. Through Aichi Target 11, the Convention on Biological Diversity (Convention on Biological Diversity, 2010) announced a goal to protect 10% of marine habitats by 2020, although this target was not met (Convention on Biological Diversity, 2020). In 2003 and later in 2014, the World Parks Congress (International Union for the Conservation of Nature, 2005, 2014) advocated for a more ambitious 30% protection of global habitats. Using the same target as the World Park Congress, Global Ocean Alliance announced their '30by30' initiative to protect at least 30% of global oceans as Marine Protected Areas (MPAs) and Other Effective area-based Conservation Measures (OECMs) by 2030. All three commitments specify that protected habitats are representative of the wider marine environment to ensure ecological coherence of protected area networks. As a result, there are a number of national and international conventions and processes that seek to facilitate this management and protection, both within nation's waters, and in areas beyond national jurisdiction (ABNJ).

Marine spatial planning (MSP) is the process by which ocean areas are spatially sectioned into different zones of use, and is defined by Ehler and Douvere (2007) as "a public process of analysing and allocating the spatial and temporal distribution of human activities in marine areas to achieve ecological, economic and social objectives that are usually specified through a political process". Whilst the concept and implementation of MSP principles in national waters is relatively advanced (e.g. the UK's Blue Belt Programme), MSP in ABNJ is significantly less developed, despite ABNJ constituting almost half the Earth's surface. Wright *et al.* (2019) explore the challenges of MSP in ABNJ, summarising them under three categories: technical, legal/policy framework, and social context. The fragmented nature of management in ABNJ is a key stumbling block when attempting MSP, both at the cross-sectoral (Ban *et al.*, 2014; Wright *et al.*, 2019; Ortuño Crespo *et al.*, 2020) and sectoral levels, particularly for fisheries in ABNJ (Cullis-Suzuki & Pauly, 2010; Wright *et al.*, 2015; Bell *et al.*, 2019). Member states endorsed more collaborative management of ABNJ in 2017 through UNGA Resolution 72/249, and the United Nations are now in the process of developing the legal instrument to support conservation and sustainable use of marine biological diversity within areas beyond national jurisdiction (coined the 'BBNJ negotiations'). While draft legal texts do not explicitly discuss MSP, they do provide an opportunity to begin thinking about how MSP in ABNJ may be undertaken, and the types of area-based management tools that could be employed to enable protection of habitats and species, while interlinking with existing Marine Protected Area (MPA) networks.

5.2.2 Habitat mapping and classifications

The technical challenge outlined by Wright *et al.* (2019) refers to the lack of data to support MSP in vast areas of the ocean – you cannot yet manage what you cannot yet map. For ocean areas that have previously undergone little scientific exploration, there are often too few data to characterise the spatial distributions of benthic communities based on biological records alone; consequently, it is difficult to identify areas for protection/exploitation. Therefore, scientists and managers need to employ different strategies and tools to fill these data gaps while making use of the best available data. Examples of these tools include model transfer techniques (e.g. Chapter 4) and habitat classifications or bioregionalisations (e.g. Howell, 2010; McQuaid *et al.*, 2020).

Perhaps the most basic form of bioregionalisation or habitat mapping is one based on global biogeography that seeks to outline species ranges and patterns of endemicity. Efforts to develop biogeographies for different deep-ocean ecosystems (benthic, pelagic etc.) have been made previously at both global (e.g. Menzies *et al.*, 1973; Zezina, 1973, 1997; Belyaev, 1989; Vinogradova, 1997; Spalding *et al.*, 2007; Watling *et al.*, 2013; Costello *et al.*, 2017; Sayre *et al.*, 2017; Sutton *et al.*, 2017) and regional scales (e.g. O'Hara *et al.*, 2011; Summers and Watling, 2021). A cognizance of biogeography is crucial in understanding the spatial distribution of organisms, but biogeographic maps provide only a very coarse representation of biological variation, typically overlooking community types, instead representing evolutionary similarity and broad-scale environmental similarities.

When seeking to map finer-scale distributions of biological communities, a popular methodology is a top-down approach using environmental surrogates (Roff & Taylor, 2000); this is particularly relevant for the deep sea as continuous environmental data layers are more readily available for the deep-ocean than biological datasets (Howell, 2010). The method typically works by classifying (either in a supervised or unsupervised manner) environmental data into biologically-relevant classes and then combining multiple input datasets together, to create maps of different environments which are assumed to harbour distinct biological communities. The use of broad-scale environmental parameters as surrogates for ecological variation in habitat mapping has been applied at different scales, sometimes with the addition of a hierarchical framework, in national waters (Greene *et al.*, 1995; Roff & Taylor, 2000; Roff *et al.*, 2003; Harris, 2007; Harris *et al.*, 2008; Verfaillie *et al.*, 2009; Huangn *et al.*, 2011; McBreen *et al.*, 2011; Robinson *et al.*, 2011; Hogg *et al.*, 2016; Sink *et al.*, 2019), regional water bodies (Davies *et al.*, 2004; Howell, 2010; Vasquez *et al.*, 2015; Populus *et al.*, 2017; McQuaid *et al.*, 2020) and globally (Greene *et al.*, 1999; Harris & Whiteway, 2009). Whilst the global attempts are large in spatial coverage, similarly to biogeographies, they typically identify very coarse variability in biological trends, often focusing on discriminating between geomorphological features like seamounts and continental slopes rather than distinct biological communities (e.g. Harris and Whiteway's (2009) seascape classification).

5.2.3 Habitat classifications in marine spatial planning

Habitat classifications can play an important role in developing conservation policy and supporting MSP and area-based ocean management (Davies *et al.*, 2004; Harris & Whiteway, 2009; UNESCO, 2009; Howell, 2010; McQuaid *et al.*, 2020). Habitat classifications can be used to support MSP both at the plan development stage by providing a baseline spatial map of the distribution of habitats, or to assess the efficacy and ecological coherence of existing MPA networks. For example, EUSeaMap is a regional, hierarchical, broad-scale habitat map developed collaboratively over a number of phases (Populus *et al.*, 2017) that links with the European Environment Agency's EUNIS habitat classification (Davies *et al.*, 2004). The development of a broad-scale habitat map that covers all European Seas and allows for regional comparison to be made has been integral in supporting regional and transboundary MSP (e.g. in the Celtic Seas, see Mcgowan *et al.*, 2018). Additionally, the EUSeaMap has also been used to assess the ecological coherence of European MPA networks (HELCOM, 2016) and to assist in the development of ecosystem-based MSP in national waters (European Environment Agency, 2019).

As habitat classifications can identify distinct benthic biological communities, they are particularly useful when considering the representativity of MPAs to ensure global targets such as those stemming from the CBD and World Parks Congress are met/in-progress. Habitat classifications have been used in these types of analyses both in networks of MPAs in national waters (e.g. Young and Carr, 2015), and in networks of industry/Convention-specific closures in ABNJ (Evans *et al.*, 2015; McQuaid *et al.*, 2020).

5.2.4 Aims

This study aims to support the MSP process by creating a benthic habitat classification that spans the entire global ocean. Crucially, the extent will cover both EEZs and ABNJ to specifically facilitate transboundary and regional MSP. This chapter presents a top-down, broad-scale habitat classification based on environmental surrogates following both Howell (2010) and McQuaid *et al.* (2020). The habitat classification is then used to provide an example of how the basin scale representativity of habitats within an MPA network can be assessed, and a quasi-groundtruthing exercise of the habitat classification was undertaken by aligning it with a fine-scale habitat suitability model output (Chapter 4).

5.3 Methods

5.3.1 Study region

While the habitat classification was made at a global scale, the South Atlantic (Figure 5.1) is used as a case study to assess the representativity of a particular MPA network in relation to all habitat classes within the basin.

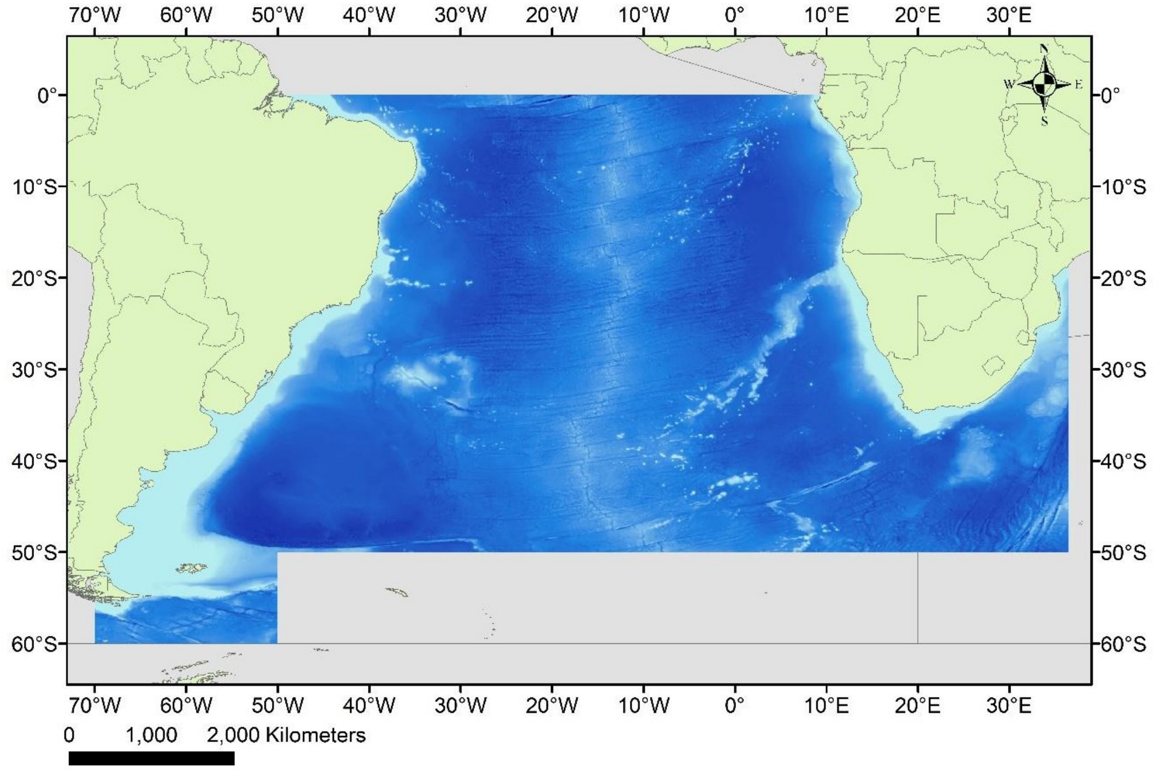

Figure 5.1: The South Atlantic Ocean. The southern boundary is determined by the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). For the purposes of this chapter, the eastern boundary of the South Atlantic is extended to the eastern edge of the South African EEZ. Bathymetry provided by GEBCO 2020 Grid. Map projected in WGS84.

The UK Overseas Territory (UKOT) of Saint Helena, Ascension and Tristan da Cunha is made of three separate oceanic islands in the South Atlantic (Figure 5.2). All three islands have implemented marine protection regimes in their Exclusive Economic Zones (EEZs) that range in protection level. The Ascension Island MPA covers the whole EEZ at just over 440,000 km^2 and was designated in 2019; within the MPA, both commercial fishing and mining are prohibited. Saint Helena designated their whole 451,000 km^2 EEZ an IUCN Category VI MPA in 2016, allowing for ‘sustainable use of natural resources’. Whilst commercial fishing is allowed on a permit basis, bottom trawling is prohibited throughout the whole MPA. In late 2020, Tristan da Cunha announced the designation of their Marine Protection Zone (MPZ). Unlike the other two islands, the MPZ is sectioned into 'fully protected' (i.e. no-take) and 'sustainable fishing' zones; the latter surround the two island groups and sections of four seamounts. Again, bottom trawling is banned throughout the whole EEZ. The Ascension Island and Saint Helena MPAs and the Tristan da Cunha MPZ are henceforth referred to as the South Atlantic UKOT MPA network.

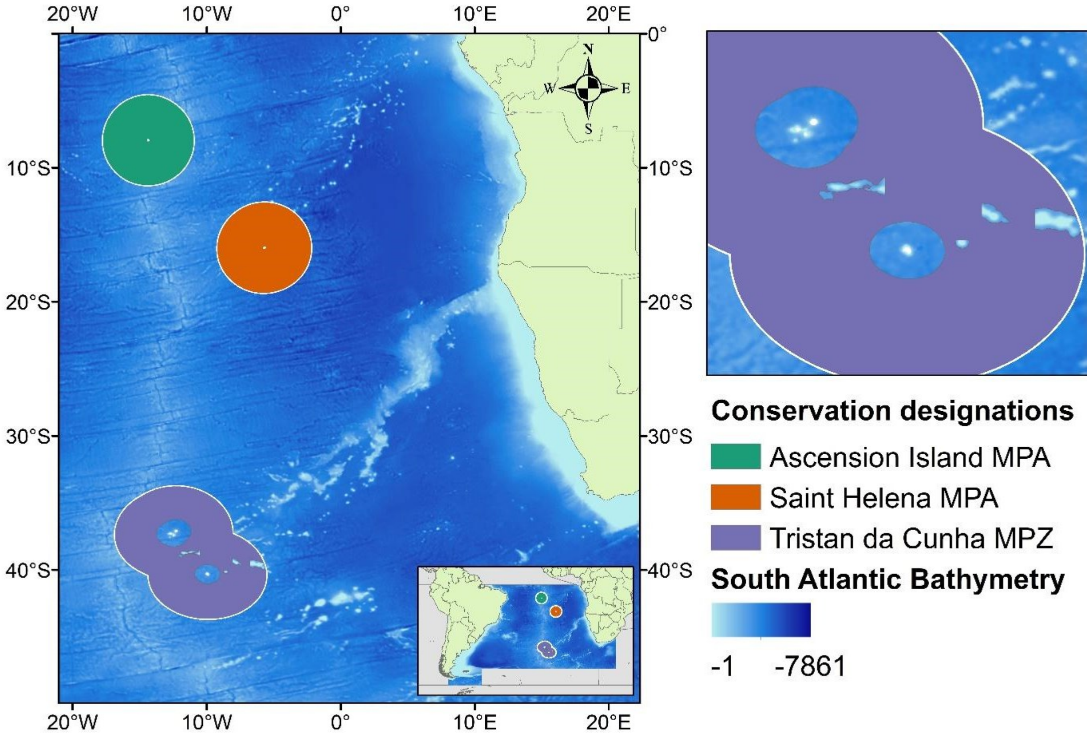

Figure 5.2: UK Overseas Territory of Saint Helena, Ascension Island and Tristan da Cunha in the South Atlantic. Marine Protected Areas (MPAs) and Marine Protection Zones (MPZs) are shaded. The map on the right hand side shows the location of the (unshaded) sustainable fishing zones within the Tristan da Cunha EEZ. Underlying bathymetry provided by GEBCO. Map projected in WGS84.

5.3.2 Habitat classification

The multi-step classification process of McQuaid *et al.* (2020) was followed with minor alterations to develop the habitat classification presented here. Areas with different environmental conditions were identified by clustering environmental variables (either individually or in groups of related variables) using a k-medoids, non-hierarchical clustering algorithm. The outputs of the clustering algorithms for each variable were then combined using a stepwise approach to give a final habitat classification.

5.3.2.1 Variable selection

Selection broadly followed the suggestions laid out in Howell (2010) and adopted by other regional broad-scale habitat classifications such as the EUNIS classification system (Davies *et al.*, 2004). Variables were selected following an extensive literature review, and review by Howell (2010) who proposed a four-tier hierarchical classification system for the deep-sea structured by biogeography, depth, substrate and biology. Selection was also based on expert judgement of ecological relevance and availability of continuous datasets at an appropriate resolution. The variables used in this study were acquired from multiple sources (Table 5.1).

Table 5.1: Original data layers used in this study to create the environmental variables used to build the habitat classification. The native projection of all layers is WGS84.

Variable	**Source**	**Original resolution**	**Reference**
Bottom temperature (°C)	Bio-ORACLE	~10 km (0.083°)	Assis *et al.* (2018)
Bottom salinity (PSS)	Bio-ORACLE	~10 km (0.083°)	Assis *et al.* (2018)
Depth (m)	GEBCO	~430 m (0.004°)	GEBCO Compilation Group, (2020)
POC flux to depth (UNIT)	Lutz	~10 km (0.088°)	Lutz *et al.* (2007)

Water mass structure

Water mass structure generally refers to the layering of different water masses in a body of water driven by differences in the physical properties (e.g. temperature, salinity, chemical concentrations). It is the interaction between these properties that effects the density of water masses, and therefore the layering within the water column. Water mass structure is understood to drive structuring of biological communities (Tyler & Zibrowius, 1992; Koslow, 1993; Bett, 2001; Howell *et al.*, 2002), and depth (level 2 in Howell, 2010) may be considered a proxy for water mass structure in specific regions. However, when working across multiple ocean basins, the depth of particular water masses and the number of water masses present can vary considerably. Therefore, over larger areas, temperature is a more transferable variable, and is more biologically relevant owing to its regulatory effect on metabolism. Howell (2010) acknowledge this by linking their depth classes with particular isotherms. To best utilise the available data and ensure its applicability to all regions, benthic temperature and salinity layers were clustered together to create a global water mass structure layer. For this, bottom temperature and salinity data were downloaded from the Bio-ORACLE marine database (Assis *et al.*, 2018). Data were available at a 5 arc-minute resolution (0.083 °).

Topography

Substrate is the third level in Howell's (2010) proposed classification as different substrate types are known to harbour distinct biological communities even when on the same geomorphological feature (Lundsten *et al.*, 2009). However, unlike for many shallow seas, comprehensive substrate maps for the world's oceans do not exist in a form that is biologically relevant. Major maps of substrate often focus on sediment types based on a combination of chemical composition and geological history. An example of this is Diesing (2020) who mapped global deep-sea sediments using a predictive modelling approach, describing five lithology classes of sediment: calcareous sediment, clay, diatom ooze, lithogenous sediment, and radiolarian ooze. Although these compositionally-driven classes are perhaps meaningful to certain groups such as bacteria and archaea (e.g. Hoffmann *et al.*, 2017), they are not thought to be relevant to larger animal distributions. Instead, in the context of sediments, particle size is considered the key determinant of community structure in the deep sea (Etter & Grassle, 1992). Similarly, for geomorphological classifications and descriptions (e.g. seamounts, hills etc.), the geological history of features is used to discriminate between otherwise similar environments (e.g. seamounts and continental slopes). Despite forming via different geological processes, seamounts and continental slopes do not necessarily support distinct faunal communities (McClain, 2007; Howell *et al.*, 2010b), and therefore automatically classifying these features as separate in a habitat classification input layer could lead to the identification of habitats that are not truly distinct from one another (Howell, 2010).

Topography refers to the shape of the seabed and can be used as a surrogate for broad-scale substrate (Evans *et al.*, 2015). In Chapter 3, two topographically-derived variables, fine-scale bathymetric position index (FBPI) and slope, were identified as significant explanatory variables of structure in seamount benthic communities across the 32° latitude study area. To capture the importance of substrate type, and in the absence of biologically relevant substrate maps, topographic variables can be used as a surrogate (McQuaid *et al.*, 2020). For this study slope, fine-scale bathymetric position index (FBPI) and broad-scale bathymetric position index (BBPI), were selected as potential proxies for substrate, all of which can be derived from bathymetric data.

Slope is a measure of seabed steepness in relation to the horizontal plane, and is important in driving the distribution of many deep-sea biological communities including cold-water coral (CWC) reefs and sponge aggregations (Ross & Howell, 2013; Ross *et al.*, 2015; Howell *et al.*, in prep). Slope can be interpreted as a surrogate for hydrodynamic properties such as current velocity (Guinan *et al.*, 2009b), which in turn can be used to model substrate type and grain size (Stephens & Diesing, 2015). The hydrodynamic regime in place is crucially important for deep-sea epibenthic species distributions as the vast majority of deep sea taxa are deposit or suspension feeding organisms (Sokolova, 1959), and therefore rely on currents (or the lack of) as a food supply mechanism.

Bathymetric position index is derived from slope and is the marine equivalent to topographic position index (Weiss, 2001; Lundblad *et al.*, 2006). The values reflect the elevation of a focal point (i.e. grid cell) in relation to the overall landscape (i.e. surrounding grid cells), where positive values represent raised areas and negative values are depressions. Depending on the scale factor used, bathymetric position indices can be used to identify habitats over different scales such as meso- and megahabitats *sensu* Greene *et al.* (1999). The relative height of the seabed is important for species distribution in the deep sea because again, it can act as a surrogate for environmental variables such as current velocity and substrate (Evans *et al.*, 2015; McQuaid *et al.*, 2020).

Topographic variables (slope, FBPI and BBPI) were derived from the GEBCO 2020 bathymetric grid (GEBCO Compilation Group, 2020) using the Benthic Terrain Modeller plugin (Walbridge *et al.*, 2018) in ESRI ArcMap v10.7. To calculate these derivatives, data need to be in an equal-area projection so the bathymetry raster was first re-projected from WGS84 into Mollweide and resampled to the desired grid cell size of 10 km to match the resolution of the Bio-ORACLE data layers (Assis *et al.*, 2018). This projection was chosen as it minimised problematic areas in the final data grids where layers had been reshaped; these areas are therefore confined to the extreme longitudes (i.e. 180 °W and °E) in the polar regions. Slope was calculated using the default 3x3 neighbourhood around the processing cell. FBPI was calculated using an inner radius of 1 and outer radius of 2, allowing for detection of habitats at the scale of 20 km such as seamounts and canyons (described as 'megahabitats' in Greene *et al.*, 1999). BBPI was used to identify larger habitats at the scale of 100 km using an inner radius of 1 and outer radius of 10. This facilitated the detection of, for example, abyssal plains. The topographic layers were then projected back into WGS84 at ~10 km (0.083 °) resolution for clustering so as to reduce any potential projection-related artefacts in the final outputs. Topographic variables were also clustered together as one group to avoid overweighting their importance as per previous studies employing similar habitat classification methodologies (Evans *et al.*, 2015; McQuaid *et al.*, 2020).

Particulate organic carbon flux to depth

The fourth and final data type in the Howell (2010) suggested habitat classification methodology is biological communities. While maps of distinct biological communities are somewhat accessible for shallow-water areas, continuous maps of communities (or biotopes) rarely exist for the deep sea. Particulate organic carbon (POC) flux to depth, is an important driver of a number of biological processes in the deep sea including diversity, abundance, biomass and aspects of ecosystem function (Rex *et al.*, 1993, 2000; Culver and Buzas, 2000; Lambshead *et al.*, 2000, 2002; Gage, 2004; Smith *et al.*, 2008; Rosa *et al.*, 2008; Corliss *et al.*, 2009; Bodil *et al.*, 2011; Tittensor *et al.*, 2011; McClain *et al.*, 2012; Chapter 2). POC flux to depth is therefore an important component shaping biological communities of the deep sea. POC flux to depth values were extracted from Lutz *et al.* (2007) that predicted flux as a function of seasonality of net primary production and depth. The raster dataset was available in a 0.089 ° resolution which was subsequently re-sampled to 0.083 ° using a bilinear interpolation method to match the water mass structure and topography data layers.

5.3.2.2 Cluster analysis

Prior to the cluster analysis, all individual variables were normalised between 0 and 1. An unsupervised, non-hierarchical clustering algorithm (Clustering Large Applications, CLARA) capable of working with large datasets was employed for the analysis in R (R Core Team, 2019). Whilst not all environmental parameters are equally important in driving biological distribution patterns, many regions across the globe have not been sufficiently studied and therefore confidently assigning degrees of importance for variables *a priori* is not possible. Therefore, individual cluster analyses were undertaken on each class of/individual variables to ensure equal weighting of: water mass structure (temperature and salinity), topography (FBPI, BBPI and slope) and POC flux to depth. Using the ‘fpc’ package (Hennig, 2020), cluster analyses were carried out testing two to 40 clusters for each variable/group. The average silhouette width (ASW) provides an indication of the similarity of an object in relation to its own cluster, compared to other clusters. This was used alongside the Calinski-Harabasz (CH) index and expert judgement to inform how many clusters each variable/class of variables should be split into. In both cases, the optimum number of clusters is associated with the highest ASW and CH indices (Caliński & Harabasz, 1974; Kaufman & Rousseeuw, 1990).

5.3.2.3 Demarcation of biogeographic regions

To avoid unconnected water masses with similar properties appearing together in the same habitat classes (e.g. the Arctic and Antarctic), a biogeography was imposed. A number of biogeographical classifications have been developed for the deep sea. However, due to the variability of environmental parameters often being orders of magnitude higher in shallower waters, most do not span across nation's EEZs and neighbouring ABNJ (e.g. Spalding *et al.*, 2007; Watling *et al.*, 2013). Although the reasoning behind this choice is understandable, this approach can hinder ecosystem-based management. To account for this, a biogeography that covers all the world's oceans, national waters included was created. This was developed based on the water mass structure analysis and following published biogeographies (Vinogradova, 1997; Zezina, 1997; Spalding *et al.*, 2007; Watling *et al.*, 2013; Costello *et al.*, 2017; Sink *et al.*, 2019).

Our aim was to create a simple model of biogeography for the express purpose of separating unconnected water masses. Clustering of water mass structure revealed 12 classes; 1-7 were deemed largely offshore and 8-12 inshore. Firstly, for offshore water masses (1-7) discrimination between major ocean basins was achieved by following large offshore water mass structure boundaries within each basin and following published biogeographies where possible. Secondly, for inshore water masses (8-12), Spalding *et al.*'s (2007) classification at the 'province' level was used to split coastal biogeographic regions. In the case of South Africa, their 2018 national classification (Sink *et al.*, 2019) at the ecoregion level was used to denote the split between the Atlantic (Benguela) and Indian (Algulhas) oceans. This approach allowed the offshore and inshore biogeographies to be combined on the same continuous map whilst avoiding ecologically irrelevant splits at political boundaries.

5.3.2.4 Combining of the habitat classification

Once the final number of clusters was confirmed for each variable/group, the outputs were converted into raster datasets and imported to ArcGIS. Using the 'Combine' tool from the Spatial Analyst toolbox, the water mass structure, topography and productivity clustered outputs were combined with the biogeography to create the final habitat classification, where each unique combination of values denotes a unique habitat class (and assumed distinct biological community).

5.3.3 UK Overseas Territory MPA network representativity

In order to assess the contribution of the UKOT MPA network to representative protection in the South Atlantic, the amount of each habitat class within the UKOT MPA network was calculated as a proportion of the full coverage of each habitat class within the South Atlantic basin. These were then compared against the CBD and World Parks Congress targets of 10 and 30%, respectively.

5.3.4 Comparing fine- and broad-scale habitat classification schemes

To evaluate how well fine- and broad-scale habitat classification schemes align, predictive outputs from Chapter 4 were overlaid on the habitat classification. Binary *D. pertusum* reef predictions were converted to a point shapefile and values for habitat class were extracted using the ‘Extract Values to Points’ tool from the Spatial Analyst toolbox. Proportions of predicted presences in each habitat class were calculated and visualised using histograms.

5.4 Results

5.4.1 Initial clustering of variables

Final cluster numbers were selected based on a combination of ASW (Figure 5.3), CH index (Appendix E.1) and expert judgement to ensure final variable layers accurately depicted features known to be important in the distribution of deep-sea habitats.

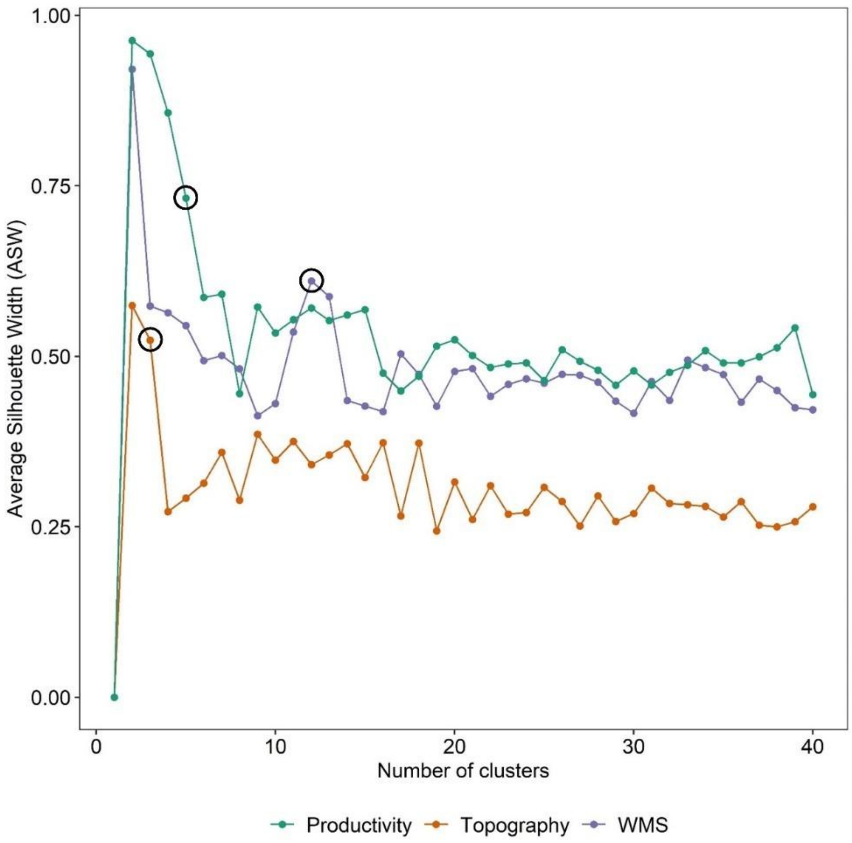

Figure 5.3: Average silhouette width (ASW) for two to 40 clusters plotted for each variable/class of variables. Higher values indicate the best performing cluster scenario. The final selected clusters based on ASW, Calinski-Harabasz Index and expert judgement are denoted by black circles.

Two clusters received the highest ASW for all variables, but this would not appropriately reflect the complexity of biologically relevant variation in each variable at the global scale. CH index values were not highest for two clusters, instead they varied across each variable/class of variables (Appendix E.1). Efforts were made to find the minimum number of clusters whilst avoiding loss of complexity in the layers, driven by expert opinion and information provided by the ASW and CH index. This resulted in the number of clusters circled in Figure 5.3 and presented in Table 5.2 being used in the final classification.

Table 5.2: Number of clusters for each variable/class of variable that were used in the final habitat classification. Water mass structure clusters are grouped into inshore and offshore. Values for individual classes are available in Appendix E.2.

Variable class	**No. clusters**	**ASW (2 d.p.)**	**Variable**	**Min**	**Max**	**Mean**	**Description**
Water mass structure	12	0.61	Sal	5.0	35.6	33.4	Offshore (1-7)
			Temp	-1.8	10.1	1.0	
			Sal	9.9	40.8	35.5	Inshore (8-12)
			Temp	4.9	31.4	16.8	
Topography	3	0.52	Slope (°)	0	7	1.4	Hills and ridges
			BBPI	-1903	4827	124	
			FBPI	-1117	3936	37	
			Slope (°)	0	1	0.3	Plains and shallow slopes
			BBPI	-3318	3218	-43	
			FBPI	-1258	1635	-6	
			Slope (°)	1	17	3.9	Seamounts and other complex features
			BBPI	-5861	4876	17	
			FBPI	-5710	3073	-56	
Productivity (g C_{org} m^{-2} y^{-1})	5	0.73		0.1	3.0	1.4	Very low
				3.0	18.4	6.5	Low
				18.4	41.2	28.0	Medium
				41.2	90.8	61.8	High
				90.8	217.0	120.4	Very high

The 12 clusters within water mass structure show clear tendencies to being either ‘inshore’ or ‘offshore’ (Figure 5.4). Topography clusters into three classes (Figure 5.5) that when assessed against GEBCO bathymetry can be described as ‘hills and ridges’, ‘plains and shallow slopes’ and ‘seamount and complex features’. In the absence of accurate substrate maps, topography is our surrogate and while authors are not claiming that each class is solely constituted of one substrate type, generalisations can be made such as plains and shallow slopes being largely soft sediment habitats, whilst seamounts and complex features are more likely to provide large areas of hard substrate. The majority of the globe is covered by the ‘very low’ productivity class (Figure 5.6); an unsurprising find as POC flux is known to decrease with depth (Lutz *et al.*, 2007). Crucially, the five classes of productivity allow for the separation of areas in temperate latitudes that are known to receive higher POC flux to depth than adjacent areas (e.g. around Tristan da Cunha in the South Atlantic).

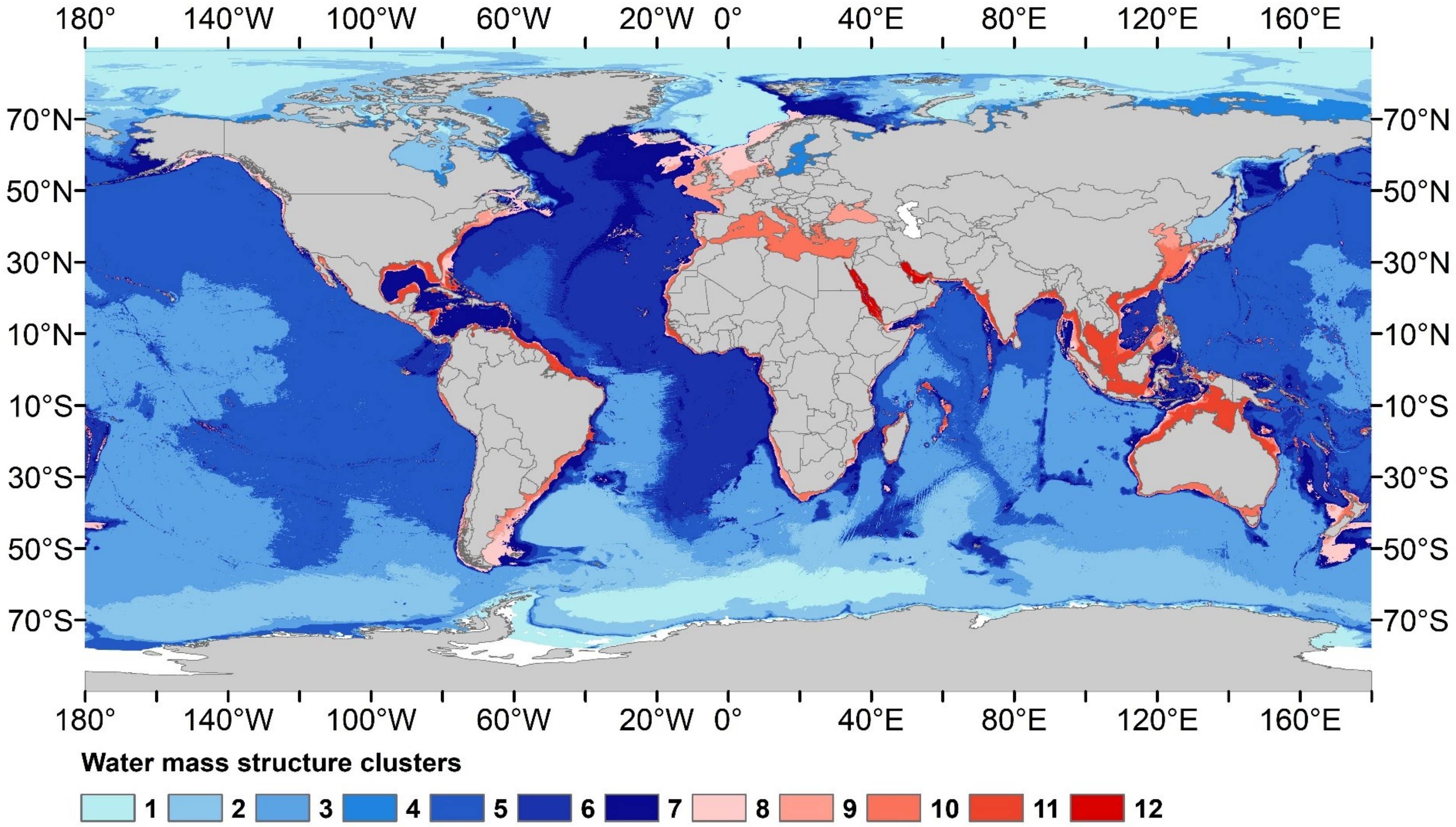

Figure 5.4: Outputs of the CLARA clustering to create the final water mass structure layer used in the habitat classification. Water masses are separated into offshore (blue) and inshore (red). Class input variable values can be found in Table 5.2.

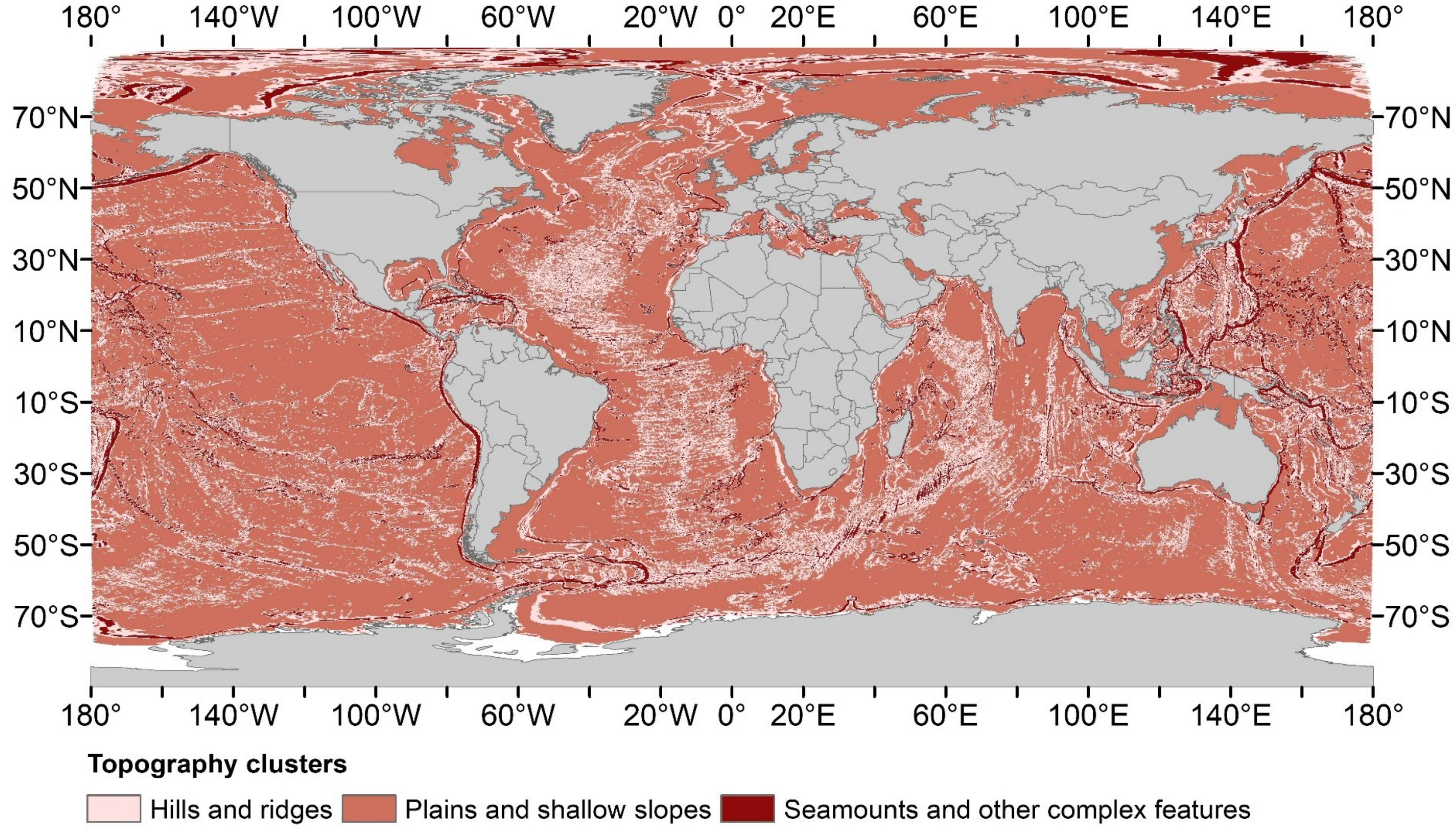

Figure 5.5: Outputs of the CLARA clustering to create the final topography layer used in the habitat classification. Colours denote the descriptive labels given to each cluster. Class input variable values can be found in Table 5.2.

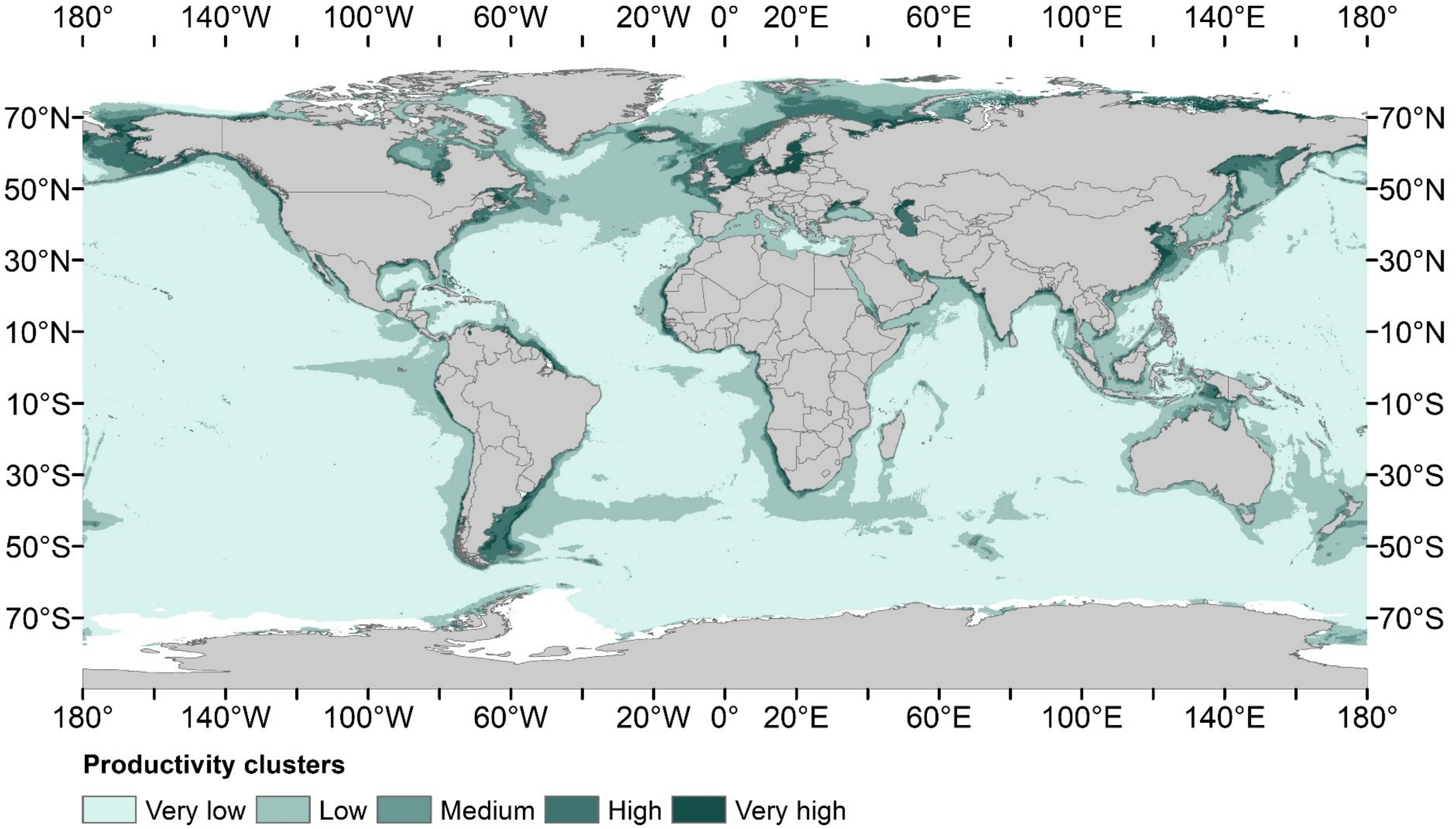

Figure 5.6: Outputs of the CLARA clustering to create the final productivity layer used in the habitat classification. Colours denote the descriptive labels given to each cluster. Class input variable values can be found in Table 5.2.

Biogeographic regions (Figure 5.7) were not determined using clustering, although the water mass structure layer did contribute to decisions regarding where splits between major ocean basins should be. In total, 53 biogeographic regions were identified, 48 of which were deemed ‘inshore’ based on existing biogeographies (Spalding *et al.*, 2007; Sink *et al.*, 2019). Offshore biogeographic regions were Arctic, Antarctic, Atlantic, Indian and Pacific.

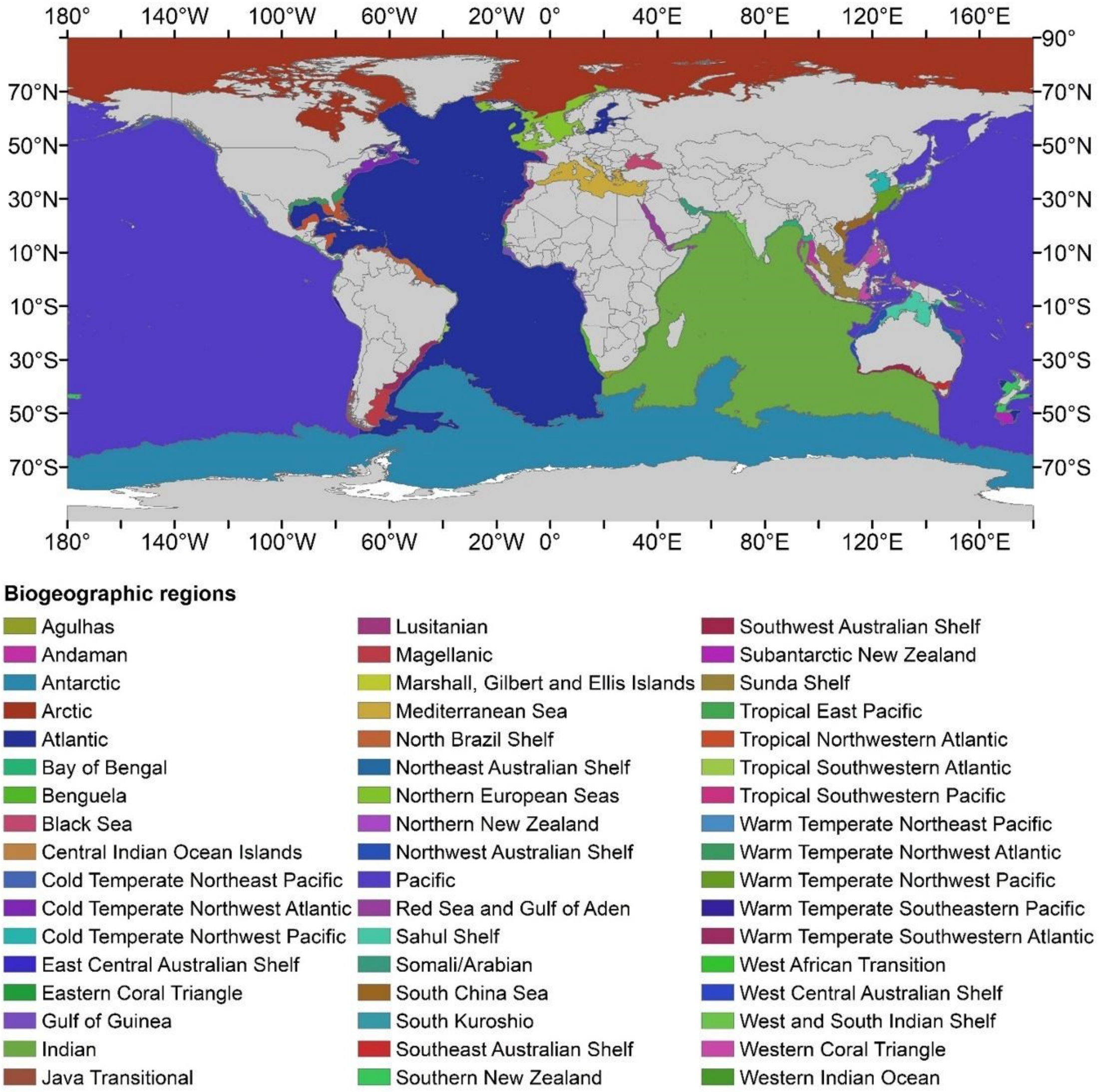

Figure 5.7: Biogeographic regions used in the final habitat classification.

5.4.2 Final habitat classification

The final habitat classification produced revealed 1,750 benthic habitat classes globally (Figure 5.8) that are assumed to support distinct faunal communities. These classes are based on differences in environmental conditions at 10 km resolution. Broadly speaking, large areas of major ocean basins such as the Pacific and Indian are dominated by individual habitat classes, whilst the Atlantic appears more complexly split. Inshore areas (based on clusters 8-12 of the water mass structure layer, Figure 5.4) contain 1,346 of the 1,750 habitat classes, whilst offshore contain far fewer at 484.

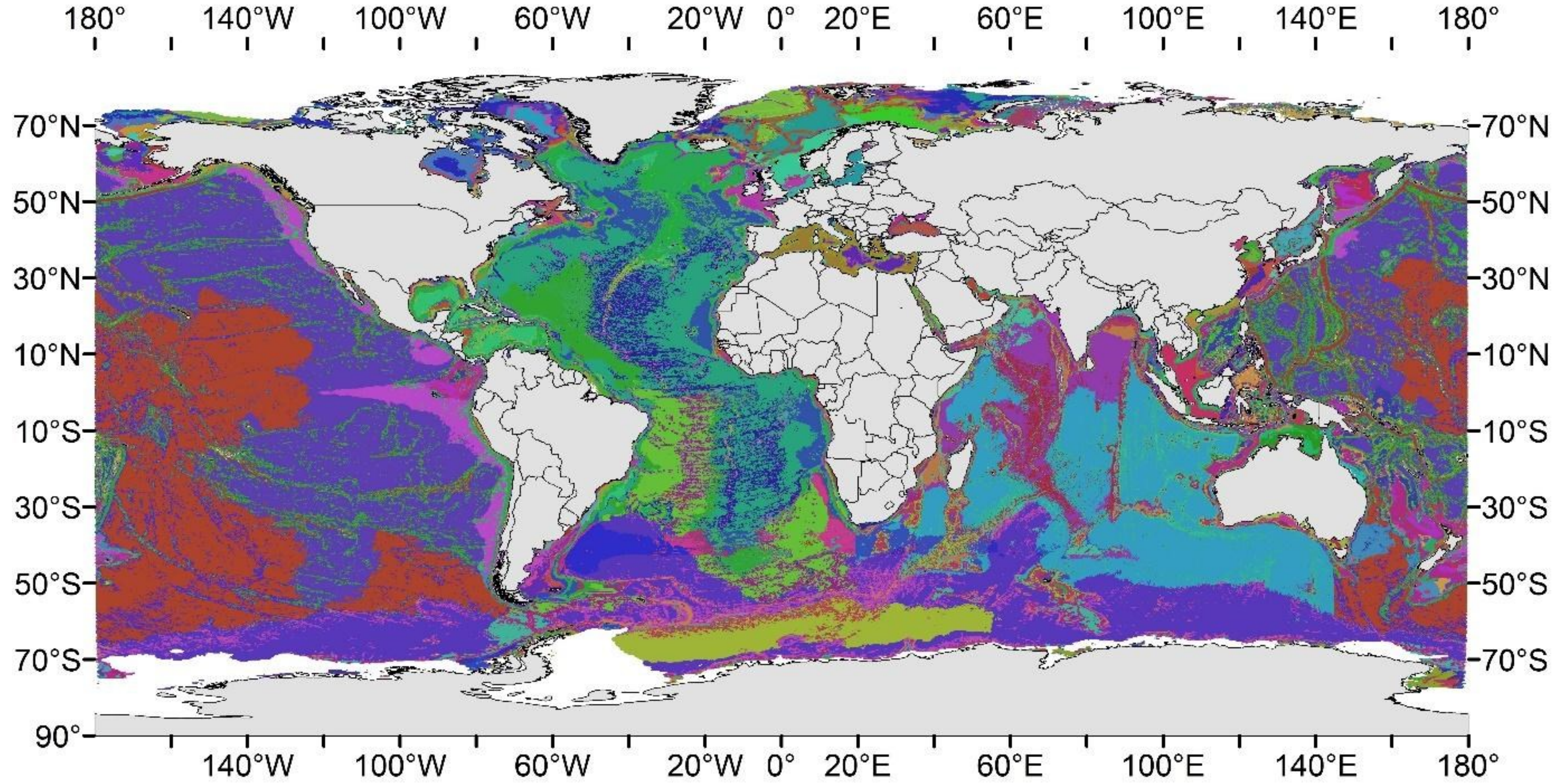

Figure 5.8: Final global, benthic habitat classification with 1,750 classes; each class is assumed to harbour a distinct biological community.

The most dominant habitat class in terms of spatial coverage is the purple class seen covering a large amount of the Pacific Ocean (Figure 5.8), calculated to cover approximately 75 million km^2. However, the majority of distinct classes have smaller geographical extents between 100 and 10,000 km^2 (Figure 5.9).

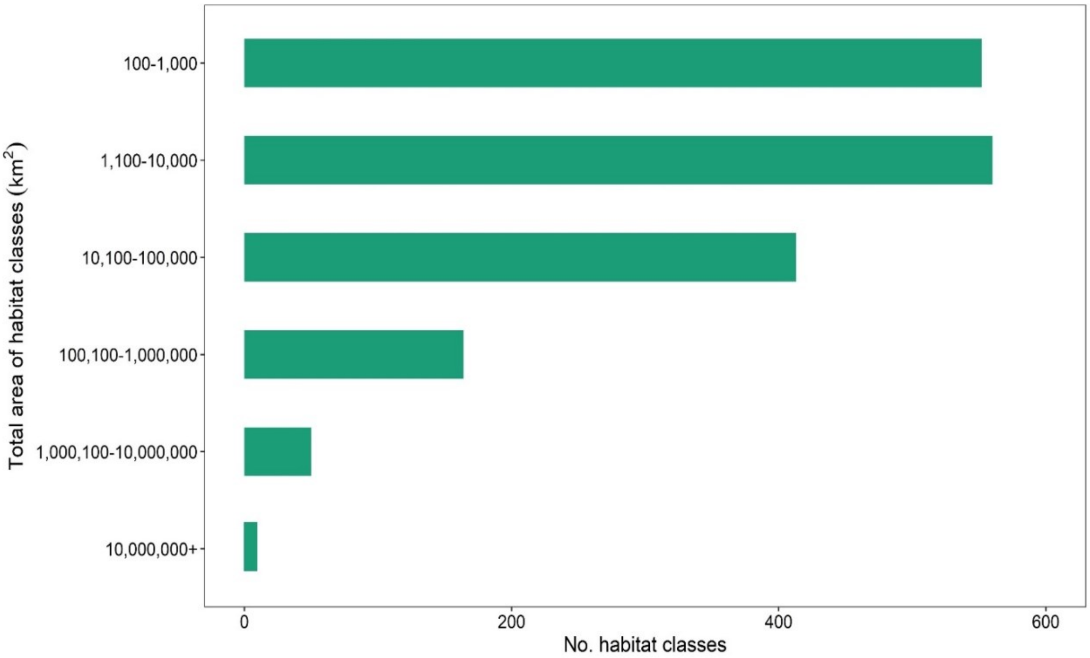

Figure 5.9: Distribution of the geographical extent of habitat classes identified in the habitat classification.

5.4.3 South Atlantic UKOT MPA network representativity

In the South Atlantic (Figure 5.1), 313 habitat classes were identified over the 53.5 million km^2, 34 (~11%) of which were also found in the UKOT MPA network (1.64 million km^2). Of those 34 classes, eight classes were calculated as having ≥10% of their full South Atlantic area in the UKOT MPA network (Table 5.3), thus satisfying the CDB 10% representativity target. However, of the eight classes with ≥10% of their

South Atlantic area in the UKOT MPA network, only two were deemed to have less complex topography (plains and shallow slopes).

None of the habitat classes within the UKOT MPA network had more than 30% of their South Atlantic area protected, and no classes existed solely in the UKOT MPA network.

Table 5.3: Habitat classes in the South Atlantic with ≥10% of their area within the UKOT MPA network. BG = Biogeographic.

Habitat Class	**BG. region**	**Water mass structure class**	**Topographic class**	**Productivity class**	**Area in whole SA (km^2)**	**% of area in UKOT MPA Network**
379	*Atlantic*	*Inshore: 9*	*Seamount and complex features*	*Low*	2,400	25.0
149	*Atlantic*	*Offshore: 7*	*Hills and ridges*	*Very low*	285,800	14.6
163	*Atlantic*	*Offshore: 6*	*Hills and ridges*	*Low*	1,196,300	13.2
104	*Atlantic*	*Offshore: 6*	*Plains and shallow slopes*	*Low*	2,595,000	12.6
206	*Atlantic*	*Offshore: 6*	*Hills and ridges*	*Very low*	3,746,900	11.5
378	*Atlantic*	*Offshore: 5*	*Plains and shallow slopes*	*Very low*	1,967,200	10.7
386	*Atlantic*	*Inshore: 8*	*Seamount and complex features*	*Very low*	4,900	10.2
503	*Atlantic*	*Inshore: 9*	*Hills and ridges*	*Very low*	1,000	10.0

5.4.4 Merging of fine- and broad-scale habitat classification/identification systems

Over a third (37.6%) of *D. pertusum* reef presence predictions in the South Atlantic from Chapter 4 were found in habitat classes 132, 638 and 1,531, with the remaining 62.4% split across 34 different habitat classes (Figure 5.10). These classes represent three habitats across three biogeographic regions (Atlantic, Indian and Agulhas) that are characterised by complex topography with low to medium productivity; 3.4% of the area of habitat class 132 within the South Atlantic is found within the UKOT MPA network. The strong affinity between presence predictions and particular habitat classes suggests a level of alignment between fine- and broad-scale habitat classifications is possible. However, the predictions from Chapter 4 are limited to areas for which multibeam data were available, and thus these results are somewhat biased to particular features and substrate types.

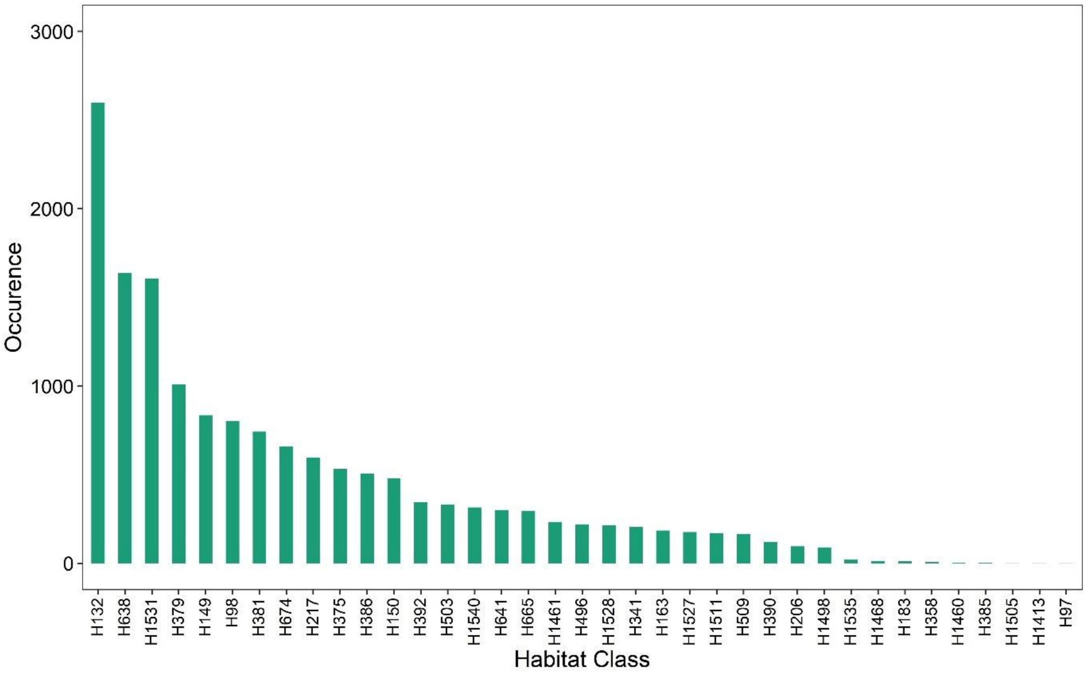

Figure 5.10: Frequency of occurrence of Desmophyllum pertusum reef presence predictions (n=15,531) from Chapter 4 in habitat classes in the South Atlantic.

5.5 Discussion

The final habitat classification presented here identified 1,750 benthic habitat classes assumed to each support distinct faunal communities, the majority of which covered areas between 100 and 10,000 km^2. Inshore areas harbour the majority of habitat classes (1,346 of 1,750), likely owing to the more complex biogeographic regime and larger variability in environmental parameters in shallower waters.

Without an equivalent global habitat classification to compare this with, it is difficult to assess whether the final habitat classification produced here has biological relevance. However, some comparisons can be made between the clustered input layers and patterns observed in previous studies that have investigated the effects of particular environmental parameters on the distribution of faunal communities. Additionally, drawing comparisons on the number and distribution of habitat classes in areas where the faunal zonation patterns are reasonably well-described can contribute to understanding whether the final habitat classification aligns with empirical observations.

5.5.1 Comparison of input variables with existing literature

5.5.1.1 Water mass structure and biogeography

Perhaps the most basic of habitat classifications are biogeographic regionalisations. These typically combine environmental data such as water mass structure with data on species' ranges to infer regions of shared species. It is therefore possible to compare published biogeographic regionalisations with the combined biogeography and water mass structure input layers from our habitat classification. As our inshore biogeography is directly extracted from published literature (Spalding *et al.*, 2007; Sink *et al.*, 2019), only the offshore biogeography and water mass structure will be considered in this comparison (Figure 5.11).

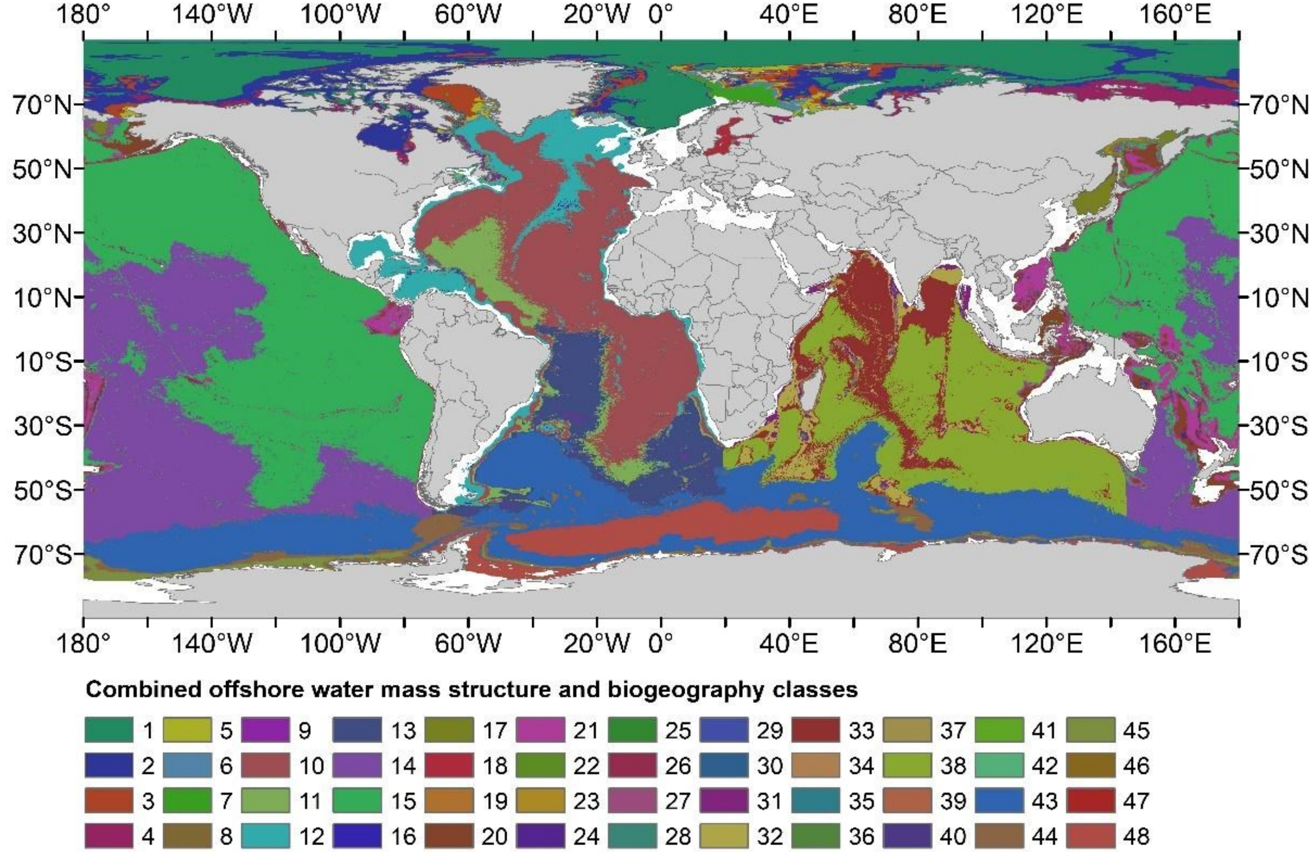

Figure 5.11: Clustered offshore water mass structure output combined with the biogeography input layer.

Menzies *et al.* (1973) provides a global scheme of abyssal biogeographic provinces. Compared to a combined product of our offshore water mass structure and offshore biogeography (Figure 5.11), there is notable agreement between the two. A major similarity is the way in which both classifications keep the east Atlantic as one, contiguous unit spanning from western Europe to west of South Africa (class 10, Figure 5.11), a feature that is also seen in Vinogradova's (1997) abyssal provinces. However, this is not observed in Watling *et al.*'s (2013) proposed biogeography of the seafloor. Instead, these authors distinguish between the northeast and southeast Atlantic approximately at the equator. For the southwest Atlantic, both Menzies *et al.* (1973) and Watling *et al.*'s (2013) identify a distinct biogeographic region. Although the southwest Atlantic is separated from the north Atlantic and the majority of the southeast Atlantic, class 13 in Figure 5.11 does also appear off the western coast of South Africa. Due to the paucity of data in this region, there is very little evidence to determine whether the southwest Atlantic is truly distinct from this region and therefore the class is left unedited. Interestingly, Vinogradova (1997) present the northwest and southwest Atlantic in a single province.

The North Atlantic just south of Greenland and Iceland is separated from the rest of the Atlantic in multiple biogeographies (Menzies *et al.*, 1973; Vinogradova, 1997; Watling *et al.*, 2013). This northern North Atlantic boundary is represented in our input layers as the distinction between classes 10 and 12 in Figure 5.11. Again focusing on bathyal biogeography, Zezina (1997) place the 'limits for most cold-water species' in this region, further supporting the biological relevance of our biogeography and water mass structure input layers. Costello *et al.* (2017) differ from other biogeographies in this region by introducing a boundary along ~30 °N, splitting the Atlantic into just two offshore regions. Costello *et al.* (2017) use both benthic and pelagic data from repositories to characterise global biogeographic provinces. However, due to increased data availability for pelagic taxon, the resulting provinces may be overly sensitive to pelagic taxa distributions and thus present a less relevant comparison for this work (Summers & Watling, 2021).

In the Pacific, there are more inconsistencies between our offshore biogeography and water mass structure and published biogeographic regionalisations. We identify two major regions, one constrained to the central and southern Pacific (class 14, Figure 5.11), and the other surrounding this from east to west (class 15, Figure 5.11). The abyssal provinces from Menzies *et al.* (1973) are most similar to ours, but introduce further discrimination between provinces in the east; one province does continue around the Pacific from east to west, but this band is thinner than ours and is confined to water nearer the continental shelf. Vinogradova (1997) also have few splits in the Pacific Ocean, although they separate the north from the east and west and thus lack a continuous band around the basin. Other biogeographic regionalisations of the Pacific identify significantly more provinces in the central and southern Pacific (Watling *et al.*, 2013; Costello *et al.*, 2017). For offshore areas, it was felt there was not enough biological evidence applicable to split the Pacific Ocean into further subdivisions (e.g. east and west). This decision is somewhat driven by the relative scale of the habitat classification because although there may be differences in offshore biological communities between the east and west Pacific, the variability is small compared to, for example, inshore *versus* offshore communities. Therefore offshore areas with the same environmental conditions on either side of the basin are in the same habitat class. If in the future there are data to evidence further biogeographic splits between areas, the benefit of this classification methodology is that a new biogeography can be easily retrospectively applied.

Compared to published biogeographic regionalisations, the Indian Ocean input layers also show broad similarities; this is particularly true for Watling *et al.* (2013) where the only noticeable difference is the intrusion of Antarctic water that protrudes north in our water mass structure input layer (Figure 5.4). Costello *et al.*'s (2017) regionalisation also shows a high affinity with our input layers for the Indian Ocean, excluding the province that wraps around the cape of South Africa. In our biogeography input layer, the demarcation between the Atlantic and Indian oceans is a continuation of the inshore Algulhas-Benguela division, based on the South African national habitat classification that reports differences in the offshore fauna on the east and west coasts of South Africa (Sink *et al.*, 2019).

While it is difficult to compare due to fewer broad-scale biogeographic regionalisations in the polar regions and a general lack of continuous data layers, the identification of the Southern Ocean in our input layers appears to broadly follow existing classifications, albeit with fewer subdivisions (Menzies *et al.*, 1973; Vinogradova, 1997; Watling *et al.*, 2013). Somewhat surprisingly, pelagic classifications typically identify the Southern Ocean as one continuous province, and are therefore more akin with our input layers (Longhurst, 2006; Costello *et al.*, 2017; Sutton *et al.*, 2017). Similarly, the Arctic provinces identified in published biogeographic regionalisations are similar (Menzies *et al.*, 1973; Vinogradova, 1997), particularly those identified in Watling *et al.*'s (2013) bathyal classes.

5.5.1.2 Productivity

Rice *et al.* (1994) used time-lapse photography to compare the input of phytodetritus on the Porcupine Abyssal Plain with the Madeira Abyssal Plain, both located in the northeast Atlantic. Results confirmed that the Porcupine Abyssal Plain receives more phytodetritus that the Madeira Abyssal Plain, with the suggestion from authors that this was due to differences in the overlying water column structure. The expectation was that this difference in phytodetritus input at depth would play a significant role in structuring the faunal communities found at each location. In our clustered productivity input layer, the Porcupine Abyssal Plain is in an area of 'low' POC flux to depth, whereas the Madeira Abyssal Plain is within an area of 'very low' flux (Figure 5.6). The ability of our clustered productivity layer to discriminate between these two locations suggests that the variability in productivity captured by our clusters is biologically relevant for this site. This is reflected in the final habitat classification where abyssal habitat classes at each location are different.

On the other hand, work around the Crozet Islands in the Southern Ocean has previously focused on comparing the distribution and ecology of faunal communities between two sites with different productivity regimes driven by natural iron-enrichment at one location (Wolff *et al.*, 2011; Billett *et al.*, 2013). On our clustered productivity input map (Figure 5.6), the locations of sites used to represent the two productivity regimes both fall within areas of 'very low' productivity, suggesting that the biologically relevant gradient in POC flux in this region is not captured. This is possibly driven by the fact that the Lutz *et al.* (2007) model is based on remotely sensed primary productivity data and is therefore at a resolution of ~10 km. Therefore, it is less likely to capture fine-scale variation in primary productivity driven by local effects such as volcanic iron-enrichment. This highlights a generic limitation in broad-scale habitat classifications where variation at the local level is often unreported due to the coarse resolution of continuous data layers, thus leading to underestimations of faunal diversity.

5.5.1.3 Topography

McQuaid *et al.* (2020) built a habitat classification using the same methodology as this study for the Clarion-Clipperton Fracture Zone (CCZ) in the central Pacific; using the same topographic variables, they identified two topography clusters. For the CCZ region, all three of the classes from the clustered topography input layer are present, although 'seamounts and complex features' are very sparse. The majority of the area is covered by the 'plains and shallow slopes' topography class that aligns well with McQuaid *et al.*'s (2020) 'flat, with less prominent peaks' class. There is also strong alignment between their 'sloped, with more prominent peaks' class and our 'hills and ridges' class (Appendix E.3).

Using a combine and then classify protocol, Evans *et al.* (2015) developed a classed topography layer for a habitat mapping exercise in the northeast Atlantic, identifying five topography classes. Comparison of our clustered topography input layer with the equivalent from Evans *et al.* (2015) finds similarities in the patterns identified. The 'steep' and 'steepest' classes equate to our 'seamounts and other complex features' class, whilst their 'flat' and 'gentle' classes equate to our 'plains and shallow slopes' class (Appendix E.3).

The lack of reliable deep-sea substrate maps make it difficult to validate the clustered topography input layer with regards to its biological relevance. However, the similarities between our input layer and similarly derived topography layers used in two other habitat classifications suggests our input data are at least similar to other topography layers used as surrogates for broad-scale substrate in peer-reviewed works. This said, both Evans *et al.* (2015) and McQuaid *et al.* (2020) used GEBCO bathymetry to develop their topography layers, albeit different versions. Therefore, it is perhaps not surprising that our study yields similar results. More mapped data are required on both substrate type itself, and its role as a driver of community structure at broad spatial scales to truly ascertain the biological relevance of our clustered output.

5.5.2 Comparison of final habitat classification with existing literature

Carney (2005) reviewed the literature on faunal zonation (sometimes referred to as faunal change) along the depth gradient, reporting a consistent finding across most studies was the identification of a zone of more rapid change (i.e. high species turnover) between 1,000 and 1,200 m. The following section compares the final habitat classification with faunal zonation literature for three areas. Figures of the habitat classification produced here for each area are available in Appendix E.4-E.6.

5.5.2.1 Porcupine Seabight

The Porcupine Seabight is a well-studied oceanic basin in the northeast Atlantic (Rice *et al.*, 1991). In this region we observe a zone of rapid change in habitat classes (i.e. high turnover) between 1,000 and ~1,300 m (figure available in Appendix E.4). This is in agreement with Howell *et al.* (2002) who used depth distributions over 47 species of seastar to describe an upper bathyal zone between ~700 and 1,100 m within which species succession is very rapid. However, it would appear that the exact location of this zone shifts up and down the depth gradient based on taxa, as Olabarria (2005) described a combined upper and mid-bathyal zone from ~750 to 1,900 m, with the highest rate of faunal change observed around 1,800 m based on bivalve depth distribution.

Above the bathyal zones, both Howell *et al.* (2002) and Olabarria (2005) report an upper slope zone from around 200 m, an area also visible in our final habitat classification by the presence of a distinct band of the same few habitat classes between the 250 and 750 m isobaths. There is also a distinct change in dominant habitat classes in our classification just above the 2,000 m isobath, possibly corresponding with the 1,700 m and 1,900 m boundaries described in Howell *et al.* (2002) and Olabarria (2005), respectively.

Howell *et al.* (2002) also identify a lower slope zone between 2,500 and 2,800 m and an abyssal zone from 3,300 m. Our habitat classification does not identify the equivalent to Howell *et al.*'s (2002) lower slope zone, possibly due to coarse (10 km) resolution of the classification compared to their sampling regime. However, there is a change in dominant habitat classes around the 3,000 m isobath, congruent with both the abyssal zone in Howell *et al.* (2002) and the bathyal-abyssal overlap zone described in Olabarria (2005).

5.5.2.2 Gulf of Mexico

The Gulf of Mexico has also been the focus of a number of zonation studies over previous decades (e.g. Culver, 1988; Pequegnat *et al.*, 1990; Wei *et al.*, 2012). In our habitat classification, there are marked shifts in habitat classes at ~100 and ~1,000 m and ~2,500 m in the Gulf of Mexico (figure available in Appendix E.5). The shift at ~100 m marks the end of what appears to be shelf habitat classes and is consistent with the shelf-slope transition zone identified by Pequegnat *et al.* (1990), but slightly shallower than some other studies have found (Culver & Buzas, 1981). Using benthic foraminifera as a model taxon, Loubere *et al.* (1993) identified a shelf-slope transition slightly deeper at 170 – 200 m, attributing this to sediment shift from sandy to finer silts and clays. The shelf-slope transition zone in our classification corresponds with an underlying change in the clustered topography input layer, thus suggesting the topography input layer is appropriately capturing variability in substrate at a biologically relevant scale.

Rapid turnover in habitat classes down to 1,000 m is congruent with the archibenthal zone in Pequegnat *et al.* (1990), although we cannot identify a significant change in habitat classes to discriminate between Culver and Buzas' (1981) upper and middle bathyal at 500 m. The upper boundaries of the lower bathyal zone described in Culver and Buzas (1981) and the upper abyss described in Pequegnat *et al.* (1990) are both 1,000 m, aligning well with a shift in our habitat classification to fewer and more dominant classes. Pequegnat (1983) postulated that the distinct boundary at ~1,000 m, was a result of different oceanographic conditions below the thermocline. The clustered water mass structure identifies different water masses above and below 1,000 m, again signifying that the variability captured in water mass structure by the clustered input layer is biologically meaningful.

The boundary at ~2,500 m in our habitat classification aligns with the beginning of previously described mesoabyssal zones (Pequegnat *et al.*, 1990). Wei *et al.* (2010) used a dataset of 271 box cores across 51 locations to identify six faunal zones based on macrofaunal communities. Zones 3E and 3W have upper boundaries at 2,275 and 2,042 m, respectively, somewhat agreeing with our boundary at ~2,500 m. The study assessed the importance of environmental variables on the structure of faunal communities, concluding that differences in POC flux to depth had a significant effect on community structure. The underlying clustered POC input layer shows a strong stratification of

POC flux to depth, demonstrating that this input layer is capturing biologically-relevant variability.

5.5.2.3 Central Pacific

Shifting focus to the Pacific, Yeh and Drazen (2009) identified four main faunal zones around the Hawaiian archipelago based on the depth distributions of megafaunal scavengers. The major faunal break was identified between 500 and 1,000 m where species turnover was high; additional zones were identified at 250-500, 1,000, 1,500-3,000 and ≥4,000 m. Around Hawaii, our habitat classification displays a break in habitat classes at approximately 500 m (figure available in Appendix E.6), congruent with Yeh and Drazen (2009). However, in the deeper areas, the steepness of the terrain means that, at 10 km resolution, it becomes increasingly difficult to identify comparable faunal breaks. This is because the horizontal distance travelled to achieve a 1,000 m increase in depth is far less than 10 km.

McQuaid *et al.* (2020) represents one of the few habitat classifications with which results can be compared, albeit a regional classification for the CCZ. Regional classifications are understandably more detailed than global classifications due to both the differences in resolution of available data for the area (McQuaid *et al.* (2020) use 1 km grids whereas this study used 10 km grids) and less variation in regional data allowing for more nuanced differences between environmental clusters to be identified. This is seen here where our habitat classification identifies 11 distinct classes in contrast with the 24 described previously (McQuaid *et al.*, 2020). This highlights an important point about broad-scale habitat classifications – while undoubtedly useful for areas where empirical data collection is logistically challenging, they will more than likely be superseded by national/regional classifications where higher-resolution data are typically more readily available, and local-scale drivers of faunal distributions can be included. However, broad-scale habitat classifications can offer significant advances in transboundary, regional and global assessments that link national classifications with neighbouring ABNJ, thus facilitating management at the ocean basin level.

5.5.3 Contribution of the UKOT MPA network to conservation in the South Atlantic

While there is a global drive to protect 30% of the global oceans by 2030, it is important to ensure that these areas are representative of the wider marine environment. The UKOT MPA network represents a total of ~1.64 million km^2 of protection in the South Atlantic. Bottom trawling is one of the most destructive fishing methods for benthic habitats, particularly on seamounts and continental slopes (Koslow *et al.*, 2001; Weaver *et al.*, 2011; Clark *et al.*, 2016), and is prohibited in all three areas. This means that the protection afforded by the UKOT MPA network is particularly relevant for benthic habitats.

In the South Atlantic, 11% of the distinct habitat classes were identified in the UKOT MPA network, suggesting that these large-scale MPAs are set to play an important role in conservation at the ocean basin scale. However, only eight of the 34 habitat classes (2.6% of South Atlantic habitats) have ≥10% of their area within the UKOT MPA network which when assessed against the CBD target of 10% protection of all habitat types is low. Of course, the UKOT MPA network is not the only protection network in the South Atlantic – other prominent networks include the extensive South African and Brazilian MPA networks, and the South East Atlantic Fisheries Organisations bottom fisheries closures. However, it is the only truly cross-sectoral protection in the South

Atlantic section of the offshore Atlantic biogeographic region used in this study, suggesting it is of significant importance in the protection of habitats more commonly observed in South Atlantic ABNJ.

Habitat class 379 is found in all three UKOTs, and 25% its area in the South Atlantic falls within the UKOT MPA network (Table 5.3). Compared to the other habitat classes found within the UKOT MPA network, this percentage representation is high and surpasses the CBD's 10% protection goal, almost achieving the World Park's Congress 30% target. Although it is important to acknowledge that the total area of habitat class 379 in the South Atlantic is only 2,400 km^2 and therefore 25% represents a relatively small area, Johnson *et al.* (2014) propose that less common habitats require a greater proportion of protection than more widely distributed habitats. Therefore, it would appear that the UKOT MPA network is assisting the conservation of this habitat class at the basin scale.

Habitat class 206, characterised by semi-complex topography, has 11.5% of its South Atlantic area within the UKOT MPA network, equating to 430,800 km^2, and therefore this MPA network alone achieves the CBD protection target. This is an example of a habitat class that is geographically widespread throughout the South Atlantic, but is also well represented within the UKOT MPA network. Additional MPAs and OECMs, either already designated or to be designated, in the near future mean it is plausible that this class, among others, will achieve the World Park's Congress 30% target.

The majority of the eight habitat classes with ≥10% of their area in the UKOT MPA network are characterised as having more complex topography (hills, ridges, seamounts etc.). This is not surprising as these oceanic islands are associated with large ridge systems (Mid-Atlantic Ridge, Guinea Seamount Chain and the Walvis Ridge). Abyssal plains and similar environments are currently underrepresented in terms of basin-wide protection in the South Atlantic, though of course, this is not a failing of the UKOT MPA network as such, and instead demonstrates the importance of having protected area networks at basin scales.

5.5.4 Aligning fine- and broad-scale habitat classifications

Desmophyllum pertusum reef suitable habitat as predicted by Chapter 4 shows a strong affinity for habitat classes 132, 638 and 1531 (Figure 5.10), confirming that broad-scale habitat classifications such as this align with finer scale habitat suitability models. This result can be interpreted as a successful quasi-groundtruthing of the habitat classification as confidence in fine-scale maps is often high (Ross *et al.*, 2015).

All three classes are characterised by areas of complex topography ('seamounts and complex features') and low to medium productivity. These environmental parameters align with current understanding of the *D. pertusum* niche (Rogers, 1999; Roberts *et al.*, 2006; Dodds *et al.*, 2007; Howell *et al.*, 2011). This result is of great importance for marine spatial planning as there are many areas, particularly within ABNJ, for which high-resolution environmental data (i.e. ≤200 m grid cell size) do not exist. This lack of available data means that fine-scale habitat suitability models are often unable to be either calibrated within, or transferred to these areas (e.g. the southwest Atlantic), representing a vast knowledge gap in terms of the faunal communities that may inhabit areas (Yates *et al.*, 2018). HSMs built with lower resolution data for broader areas have been shown to perform worse than fine-scale models built using high-resolution data (Ross *et al.*, 2015); therefore broad-scale habitat classifications may provide 'the missing link' for spatial planners working at the ocean basin scale when high-resolution data are not available.

5.5.5 Applications in marine spatial planning

With multiple global conservation initiatives such as '30by30' gaining more traction, and the BBNJ negotiations in their latter stages, this study provides an example of a habitat classification that could be used to inform marine spatial plans for vast areas of the deep-sea for which there are few available data on the distribution of habitats. This is particularly valuable to ABNJ in the Southern hemisphere which is comparatively undersampled (Howell *et al.*, 2020b), and supports claims made by scientists and policy makers for better provisioning of MSP in ABNJ (Wright *et al.*, 2019; McQuaid *et al.*, 2020).

In addition to its application to multi-sectoral management, habitat classifications such as this may also prove useful in individual sector-based marine spatial plans. For example, in 2018 the International Seabed Authority announced they would develop Regional Environmental Management Plans (REMPs) for new areas, including the South Atlantic, following increased interest in the prospective mining of seabed resources. Habitat classifications such as this one would prove useful in ascertaining whether draft REMPs are best positioned and adequately represent the habitats where potential mining activities may occur, and consequently benthic habitat lost (Van Dover *et al.*, 2017). This could help to avoid a situation like the CCZ where the efficacy of the current Areas of Particular Environmental Interest network has been questioned (Taboada *et al.*, 2018; McQuaid *et al.*, 2020; Washburn *et al.*, 2021). Moreover, habitat classifications could also be used to identify links between existing anthropogenic activities (e.g. fishing effort) and habitat type. Should particular habitat types be continually exposed to certain pressures, this would provide an argument to ensure their protection in regional MPA networks.

While authors advocate for the use of habitat classifications in the design of new MPA networks/marine spatial plans, they can also be used to assess efficacy of, and provide evidence to support, existing MPAs. Hogg *et al.* (2016) use a similar landscape mapping approach to underpin the South Georgia and South Sandwich Islands MPA, again demonstrating that habitat classifications are useful in MSP. As demonstrated with the UKOT MPA network, habitat classifications can shed light on the importance of certain MPAs in achieving protection targets at ocean basin levels. This is particularly important because over the last several years, marine spatial planning and MPA designations have increased rapidly (UNEP-WCMC, 2018). Understanding the contribution of individual MPAs/regional networks to global targets will facilitate marine spatial planning in the future that compliments existing networks and find the most parsimonious protection scenario that ensures ecological protection while allowing for sustainable development to support blue growth.

Fine-scale maps of habitats are useful and shed light on the intricate nature of individual species and habitats, but building continuous habitat classifications from them in a holistic, bottom-up approach is not often possible due to the paucity of data (Hogg *et al.*, 2016). Moreover, whilst species distribution models can predict species ranges accurately, Vilhena and Antonelli (2015) suggest they are not appropriate for delineating between biogeographic boundaries. In the future, MSP may benefit from aligning fine- and broad-scale habitat models and classifications together as demonstrated here with *D. pertusum* reef to designate MPAs based on a suite of the best-available ecological data.

5.5.6 Limitations

The habitat classification here follows standard approaches developed across multiple studies (e.g. Roff and Taylor, 2000; Howell, 2010; McQuaid *et al.*, 2020) and while results are promising, the arbitrary nature of this type of mapping does need to be acknowledged. Although the variables considered have clear and well-known causal links with ecological variability based on a literature review, the choice of variables used in the classification is partially subjective and driven somewhat by data availability. Be that as it may, the non-hierarchical methodology applied here does mean that decisions regarding the importance of certain variables above others were not required. Moreover, the choice of how many clusters to allow each variable to group into is driven somewhat by established metrics such as average silhouette width (Kaufman & Rousseeuw, 1990), but expert judgement was also required to select the most biologically-relevant clustering regimes, again leading to the possibility of unrealistic results.

The creation of continuous data layers for environmental parameters such as depth, temperature and salinity is facilitated through remote-sensing technologies, and whilst there is understood to be error associated with the data, this is often unquantified and geographically unequal. In areas for which there are more *in-situ* records to groundtruth remote sensed data, the error will be lower. For example, bathymetry products from GEBCO will undoubtedly have more error (both horizontally and vertically) associated with them for the South Atlantic compared to the North Atlantic because of the lack of *in-situ* data, and thus interpolation will be more frequently used.

Finally, as with any modelled output, results should be independently validated using biological datasets to determine whether the maps are biologically relevant. Although a quasi-groundtruthing of the habitat classification was attempted using the *D. pertusum* reef predictions from Chapter 4, this is ultimately validating one model with another. However, sufficient numbers of biological records for vast areas of the ocean are simply unavailable and therefore, the extent to which this classification is biologically relevant remains unclear. This said, it does represent the best available data for vast areas of the world's oceans including the South Atlantic and therefore provides a useful tool in MSP in the short to medium term.

5.6 Conclusion

This study provides a baseline map of the spatial patterns of benthic marine habitats across the globe. Compared to published literature on biogeographic and faunal zonation patterns, some significant similarities are present. Habitat classifications can be employed in national and international efforts to develop marine spatial plans (e.g. Sink *et al.*, 2019), yet they are not frequently used (Hogg *et al.*, 2016). However, if evidence-based ocean-basin management is to become a reality, data derived from sources such as broad-scale habitat maps will be needed.

Using the UKOT MPA network as an example, this study demonstrates how habitat classifications can further enhance our understanding of representative protection of habitats at geographically broad scales, suggesting that this particular MPA network is important in achieving representative protection in the South Atlantic. Strong alignment between fine- and broad-scale habitat models, also in the South Atlantic, demonstrates how habitat classifications such as ours remain biologically relevant, whilst facilitating MSP through the creation of continuous maps.

To fulfil international protection targets, designate ecologically coherent MPA networks, and to develop suitable marine spatial plans to support blue growth, habitat classifications will likely need to feature prominently in the tools used by marine spatial planners in the near future. Habitat classifications should not replace fine-scale mapping efforts, but complement them to fill often vast data gaps, particularly in data-poor regions where few empirical biological data are available.

CHAPTER 6: GENERAL DISCUSSION

This general discussion briefly contextualises the thesis by revisiting the background and rationale, provides a synopsis of key findings from each Chapter and considers how these contribute to the existing body of research. It then reflects on the limitations of the thesis within the broader context of the challenging nature of deep-sea research, and identifies future areas of work that are highlighted by Chapter results.

6.1 Thesis background and rationale

Despite being an inextricably remote and unfamiliar environment for most of the world's human population, the deep sea is subject to/at risk from increasing pressure from extractive industries such as fishing and mining, and anthropogenically-driven climate change (Halpern *et al.*, 2015; Van Dover *et al.*, 2017; Kroodsma *et al.*, 2018; Levin *et al.*, 2020). While this is somewhat due to activities undertaken by humans on land (e.g. rising carbon emissions), significant advances in the technological capabilities of humankind have allowed industry to penetrate deeper into the oceans and further from land, increasing the footprint of such direct pressures in the deep sea (Petersen *et al.*, 2016). In parallel our knowledge on the spatio-temporal distribution and connectivity of deep-sea habitats is improving, however the rate of progression in scientific fields often lags far behind industry development.

6.1.1 Diversity gradients

Our current understanding of deep-sea ecosystems is geographically biased towards the northern hemisphere (Ho*well et al*., 2020b), raising uncertainty as to whether particular observations are equally applicable to all areas of the deep sea. Specifically, there is a lack of information to ascertain whether ecosystems in the South Atlantic deep sea adhere to previously described deep-sea diversity gradients, of which there are multiple, that are often characterised using data collected in the northern hemisphere. Understanding the drivers and distribution of diversity across all deep-sea ecosystems is crucial so as to ensure management of the deep sea is evidence-based, ecologically coherent and fit for purpose.

Furthermore, seamounts and oceanic islands represent areas of hard substrate in an otherwise relatively soft-sediment deep sea. Their topographic setting combined with their complex hydrodynamic regimes mean that these features are described as 'stepping stones', facilitating the incremental movement of species across vast ocean areas (Hubbs, 1959). This may be in the form of enabling larval dispersal across the same (Miller & Gunasekera, 2017) and/or similar features (Ross *et al.*, 2017), or providing areas of increased food availability/trophic activity linked to heightened primary productivity in otherwise comparatively oligotrophic seas (Hosegoo*d et al.*, 2019; Bell *et al.*, 2021; Thompson *et al.*, 2021). The idea that more species may reside on seamounts both due to the substrate and hydrography has led to their previous description as 'oases of biodiversity' (Samadi *et al.*, 2006). However, early work characterising deep-sea latitudinal and bathymetric diversity gradients typically used largescale datasets from soft-sediment habitats. The rationale for parts of this thesis was to determine whether similar gradients are observed on hard substrate features in the deep sea.

6.1.2 High-resolution habitat suitability modelling

Predictive models have long been used to drive policy, one of the best known examples of which is the use of the Intergovernmental Panel on Climate Change models influencing global commitments to reduce carbon emissions through the Paris Agreement (United Nations Framework Convention on Climate Change, 2016). However, despite regular inclusion in terrestrial equivalents and continued technological advancement, predictive habitat models are only just beginning to feature in discussions surrounding ocean management. This is despite their demonstrable use in the sector (Ross & Howell, 2013; Howe*ll et al*., 2016) particularly in management of deep-sea fisheries on, for example, seamounts (Rowden *et al.*, 2017; Georgian *et al.*, 2019).

One of the biggest barriers to ecosystem-based management in the deep sea is the fundamental lack of biological distribution data to underpin our understanding of where particular species and/or habitats are present or absent. In general, increasing sample size facilitates more reliable outputs from habitat suitability models (Stockwell & Townsend Peterson, 2002; Wisz *et al*., 2008), and therefore a lack of biological data hinders the performance of models calibrated in data-poor regions.

In theory, model transferability can provide a solution to this problem if good performance across this data gradient is attainable. However, this is based on the assumptions that: (i) the drivers of benthic assemblage distribution in the northern and southern hemispheres are the same, and (ii) the environmental profiles of the northern and southern hemisphere are comparable and thus offer the same niche space.

6.1.3 Lack of baseline data for marine spatial planning

A major obstruction for area-based management and marine spatial planning in the deep sea is the lack of continuous maps of habitat distribution that can act as a baseline on which to overlay fine-scale models and datasets.

The use of environmental surrogates to model the broad-scale distribution of habitats has a relatively long history of use in marine spatial panning within national jurisdiction, and is now widely used in EEZs across the world (see reviews by Brown *et al.*, 2011; Strong *et al.*, 2019). Conversely, for ABNJ, there are far fewer habitat classifications (Howell, 2010; Evans *et al.*, 2015; McQuaid *et al.*, 2020), with analyses instead tending to focus on identification of broader scale biogeographies as opposed to distinct habitats (Menzies *et al.*, 1973; Zezina, 1997; Watling *et al.*, 2013; Costello *et al.*, 2017).

Whilst there are a number of other challenges facing the implementation of MSP in ABNJ, ‘lack of data’ is considered a key problem (Wright *et al.*, 2019). Specifically, the lack of continuous habitat map for the world’s oceans, particularly one spanning ABNJ and EEZs, hinders transboundary, intra- and inter-ocean basin comparisons which in turn hinders management at the ocean-basin scale, and limits our understanding of the connectedness of current protection networks. However, with the advent of now readily available, continuous environmental data layers in online repositories (e.g. Assis *et al.*, 2018), application of top-down approaches using environmental surrogates could stand to fill these gaps, facilitating greater collaboration in both science and management across ocean basins.

6.2 Thesis objectives

The objectives of this thesis and thus the aims of the individual data chapters can be broadly split into two categories: (i) characterise the ecology of the South Atlantic deep sea, and (ii) trial new methodologies to support sustainable management.

To further our limited understanding of South Atlantic deep-sea ecology, I first investigated the changes in seamount diversity and community structure across depth and latitude in the South Atlantic, linking these with environmental drivers of change (Chapter 2). Continuing on from this, community structure was also investigated allowing for: identification of broad-scale environmental drivers of seamount benthic assemblage structure in the South Atlantic; characterisation of benthic assemblages in terms of their taxonomic identity, and; identification of VMEs (Chapter 3).

To address the second objective regarding sustainable management, I transferred a high-resolution habitat suitability model from a data-rich to a data-poor ocean basin and validated it with an independent dataset to trial whether model transfer performed well (Chapter 4). Finally, I used a top-down, non-hierarchical approach to develop a broad-scale habitat map, using ecologically relevant environmental variables identified from Chapters 2 and 3, that can facilitate ecosystem-based management at the ocean basin scale, providing a South Atlantic example of how the basin scale representativity of habitats within an MPA network can be assessed (Chapter 5).

6.3 Synopsis of data chapters

Using imagery collected between depths of 250 and 950 m from the UKOT of Saint Helena, Ascension and Tristan da Cunha, species richness, a measure of α-diversity, was calculated for each of 39 transects covering 32 degrees of latitude in Chapter 2. Environmental data were extracted for each transect, facilitating the identification of relationships between the environment and α-diversity. Species richness was significantly higher at Tristan da Cunha in the temperature latitudes than the tropical sites. Primary productivity in the overlying surface waters (acting as a proxy for latitude) along with substrate hardness (controlled for across territories) were found to have significant positive effects on α-diversity. Although no significant relationship between α-diversity and depth was identified, depth was identified as a significant predictor of β-diversity (species turnover). This suggests that seamount benthic communities do not display the well-documented peak in diversity at bathyal depths, but instead display a more constant diversity along the depth gradient, with the high overall diversity being driven by change in taxon identity down the slopes. Whilst the limited depth range in this study (<1000 m) may be too shallow to identify a diversity peak in bathyal depths, if one were to exist, a gradual increase in diversity with depth would perhaps be expected. This finding holds true for the multiple (nine) seamounts and oceanic islands for which data were available and therefore the lack of significant trend in α-diversity with depth on any feature suggests a lack of a significant peak in diversity is a widespread observation.

Chapter 3 used the aforementioned dataset along with extra transects to describe seamount benthic communities found across the South Atlantic, again identifying environmental drivers of distribution. Benthic communities from temperate latitudes were both significantly different from, and more numerous than, those found in tropical areas. Results showed that community structure was significantly driven by latitude and depth, and to a lesser extent, longitude, FBPI and slope. Latitude, in and of itself, is biologically irrelevant, and therefore the identification of this as a key driver of community structure is thought to truly reflect the vast difference in surface primary productivity between temperate and tropical sites, evidenced by the strong dominance of filter-feeding taxa at Tristan da Cunha. The identification of depth as a significant predictor of community structure was attributed to the complex nature of water mass structure found near temperate fronts creating bands of different communities down the slopes of seamounts, a result that is also observed in Chapter 2. Of the 74 transects analysed, 28 (37.8%) were deemed to satisfy criteria required to consider the communities a VME, signifying that the South Atlantic basin harbours significant numbers of protected ecosystems.

One of the VMEs identified in Chapter 3 was *Desmophyllum pertusum* reef. For Chapter 4, a good-performing, high-resolution habitat suitability model was built for *D. pertusum* using data from the North Atlantic. This model was then transferred onto equivalent environmental data from the South Atlantic and validated using a small independent dataset of presence and absence points for *D. pertusum* reef obtained from Chapters 2 and 3. The transferred model outputs were used to assess the current VME protection network in the South Atlantic, considering both the UKOT MPA network and SEAFO VME closures. Results showed that of the 27 features considered, 21 provided suitable habitat for *D. pertusum* reef. This suggests that the South Atlantic basin likely contains a large amount of this particular VME, agreeing with prior records (Zibrowius & Gili, 1990; Pires, 2007). The vast majority of predicted presences were in areas where bottom trawling, the most destructive fishing practice for this habitat (Roberts *et al.*, 2006), is legislated against and therefore offer relevant protection.

The final data chapter in this thesis explored a potential spatial management tool in the form of a top-down, non-hierarchical, broad-scale benthic habitat classification, the benefit of which is the provision of a baseline map of the spatial distribution of benthic habitats in data-poor regions. Globally, 1,750 distinct habitats were detected, 313 of which occurred in the South Atlantic. To provide a contextualised example of its use in MSP, an assessment of the contribution of the UKOT MPA network towards protection targets of representative habitats at the ocean basin scale was undertaken. This showed that the UKOT MPA network is an important contributor towards the representative protection of a number of habitats in the South Atlantic, particularly those occurring on hills and ridges, and seamounts and other complex topographic features. This is intuitive as the UKOT forms part of larger ocean ridge systems and seamount chains, and thus are heavily characterised by this terrain. The representativity analysis did identify shortfalls in the UKOT network whereby they do not protect habitats found on less complex terrain such as abyssal plains and shallow slopes, although this is directly due to the lack of these topographic seascapes due to the geology and positioning of the UKOTs themselves.

6.4 Contribution to knowledge

6.4.1 Biodiversity of the South Atlantic

This thesis has found the South Atlantic to be a biodiverse region supporting a range of benthic assemblages and species consistent with those observed in the North Atlantic but with notable regional differences (Chapter 3). For the upper bathyal environment, α-diversity is higher in the temperate region examined in comparison to the tropical regions examined, driven by the difference in surface primary productivity. While α-diversity on seamount communities does not appear to change with depth, β-diversity is high along the bathymetric gradient, resulting in high turnover of communities on the flanks of seamounts and oceanic islands (Chapter 2).

Although low in number, almost all previous studies from the region have found South Atlantic deep-sea ecosystems to be diverse, identifying VMEs and/or VME-indicator taxa including multiple species of cold-water coral (CWC) reef (Zibrowius & Gili, 1990; Pires, 2007; Durán Muñoz *et al.*, 2014; Bergstad *et al.*, 2019; Barbosa *et al.*, 2020; Sink, pers. comm.), coral gardens (Durán Muñoz *et al.*, 2014; Caselle *et al.*, 2018; Bergstad *et al.*, 2019a; Sink *et al.*, 2019) and deep-sea sponge aggregations (Portela *et al.*, 2012; Durán Muñoz *et al.*, 2014; Hajdu *et al.*, 2017). Notable agreements between the published literature and findings from this thesis include the presence of large amounts of dead reef framework in the southeast Atlantic, particularly towards the tropics (Durán Muñoz *et al.*, 2014; Bergstad *et al.*, 2019; Chapter 3) and the prevalence of coral gardens characterised by antipatharians, stylasterids and solitary scleractinian cup corals. Regarding the latter, data from this thesis (Chapter 3) evidenced the decision to add hard-bottom cup coral fields as a new VME sub-type by ICES/NAFO Joint Working Group on Deep-water Ecology (ICES, 2019).

Whilst there are clear similarities in findings, previous studies were purely descriptive and did not characterise *how* community composition and species' distributions are driven by particular environmental parameters. With confirmation that the communities observed within this thesis (Chapter 3) are representative of the wider South Atlantic based on the best available data, it is appropriate to extrapolate the ecological relationships characterised in this thesis and apply them to other, likely unsampled, features to better understand the distribution of biodiversity in the South Atlantic and support sustainable management.

6.4.2 Area-based management of the South Atlantic

Good baseline knowledge of the ecology and environmental drivers of biodiversity is key if we are to understand how existing and future industry may affect species and habitats. Similarly this knowledge is essential in making informed decisions in the use of area-based management tools and marine spatial planning (MSP). The data for this thesis have already contributed to MSP in the South Atlantic. In 2020, Tristan da Cunha announced the designation of a new Marine Protection Zone (MPZ) covering their entire EEZ. Many species and ecosystems were considered when designing the MPZ including seabirds, pelagic fishes and benthic ecosystems. For the latter, VME mapping from Chapters 3 and the model outputs from Chapter 4 provided significant insight into the spatial distribution of benthic habitats in Tristan da Cunha's EEZ. These data were used to inform the zoning scenarios on the seamounts, allowing for sustainable fishing whilst adopting the precautionary principle and avoiding known VME distribution. In addition, the model outputs were also used to inform on the potential environmental impacts of a sunken vessel off Gough Island in October 2020. MV *Geo Searcher* is thought to have settled on an area of steep, rocky terrain at approximately 360 m after colliding with rocks. The model outputs from Chapter 4 suggest this is an area of highly suitable habitat for *D. pertusum* reef. Whilst the extremely remote nature of the wreck site presents a significant challenge in terms of physically sampling and monitoring the wreck, this finding was used to advocate for the pursuit of additional funding to conduct a scientific research survey of the affected and surrounding areas.

Outside of EEZs, conservation and sustainable use of ABNJ is set to drastically evolve owing to the inclusion of ABMTs including MPAs in the draft text from the BBNJ negotiations. Although the CBD is not officially tied to the BBNJ negotiations, there are some suggestions that the EBSA identification process will help shape what MPAs in ABNJ may look like in the coming years, perhaps by becoming candidate MPAs.

The large temperate EBSA in the southeast Atlantic that follows the Tristan da Cunha EEZ (Figure 1.6) is likely important in protecting areas of high diversity including VMEs (Chapter 2), as is the Walvis Ridge EBSA (Chapter 4). This said, protection of the Walvis Ridge is particularly complex as some areas are still open to bottom fishing and the entire ridge extending southwest to Tristan da Cunha is claimed by Namibia as extended continental shelf. Nonetheless, the high number of EBSAs off the temperate west African coast, combined with large numbers of MPAs in South Africa's EEZ (including offshore) means that conservation of the deep sea in the southeast Atlantic is steadily progressing. As well as allowing nations to achieve conservation targets set out in legislation, national protection designations also have the power to significantly improve basin scale conservation efforts (Chapter 5) and therefore national marine protection/spatial planning initiatives should be encouraged.

In comparison with the east, there is a distinct lack of protection in the southwest Atlantic both in terms of fisheries closures (due to the lack of RFMO) and fewer EBSAs, particularly at temperate latitudes where biodiversity is likely higher (Chapter 2). Additionally, the temperate southwest Atlantic is home to the Rio Grande Rise, the only area of the basin currently undergoing exploration for deep seabed mining. Due to a lack of similar environments in the southwest, the Rio Grande Rise may represent an important feature in terms of basin connectivity and provision of hard substrate, and may harbour significant biodiversity in the southwest Atlantic (Chapter 2; 3). Additionally, if the temperate southwest Atlantic is similarly dominated by filter-feeding taxa like the southeast (Chapter 3), it may mean that communities in these areas are more susceptible to adverse impacts of mining activities, particularly those involving sediment plumes. This should be considered in the designation of APEIs and PRZs in the future.

Abyssal environments across the whole basin are currently underrepresented in existing protection networks (Chapter 5). Although there are large EBSAs overlapping some abyssal areas in the Brazil and Angola Basins, these are in the tropics and therefore likely to harbour significantly different communities to equivalent ecosystems in temperate latitudes (Chapter 3), perhaps with lower overall diversity (Chapter 2). This gap in protection could be rectified by ensuring that an MPA in the future includes abyssal environments in the Argentine Basin, particularly due to the predicted high prevalence of manganese nodules and consequent mining interest (Hei*n et al.*, 2013; Figure 1.4).

Seamounts in the southeast Atlantic provide significant amounts of suitable habitat for *D. pertusum* reef (Chapter 4) and display high habitat heterogeneity (including VMEs) in relative close proximities (Chapter 3), thus leading to the suggestion that some of the fisheries closures designated by SEAFO should be expanded and that seamounts should be considered on an individual basis in management scenarios. Also with a focus on the southeast Atlantic, the ISA will soon begin developing the REMP to provide management tools for South Atlantic seamounts. With no current guidance on how protection mechanisms will interact between multiple sectors, we are facing a situation where an area that has been identified as supporting VMEs, and has therefore been closed to bottom fishing, could be subject to mining exploration. While *in-situ* data for this region remain sparse, modelled outputs (Chapter 4; 5) represent best available data and should therefore be incorporated in future MSP processes across sectors. Likewise, if holistic, basin scale management of ecosystems is to become a reality, the South Atlantic REMP and MPAs resulting from the BBNJ negotiations should seek to complement existing spatial management measures in the region (e.g. the SEAFO fisheries closures) rather than undermine them. This is particularly important for the protection of VMEs that are only protected from significant adverse impacts of fishing activity under current legislation. As a general point, in basins such as the South Atlantic that have previously undergone little scientific exploration, it is important to revisit protection networks to ensure the precautionary principle is followed as new data are collected.

Ribeiro (2017) tabulated countries bordering the South Atlantic and their ratification status to significant international treaties on the conservation and/or sustainable use of marine resources, reporting relatively low ratification rates. They concluded that poverty and a lack of emphasis on capacity-building historically were the greatest barriers to conservation of marine biodiversity in the South Atlantic. This, combined with the fact that the South Atlantic is very data-poor, mean that MSP in the basin is still in its infancy in large areas. Whilst the lack of substantial management framework in the basin is not necessarily conducive to conservation, it does provide an opportunity for South Atlantic bordering-nations, existing regional programmes (e.g. the Abidjan Convention) and future protection initiatives (e.g. the BBNJ negotiations) to develop a comprehensive management framework. Consideration of both EEZs and ABNJ in this process (*sensu* Chapter 5) will be central to ensuring that basin scale management is not hindered by political boundaries. Moreover, the South Atlantic region may stand to gain a lot from the development of new tools and technologies to aid MSP.

6.5 Limitations and future scientific research

The overarching limitation witnessed throughout this thesis was the lack of data available for the South Atlantic. This is true of both biological and environmental datasets, and therefore a key priority for future work in the South Atlantic must have a strong emphasis on the collection, archiving and sharing of more data.

Biological data used throughout this thesis consisted of seafloor imagery collected using the Shallow Underwater Camera System (SUCS, Appendix A). The SUCS is a drop camera that lands perpendicular to the seafloor making it useful when needing to accurately quantify the size and abundance of fauna (Barnes *et al.*, 2019). Although a recent study has found drop cameras are significantly better than remotely operated vehicles (ROVs) at capturing both abundance and diversity (de Mendonça & Metaxas, 2021), the relatively small frame size (405.7 x 340.6 mm) and lack of contextual data (i.e. surrounds) mean that in general, drop cameras are not best suited for characterising larger ecological units such as habitats (Howell *et al.*, 2019). Although the ~20 randomly captured images from each cluster transect somewhat counteract this limitation by factoring repeatability into the design, future work assessing habitats and/or VMEs in the region would benefit from the use of more appropriate equipment such as ROVs or towed video camera systems. These gears should be complemented with drop cameras with higher depth ratings than SUCS to allow for data to be collected from a wider depth range than that of this thesis. This will help clarify whether the lack of depth-related α-diversity gradient identified in Chapter 2 is a true reflection of reality, or an artefact of the limited sampling regime.

Issues arising from the comparison of multiple deep-sea image datasets include the varying levels of taxonomic resolution achieved through image analysis; the morphotype naming systems different scientists and organisations adopt (Howell *et al.*, 2019); and user-bias in identification (Durden *et al.*, 2016). To account for the latter, all images from the UKOT dataset were analysed by the same user to reduce user-bias, and a subset of these were checked by a second observer. Comparison of the two annotation datasets revealed relatively high agreement in identification of distinct morphotypes. Agreement was lowest for identification and enumeration of small taxa, particularly bryozoans and hydroids, raising the possibility of inaccuracies for these taxa. Most morphotypes were only identified to class or order rank, with further resolving hindered by the lack of images from multiple angles; few standard reference images for taxa known to occur in the South Atlantic, and; the inability to apply traditional taxonomic approaches to image data. In future data collection efforts, the use of more appropriate sampling tools such as ROVs would allow for images from multiple angles to be obtained. Future work in the South Atlantic should also involve the creation of an image reference library that would significantly contribute to the standardisation, and therefore increased comparability, of different datasets from across the basin (*sensu* Howell *et al.*, 2019).

Further research is needed to better understand the drivers of fine-scale variation in seamount benthic communities, particularly in temperate latitudes where inter-seamount variation is high (Chapter 3). This will require further biological data to be collected, but an added dimension in future work should also be the collection of fine-scale oceanographic data that can provide insight into environmental variability. High environmental variability associated with frontal regions in temperate latitudes was identified as a possible reason for the high α- and β-diversity at Tristan da Cunha (Chapter 2; 3), although it was not possible to statistically test this theory due to lack of data. Characterisation of seamounts, both environmentally and biologically, in the sub-polar region would provide valuable data to prove/disprove this theory.

In general, additional exploration of seamount ecology, particularly in the southwest Atlantic, should not only contribute to further documentation of the presence/absence of VME-indicator taxa, but also illuminate potential biogeographic regions within the South Atlantic. Bergsta*d et al*. (2019a) reported a surprising lack of *S. variabilis* on southeast Atlantic seamounts, instead reporting *Enallopsammia rostrata*. Barbosa *et al.* (2020) characterise the environmental niche of multiple scleractinian reef-building corals in Brazilian waters and find that the niches of *S. variabilis* and *E. rostrata* are similar. The presence of *S. variabilis* in the southwest Atlantic (Pires, 2007; Barbosa *et al.*, 2020; Raddatz *et al.*, 2020) and the UKOTs (Chapter 3), but not the southeast Atlantic seamounts (Durán Muñoz *et al.*, 2014; Bergstad *et al.*, 2019a) is interesting. Understanding that the UKOTs share similarities with both the east and west South Atlantic sheds light on the connectivity of the basin and potential role of the MAR and UKOTs, but requires further research to fully understand the biogeography and connectivity of the South Atlantic as a whole.

Lack of data on species and habitat distribution hinders the ability to appropriately validate transferred models to ascertain their biological relevance (Yates *et al.*, 2018), the prime example from within this thesis being the extremely limited validation of the transferred model in Chapter 4. While this was unavoidable due to the understudied nature of the region, it does mean that the transferred outputs need to be treated with caution in further use. Be that as it may, the excellent performance of the model in the North Atlantic confirms that the model itself is biologically relevant in that area, and this should be favourably considered when assessing the accuracy of the transfer. The data collection recommendations above will assist in creating more appropriate validation datasets for future transferred habitat suitability models.

Chapter 4 states that the biggest hurdle in creating transferable models at oceanographic basin scales is the lack of intermediate resolution (i.e. 200 to 300 m) environmental data. This is particularly true in the southwest Atlantic where multibeam bathymetry was not available for features which are thought to provide suitable habitat for *D. pertusum* reef (Barbosa *et al.*, 2020). Increasing the spatial coverage of high-resolution environmental data including multibeam bathymetry will mean transferred model outputs will be more usable as they will be less spatially fragmented. Moreover, *in-situ* data from the South Atlantic will allow for global data repositories that rely on groundtruthing satellite-derived data to better understand the error in widely available data layers (*sensu* Chapter 5).

With the progression of international negotiations on the conservation and sustainable use of marine BBNJ alongside significant in-country initiatives to improve conservation, marine spatial planners and stakeholders should begin thinking about how to incorporate the best available data from the South Atlantic into management plans. Evidence-based management of deep-sea ecosystems at the basin scale is growing in popularity, see for example, the Frontiers in Marine Science Research Topic “Managing Deep-sea Ecosystems at Ocean Basin Scale”. This management approach recognises that both threats to natural habitats and ecological trends do not adhere to political boundaries and as such, nature conservation needs to adopt a transboundary approach. Through future work, the outputs of both Chapters 4 and 5 have the potential to drive evidence-based management of deep-sea ecosystems at the South Atlantic scale. One approach may be to take the broad-scale habitat classification and assess the current South Atlantic EBSA network for its representativity of protected habitats. Understanding the ecological coherence of the EBSA network would prove particularly useful if EBSAs are to be used to influence the locations of future MPAs in ABNJ. Another approach would be to import the outputs from Chapters 4 and 5 into systematic conservation planning software such as Marxan (Ball & Possingham, 2000) to identify where in the South Atlantic would benefit most from future protection. Knowledge acquired in Chapter 2 and 3 regarding the distribution and variation of in biodiversity could also be applied to this process. Outputs of such a study could be used to assess the appropriateness of the current EBSA network (Figure 1.4), as well as informing other regional MSP processes including the ISA’s REMP. A project such as this should work strongly with South Atlantic bordering nations to ensure proposed management plans are equitable, fit for purpose, and complementary to existing management plans in neighbouring EEZs.

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APPENDIX A

A.1 Shallow Underwater Camera System (SUCS)

Figure A.1: British Antarctic Survey's Shallow Underwater Camera System (SUCS). Photo credit: D.K.A. Barnes.

The Shallow Underwater Camera System (SUCS; Figure A.1) is owned by the British Antarctic Survey and was deployed during the following cruises to collect data presented in this manuscript: JR864 (2015), JR16-NG (2017), JR17-004 (2018) and DY100 (2019). The SUCS captures images of the seafloor using a 5 megapixel Allied Vision Prosilica GC2450 camera, a Fujinon HF12.5SA-1 lens and twin variable intensity lights, all controlled from a desktop computer on ship.

A.2 Substrate analysis

Substrate type in each image was recorded using the following categories based on Wentworth (1922): bedrock, reef framework, live reef, cobbles, coral rubble, pebbles, coral gravel, gravel and sand. Examples of each are found in Figure A.2; Table A.1 lists the size classes associated with each category.

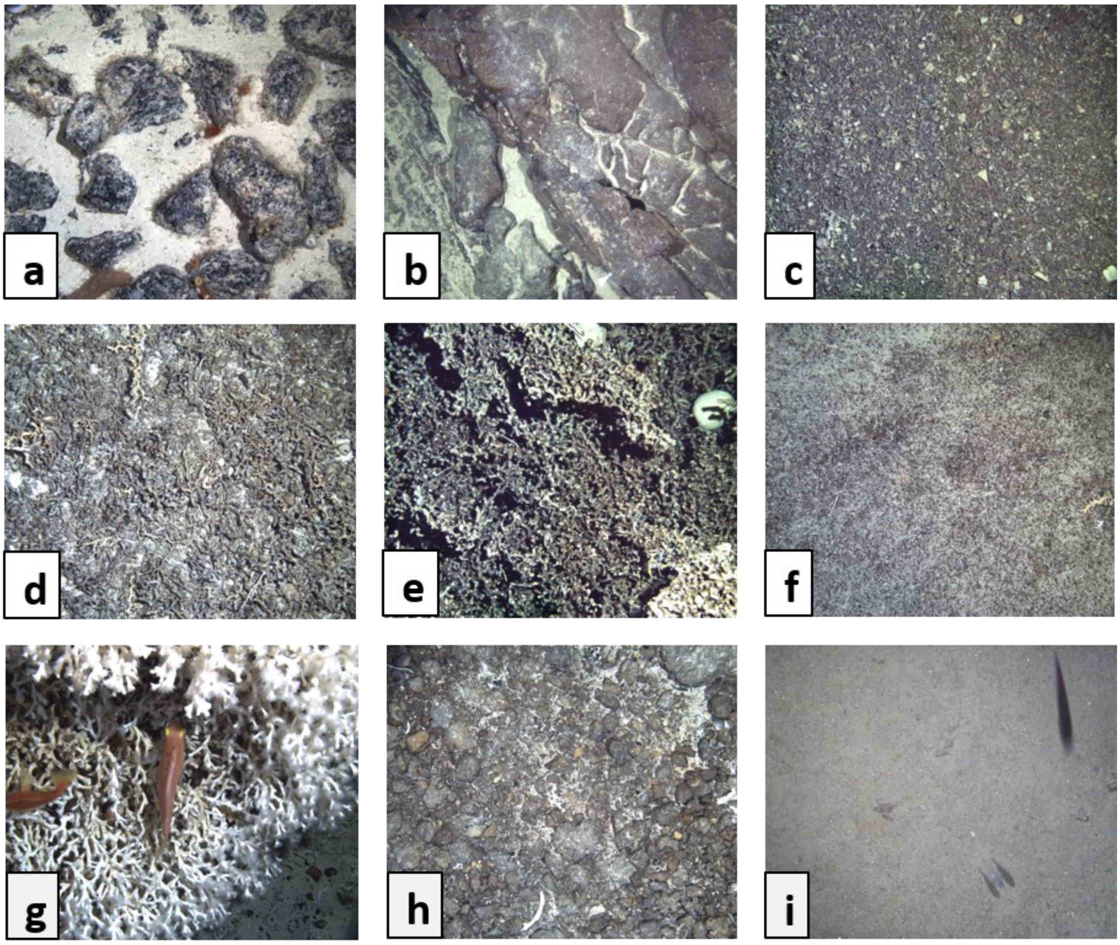


Figure A.2: Example images where the dominant substrate is one of the categories used: (a) cobbles, (b) bedrock, (c) coral gravel, (d) coral rubble, (e) reef framework, (f) gravel, (g) live coral reef, (h) pebbles, (i) sand.

Table A.1: Size classes associated with each substrate category used.

Category	**Minimum size (mm)**	**Maximum size (mm)**
Bedrock	NA	NA
Reef framework	NA	NA
Live reef	NA	NA
Cobbles	64	256
Coral rubble	NA	NA
Pebbles	4	64
Coral gravel	NA	NA
Gravel	2	4
Sand	NA	2

A.3 Bottom temperature layer

Data from 23, 26, and 19 CTD casts were used to build Generalised Additive Models (GAMs) in the 'mgcv' R package (Wood, 2011) for Ascension Island, St. Helena and Tristan da Cunha, respectively, to allow predictions of bottom temperature to be made. Casts are geographically spread out across each exclusive economic zone (EEZ; Figure A.3).

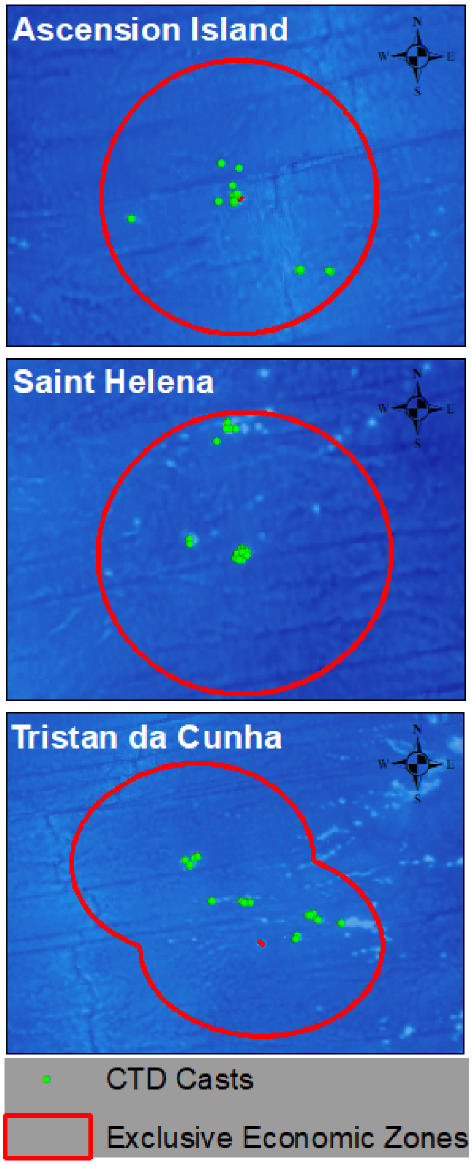


Figure A.3: Locations of CTD casts within the EEZ of each oceanic island.

Three casts within the Ascension Island EEZ were collected during The Atlantic Meridional Transect (AMT) - Phase 1 (1995-2000) funded by the Natural Environment Research Council (NERC).

For each of the three EEZs, *in-situ* temperature data were partitioned into training and test datasets at an 80/20% split, respectively. Various GAMs were built to test the usefulness of depth, latitude and longitude as predictors in each EEZ. For all three models, the single predictor of depth was used to build the model. Confidence intervals for all three models plotted tightly suggesting a reliable model (Figure A.4 – Figure A.6). For the Ascension Island layer, a k-value of seven was used to constrain the number of knots allowed in the model, resulting in a tighter fit to the *in-situ* temperatures; for St. Helena and Tristan, the authors allowed the 'mgcv' package specify the k-value as designed.

When the predicted values of each model built with the 80% training dataset are compared against the reserved 20% test *in-situ* values, a very strong Pearson's correlation of 0.99 (to 2 d.p.) is obtained for all three datasets. This is graphically represented in Figure A.7 – Figure A.9.

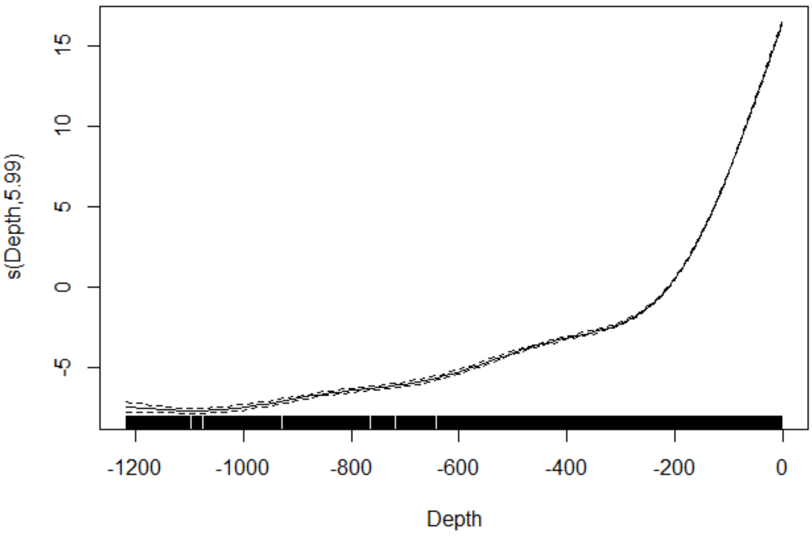


Figure A.4: Confidence intervals for the final GAM used to predict the Ascension Island bottom temperature layer.

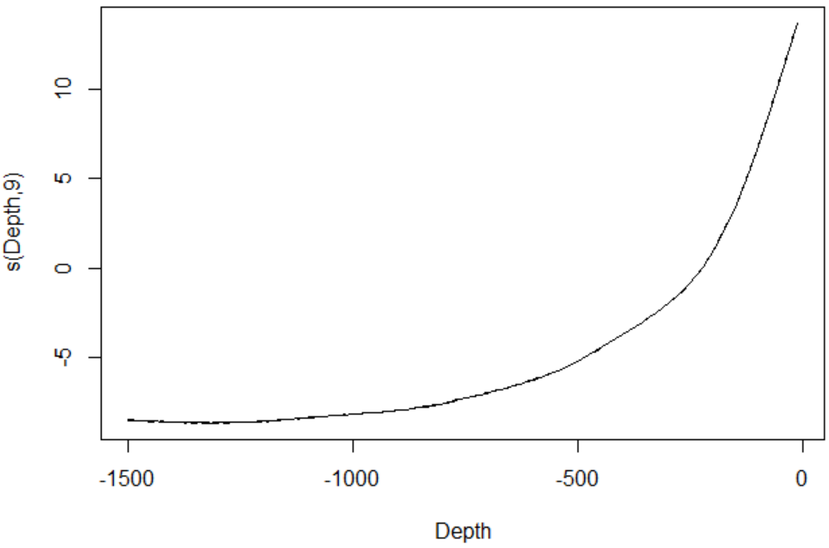


Figure A.5: Confidence intervals for the final GAM used to predict the St. Helena bottom temperature layer.

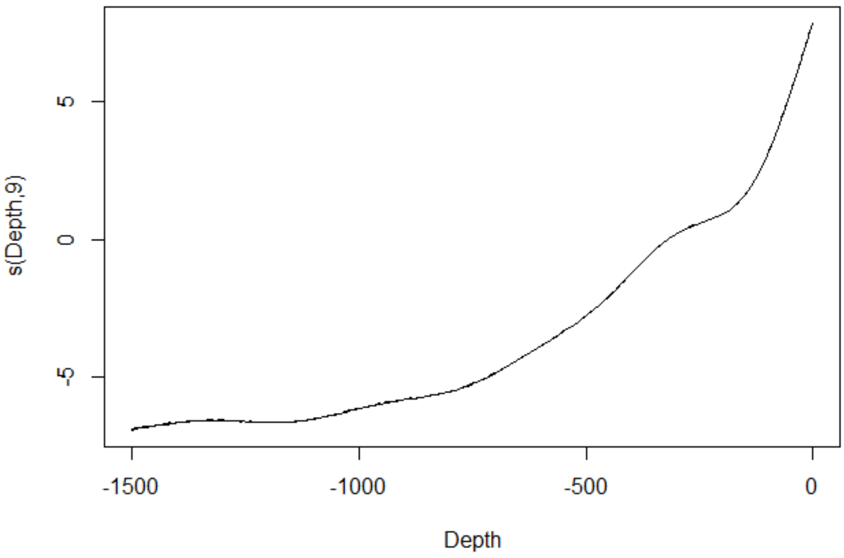


Figure A.6: Confidence intervals for the final GAM used to predict the Tristan da Cunha bottom temperature layer.

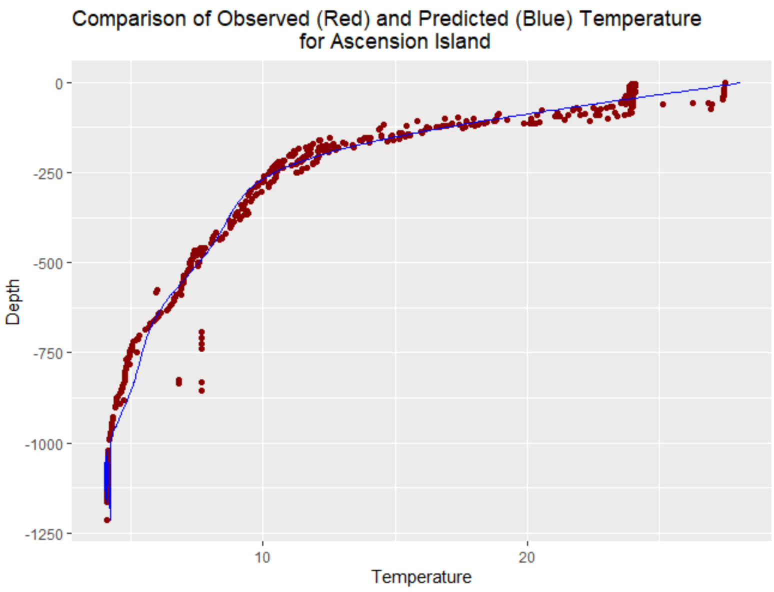


Figure A.7: Observed temperatures from CTD casts near Ascension Island are plotted in red and the corresponding temperatures as predicted by the GAM are represented by the blue line.

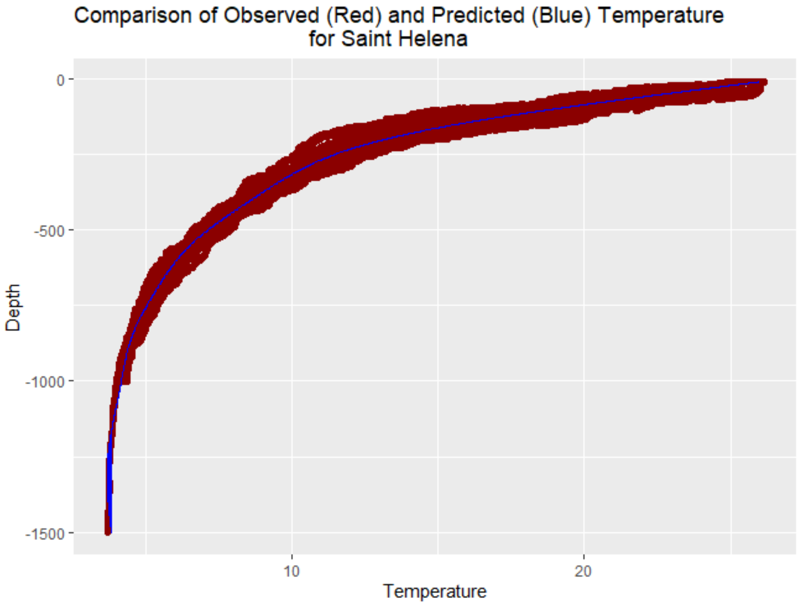


Figure A.8: Observed temperatures from CTD casts near St. Helena are plotted in red and the corresponding temperatures as predicted by the GAM are represented by the blue line.

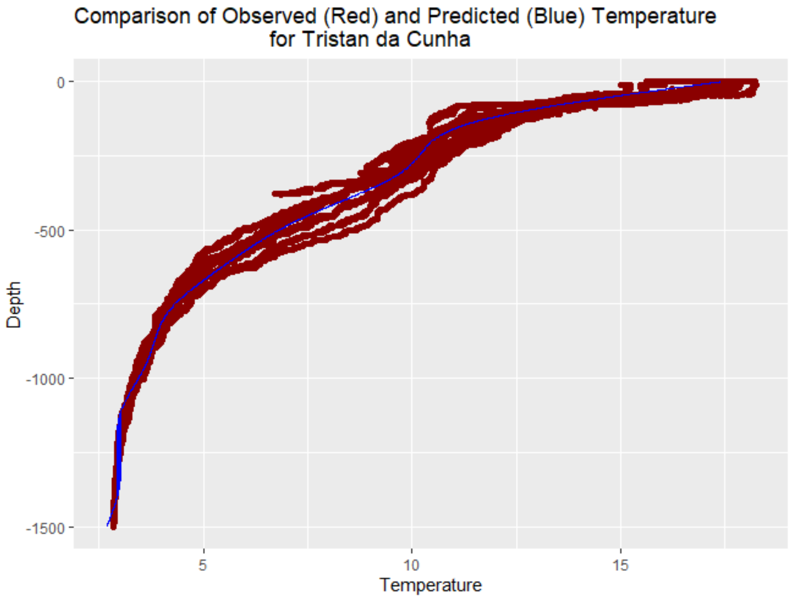


Figure A.9: Observed temperatures from CTD casts near Tristan da Cunha are plotted in red and the corresponding temperatures as predicted by the GAM are represented by the blue line.

APPENDIX B

B.1 Identification of potential confounding factors

To ensure any observed differences in species richness were attributable to factors within the model, rather than different sampling regimes across the territories, confounding factors were statistically tested for. Results of these are reported in the main manuscript, but graphical representations are in Figure B.1

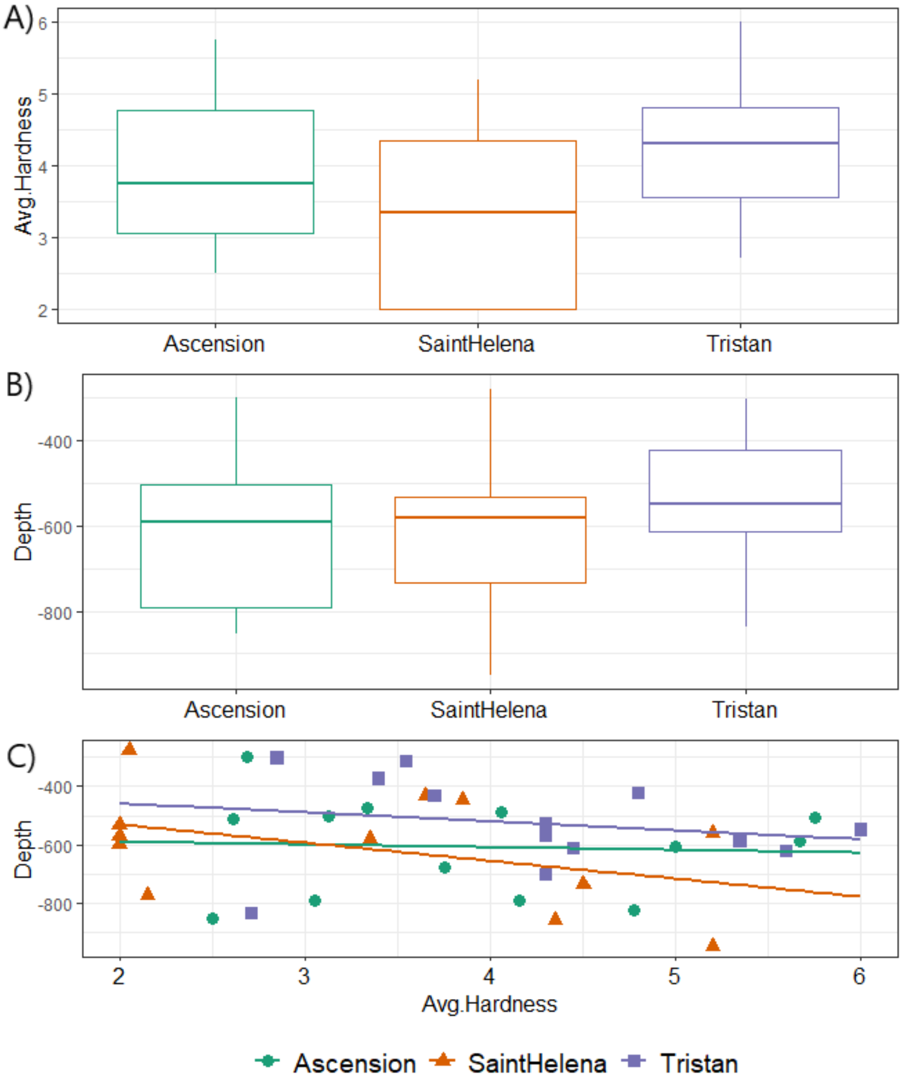


Figure B.1: Average hardness (A) and depth (B) ranges from each territory. The relationship between depth and average hardness (C) was also explored.

B.2 Correlation of variables

To avoid autocorrelation issues with the linear model, a correlation matrix was calculated for all the variables (Table B.1). Latitude and surface primary productivity, and temperature and depth were strongly correlated with coefficient values >±0.7. Generalised Additive Models (GAMs) were built to identify the variable that explained the most deviance within each correlated pair; this resulted in surface primary productivity and temperature being selected for inclusion within the linear model.

Table B.1: Correlation matrix for LM variables calculated in R Studio (rounded to 3 d.p.).

-	Latitude	Substrate hardness	POC flux to depth	Temperature	Depth	Surface primary productivity	Rugosity	Curvature	Slope	FBPI	BBPI
Latitude	-	-	-	-	-	-	-	-	-	-	-
Substrate hardness	-0.214	-	-	-	-	-	-	-	-	-	-
POC flux to depth	-0.456	0.258	-	-	-	-	-	-	-	-	-
Temperature	-0.025	-0.229	-0.066	-	-	-	-	-	-	-	-
Depth	-0.194	-0.160	0.013	**0.942**	-	-	-	-	-	-	-
Surface primary productivity	**-0.985**	0.254	0.453	0.026	0.188	-	-	-	-	-	-
Rugosity	0.140	-0.099	-0.145	-0.139	-0.160	-0.142	-	-	-	-	-
Curvature	-0.219	-0.149	-0.011	-0.052	0.008	0.178	-0.132	-	-	-	-
Slope	0.444	0.128	-0.160	-0.213	-0.298	-0.379	0.081	-0.303	-	-	-
FBPI	0.089	-0.181	-0.049	0.191	0.174	-0.090	-0.165	0.641	-0.045	-	-
BBPI	0.198	-0.078	0.037	0.421	0.423	-0.191	-0.133	0.166	0.070	0.551	-

B.3 Full data tables

Table B.2: Full environmental data table for n=39 transects.

Transect code	Lat	Long	Depth (m)	Substrate Class	Hardness	Temp. (°C)	Surface primary productivity kg/m^3/day	Rugosity (3 d.p.)	Curvature (3 d.p.)	Slope (3 d.p.)	FBPI	BBPI	POC flux to depth (3 d.p.)
Asc_21	-7.875	-14.379	299	Sand	2.684	9.39	1.083	0.005	-0.099	27.555	10	53	0.774
Asc_29	-7.966	-14.272	505	Sand	5.75	7.54	1.073	0.006	2.466	22.170	5	50	0.916
Asc_33	-8.016	-14.342	676	Sand	3.75	5.79	1.056	0.001	-0.398	6.096	2	-66	8.438
Asc_34	-8.023	-14.345	472	Dead Reef	3.333	7.89	1.056	0.003	-0.050	32.842	30	257	8.438
Asc_35	-8.027	-14.335	824	Bedrock	4.778	5.16	1.056	0.054	1.343	28.633	30	4	8.438
Asc_37	-8.034	-14.407	604	Bedrock	5	6.63	1.056	0.022	-5.437	55.803	-31	17	8.438
Asc_6	-8.043	-14.442	502	Sand	3.125	7.59	1.044	0.001	-1.792	2.321	-1	35	5.322
Grattan_143	-9.737	-12.774	855	Sand	2.5	4.96	0.692	0.002	-0.046	23.250	-8	-58	1.771
Grattan_144	-9.759	-12.837	790	Sand	3.056	5.28	0.691	3.251	-1.061	18.976	-9	-39	1.716
Grattan_39	-9.759	-12.797	487	Sand	4.056	7.77	0.683	0.001	-0.555	3.942	-4	-27	1.741
Grattan_40	-9.752	-12.791	510	Sand	2.611	7.47	0.683	0.000	-0.342	1.620	-1	-45	1.771
HS_7	-8.47	-16.99	793	Pebbles	4.158	5.23	0.806	0.016	-1.206	18.190	-9	-102	1.609

HS_8	-8.474	-16.993	590	Bedrock	5.667	6.50	0.806	0.005	-2.987	39.476	-4	31	1.609
Bon_87	-15.714	-6.985	734	Dead Reef	4.5	5.19	1.128	0.007	1.986	25.653	9	15	6.950
Bon_91	-15.609	-6.996	433	Dead Reef	3.65	8.29	1.116	0.022	-0.002	5.762	22	98	2.543
Car_105	-13.029	-6.036	445	Sand	3.85	7.92	0.707	0.004	0.289	5.4263	22	17	3.970
Car_106	-13.023	-6.038	278	Sand	2.05	10.79	0.707	0.000	0.026	2.404	4	94	3.970
Car_118	-13.04	-6.037	568	Sand	2	6.35	0.707	0.000	-0.202	1.225	1	4	3.970
Car_120	-13.056	-6.033	950	Bedrock	5.2	4.27	0.707	0.005	-0.680	7.268	-10	8	3.970
SC_128	-12.852	-5.739	533	Sand	2	6.73	0.697	0.004	1.505	17.015	7	38	3.036
SC_129	-12.852	-5.738	563	Bedrock	5.2	6.40	0.697	0.002	-0.275	12.955	-7	11	3.036
STHGI_74	-16.013	-5.611	597	Sand	2	6.09	1.793	0.003	1.589	5.918	12	104	3.094
STHGI_75	-16.013	-5.611	597	Sand	2	6.09	1.793	0.003	1.589	5.918	12	104	3.094
STHLT_61	-15.945	-5.784	581	Sand	3.35	6.17	1.674	0.009	1.669	34.375	15	13	2.975
STHLT_62	-15.945	-5.79	774	Sand	2.15	4.90	1.674	0.001	-0.202	16.639	0	-6	2.975
STHSL_80	-16.158	-5.745	860	Dead Reef	4.35	4.49	1.739	0.002	0.804	18.516	10	59	10.029
CrawE_48	-38.79	-10.548	588	Bedrock	5.35	5.79	6.022	0.001	0.691	6.540	0	-10	6.836
CrawE_49	-38.801	-10.526	571	Gravel	4.3	5.99	6.022	0.001	-0.109	5.660	1	-7	4.510
CrawE_50	-38.796	-10.497	615	Dead Reef	4.45	5.56	6.018	0.000	-0.410	0.240	0	0	4.510
CrawE_53	-38.779	-10.509	624	Dead Reef	5.6	5.45	6.022	0.000	0.488	4.497	0	-26	4.510
CrawE_54	-38.787	-10.53	434	C. Rubble	3.7	7.70	6.022	0.010	1.286	12.758	16	64	4.510

CrawE_55	-38.772	-10.556	550	Bedrock	6	6.19	6.022	0.004	1.152	3.404	7	63	6.836
JakE_36	-39.491	-7.803	303	Sand	2.85	9.74	6.053	0.001	0.414	5.406	-1	4	3.542
JakE_41	-39.265	-8.064	837	C. Gravel	2.714	3.88	5.896	0.014	0.550	27.970	0	-159	3.594
JakW_11	-39.291	-8.075	314	Sand	3.55	9.70	5.896	0.000	-0.482	2.348	0	2	3.634
RSA_33	-39.503	-6.791	374	Sand	3.4	8.77	5.716	0.001	0.635	2.857	2	7	15.303
RSA_34	-39.489	-6.792	423	Bedrock	4.8	7.97	5.743	0.001	-0.470	1.910	-1	14	15.303
RSA_36	-39.469	-6.813	703	Bedrock	4.3	4.66	5.743	0.000	0.340	4.077	-7	-28	15.303
RSA_37	-39.491	-6.806	531	Bedrock	4.3	6.43	5.743	0.002	-0.097	0.761	-7	-19	15.303

Table B.3: Species richness and location information for all transects (n=39).

Transect code	**Territory**	**Site**	**Species Richness**
Asc_21	Ascension	Asc_main	33
Asc_29	Ascension	Asc_main	20
Asc_33	Ascension	Asc_main	15
Asc_34	Ascension	Asc_main	20
Asc_35	Ascension	Asc_main	24
Asc_37	Ascension	Asc_main	10
Asc_6	Ascension	Asc_main	16
Grattan_143	Ascension	Grattan	20
Grattan_144	Ascension	Grattan	17
Grattan_39	Ascension	Grattan	21
Grattan_40	Ascension	Grattan	12
HS_7	Ascension	Harris_Stewart	14
HS_8	Ascension	Harris_Stewart	17
Bon_87	St_Helena	Bonaparte	27
Bon_91	St_Helena	Bonaparte	22
Car_105	St_Helena	Cardinot	11
Car_106	St_Helena	Cardinot	8
Car_118	St_Helena	Cardinot	7
Car_120	St_Helena	Cardinot	16
SC_128	St_Helena	SC	10
SC_129	St_Helena	SC	18
STHGI_74	St_Helena	SH_main	2
STHGI_75	St_Helena	SH_main	2
STHLT_61	St_Helena	SH_main	19
STHLT_62	St_Helena	SH_main	13
STHSL_80	St_Helena	SH_main	25
CrawE_48	Tristan_da_Cunha	Crawford	52
CrawE_49	Tristan_da_Cunha	Crawford	39
CrawE_50	Tristan_da_Cunha	Crawford	36
CrawE_53	Tristan_da_Cunha	Crawford	39
CrawE_54	Tristan_da_Cunha	Crawford	32
CrawE_55	Tristan_da_Cunha	Crawford	51
JakE_36	Tristan_da_Cunha	Jakhont	54
JakE_41	Tristan_da_Cunha	Jakhont	34
JakW_11	Tristan_da_Cunha	Jakhont	38
RSA_33	Tristan_da_Cunha	RSA	26
RSA_34	Tristan_da_Cunha	RSA	30
RSA_36	Tristan_da_Cunha	RSA	26
RSA_37	Tristan_da_Cunha	RSA	30

APPENDIX C

C.1 Correlation matrix

A Pearson's correlation matrix was calculated in Primer to identify correlated variables to remove to avoid the potential for autocorrelation issues within the DistLM (Table C.1). Coefficients >±0.7 were deemed strong, and one correlate was removed.

Table C.1: Correlation matrix for DistLM variables calculated in Primer v.6 (rounded to 3 d.p.). Coefficients ≥±0.7 are shown in bold.

	Substrate hardness	Latitude	POC flux to depth	Surface primary productivity	Depth	Log(Rugosity)	Curvature	Slope	FBPI	BBPI	Temperature
Substrate hardness	-	-	-	-	-	-	-	-	-	-	-
Latitude	0.114	-	-	-	-	-	-	-	-	-	-
POC flux to depth	0.382	-0.247	-	-	-	-	-	-	-	-	-
Surface primary productivity	-0.248	**-0.932**	0.178	-	-	-	-	-	-	-	-
Depth	-0.436	0.308	-0.467	-0.323	-	-	-	-	-	-	-
Log(Rugosity)	0.480	-0.396	-0.001	0.259	-0.297	-	-	-	-	-	-
Curvature	-0.251	-0.526	0.178	0.513	0.0237	0.378	-	-	-	-	-
Slope	0.273	-0.428	0.270	0.367	-0.3417	0.463	0.529	-	-	-	-
FBPI	-0.216	-0.438	0.021	0.333	0.443	0.412	0.496	0.086	-	-	-
BBPI	-0.379	-0.325	-0.055	0.331	0.417	-0.001	0.289	-0.406	0.451	-	-
Temperature	-0.342	0.373	-0.361	-0.410	**0.943**	-0.380	-0.142	-0.427	0.345	0.452	-

C.2 DistLM Results

To ensure the selection of latitude and depth over surface primary productivity and temperature was not changing the results, a DistLM was run allowing the model to choose from the following variables: surface primary productivity, longitude, temperature, rugosity, curvature, slope, FBPI, BBPI, substrate hardness and POC flux to depth. The best solution from the DistLM routine, selected based on AIC score, is detailed in Table C.2. The variances explained by surface primary productivity and temperature are not significantly different to those explained by latitude and depth, respectively. Using this selection, FBPI explains slightly more (+0.33%) variance, and longitude explains slightly less (-0.16%).

Table C.2: DistLM metrics for the model using surface primary productivity and temperature instead of latitude and depth, respectively.

Variable	**SS (trace)**	**Pseudo-F**	**p-value**	**% variance explained (2 d.p.)**
Surface Primary Productivity	46451	13.184	0.001	15.48
Temperature	13044	3.8488	0.001	4.35
FBPI	7937.8	2.3878	0.001	2.64
Longitude	7131.3	2.1815	0.001	2.38
Slope	6821.3	2.1205	0.001	2.27

C.3 dbRDA on SIMPROF

The 22 biological assemblages identified in the SIMPROF analysis (labelled a – v) are graphically depicted on a dbRDA plot in Figure C.1, with each assemblage coded individually. Interpretation of the dbRDA plot is found in the main text.

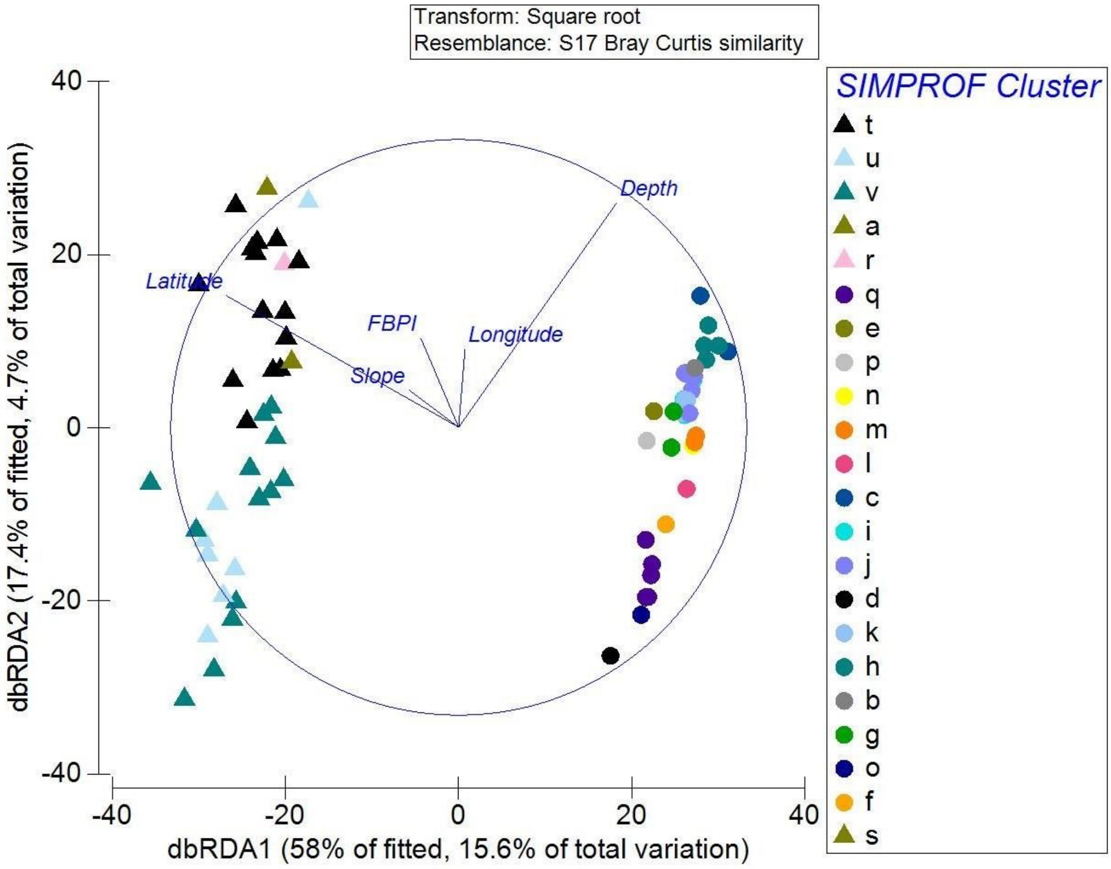


Figure C.1: dbRDA plot with each SIMPROF cluster identified. Tropical clusters are represented as coloured triangles and temperate clusters by coloured circles. Significant environmental drivers as identified by the DistLM are overlaid.

C.4 SIMPROF results

The uncollapsed dendrogram produced in Primer v.6 can be seen in Figure C.2. Lines in red depict that the transects cluster in the same group as other lines descending from each black node. The SIMPROF clusters (a – v) are identified by the text labels.

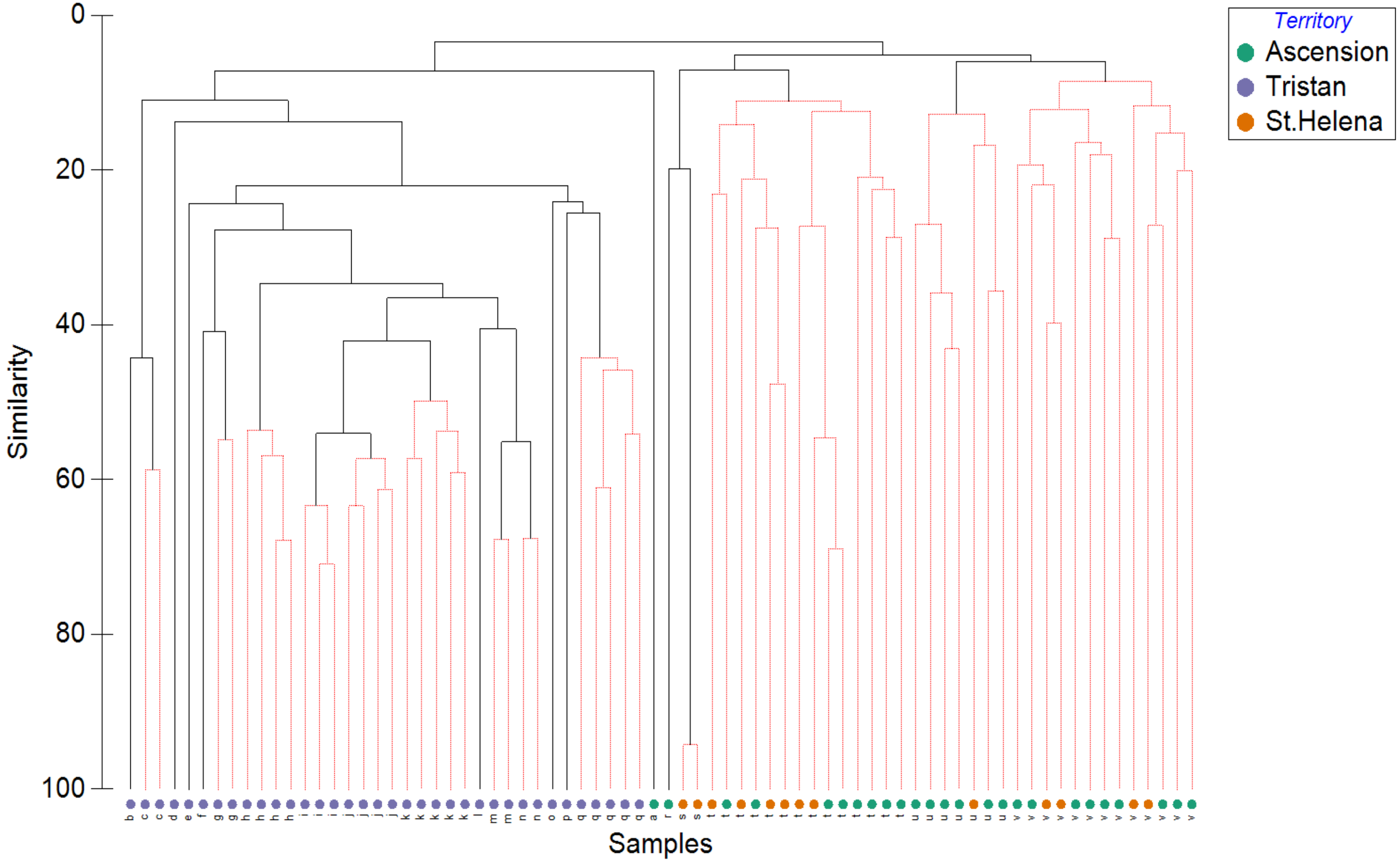


Figure C.2: Full hierarchical cluster dendrogram with SIMPROF clusters (a – v) as labels, colour-coded by territory.

C.5 Full data table

Table C.3: Full environmental data table for n=74 transects.

Transect	Hardness	Lat	Long	POC flux to depth (3 d.p.)	Surface primary productivity kg/m^3/day	Depth (m)	Rugosity (3 d.p.)	Curvature (3 d.p.)	Slope (3 d.p.)	FBPI	BBPI	Temperature (°C)
Asc_20	2.00	-7.876	-14.383	0.774	1.083	-232	0.001	0.065	26.245	0	67	10.96
Asc_21	3.00	-7.875	-14.379	0. 774	1.083	-299	0.005	-0.099	27.555	10	53	9.39
Asc_22	3.00	-7.858	-14.374	0. 774	1.083	-745	0.001	0.748	4.319	3	60	5.43
Asc_23	4.00	-7.852	-14.367	0. 774	1.083	-932	0.012	-3.752	41.048	-24	43	4.55
Asc_28	4.00	-7.966	-14.288	0.916	1.073	-190	0.004	0.443	25.2416	11	101	13.14
Asc_29	6.00	-7.966	-14.272	0.916	1.073	-505	0.006	2.466	22.170	5	50	7.54
Asc_30	4.00	-7.968	-14.261	0.916	1.073	-790	0.002	-1.455	34.261	2	8	5.25
Asc_31	6.00	-7.968	-14.255	0.916	1.073	-1011	0.003	-0.858	18.947	-9	-78	4.20
Asc_32	5.00	-8.01	-14.337	8.438	1.056	-292	0.006	0.568	33.784	22	169	9.46
Asc_33	4.00.	-8.016	-14.342	8.438	1.056	-676	0.001	-0.398	6.096	2	-66	5.79
Asc_34	3.00	-8.023	-14.345	8.438	1.056	-472	0.003	-0.050	32.842	30	257	7.89
Asc_35	5.00	-8.027	-14.335	8.438	1.056	-824	0.054	1.343	28.633	30	4	5.16

Asc_36	4.00	-8.018	-14.408	8.438	1.056	-276	0.004	0.933	7.734	13	67	9.72
Asc_37	5.00	-8.034	-14.407	8.438	1.056	-604	0.022	-5.437	55.803	-31	17	6.63
Asc_4	3.00	-8.068	-14.424	5.322	1.044	-875	0.002	-0.675	13.770	-10	-36	4.88
Asc_5	3.00	-8.063	-14.432	5.322	1.044	-768	0.001	0.004	10.684	0	-20	5.33
Asc_6	3.00	-8.043	-14.442	5.322	1.044	-502	0.001	-1.792	2.321	-1	35	7.59
Asc_7	2.00	-8.011	-14.439	5.322	1.044	-218	0.000	-0.197	1.722	0	6	11.47
Grattan_143	2.00	-9.737	-12.774	1.771	0.692	-855	0.002	-0.04	23.250	-8	-58	4.96
Grattan_144	3.00	-9.759	-12.837	1.716	0.691	-790	3.251	-1.061	18.976	-9	-39	5.28
Grattan_39	4.00	-9.759	-12.797	1.741	0.683	-487	0.001	-0.555	3.942	-4	-27	7.77
Grattan_40	3.00	-9.752	-12.791	1.771	0.683	-510	0.000	-0.342	1.620	-1	-45	7.47
HS_7	4.00	-8.47	-16.99	1.609	0.806	-793	0.016	-1.207	18.190	-9	-102	5.23
HS_8	6.00	-8.474	-16.993	1.609	0.806	-590	0.005	-2.987	39.476	-4	31	6.50
Unnamed_102	6.00	-9.763	-12.074	1.771	0.728	-371	0.000	0.176	3.055	-5	-74	8.71
Bon_87	4.50	-15.714	-6.985	6.950	1.128	-734	0.007	1.986	25.653	9	15	5.19
Bon_91	3.65	-15.609	-6.996	2.543	1.116	-433	0.022	-0.002	5.762	22	98	8.29

Car_105	3.85	-13.029	-6.036	3.970	0.707	-445	0.004	0.289	5.426	22	17	7.92
Car_106	2.05	-13.023	-6.038	3.970	0.707	-278	0.000	0.026	2.404	4	94	10.79
Car_118	2.00	-13.04	-6.037	3.970	0.707	-568	0.000	-0.202	1.225	1	4	6.35
Car_120	5.20	-13.056	-6.033	3.970	0.707	-950	0.005	-0.680	7.268	-10	8	4.27
SC_128	2.00	-12.852	-5.739	3.036	0.697	-533	0.004	1.505	17.015	7	38	6.73
SC_129	5.20	-12.852	-5.738	3.036	0.697	-563	0.002	-0.275	12.955	-7	11	6.40
STHGI_74	2.00	-16.013	-5.611	3.094	1.793	-597	0.003	1.589	5.918	12	104	6.09
STHGI_75	2.00	-16.013	-5.611	3.094	1.793	-597	0.003	1.589	5.918	12	104	6.09
STHLT_61	3.35	-15.945	-5.784	2.975	1.674	-581	0.009	1.669	34.375	15	13	6.17
STHLT_62	2.15	-15.945	-5.79	2.975	1.674	-774	0.001	-0.202	16.639	0	-6	4.90
STHSL_80	4.35	-16.158	-5.745	10.029	1.739	-860	0.002	0.804	18.516	10	59	4.49
CrawE_48	5.35	-38.79	-10.548	6.836	6.022	-588	0.001	0.691	6.540	0	-10	5.79
CrawE_49	4.30	-38.801	-10.526	4.510	6.022	-571	0.001	-0.109	5.660	1	-7	5.99

CrawE_50	4.45	-38.796	-10.497	4.510	6.018	-615	0.000	-0.410	0.240	0	0	5.56
CrawE_52	5.79	-38.788	-10.522	4.510	6.022	-376	0.015	0.854	8.706	17	119	8.67
CrawE_53	5.60	-38.779	-10.509	4.510	6.022	-624	0.000	0.488	4.497	0	-26	5.45
CrawE_54	3.70	-38.787	-10.53	4.510	6.022	-434	0.010	1.286	12.758	16	64	7.70
CrawE_55	6.00	-38.772	-10.556	6.836	6.022	-550	0.004	1.152	3.404	7	63.25	6.19
CrawW_62	3.25	-38.747	-11.663	6.764	6.083	-295	0.000	-0.619	0.785	0	2	9.85
CrawW_63	3.65	-38.761	-11.666	6.738	6.075	-318	0.000	0.301	3.281	0	3	9.63
CrawW_64	2.25	-38.758	-11.688	6.764	6.065	-297	0.000	0.112	1.989	0	1	9.84
CrawW_65	2.68	-38.749	-11.709	5.433	6.071	-307	0.000	-0.238	1.491	0	-1	9.73
CrawW_73	3.13	-38.764	-11.746	5.453	6.065	-386	0.002	-1.219	3.760	-2	7	8.61
Gough_43	4.65	-40.389	-9.885	1.210	5.599	-186	0.001	0.589	19.963	16	110	10.82

Gough_50	5.60	-40.315	-10.054	7.480	5.663	-170	0.000	0.146	1.107	1	44	10.82
JakE_28	4.90	-39.466	-7.832	3.582	6.053	-327	0.000	0.166	2.822	2	3	9.51
JakE_30	5.60	-39.455	-7.806	3.636	6.053	-285	0.002	-0.426	6.108	-1	0	9.96
JakE_35	3.19	-39.485	-7.828	3.582	6.053	-345	0.000	0.090	2.232	0	1	9.23
JakE_36	2.85	-39.491	-7.803	3.542	6.053	-303	0.001	0.414	5.406	-1	4	9.74
JakE_37	5.15	-39.462	-7.792	3.636	6.053	-273	0.000	0.362	1.519	0	0	10.02
JakE_41	2.71	-39.265	-8.064	3.594	5.896	-837	0.014	0.550	27.970	0	-159	3.88
JakW_10	3.88	-39.284	-8.059	3.594	5.896	-331	0.000	-0.034	1.261	0	15	9.44
JakW_11	3.55	-39.291	-8.075	3.634	5.896	-314	0.000	-0.482	2.348	0	2	9.70
JakW_12	4.95	-39.276	-8.087	3.668	5.907	-334	0.000	0.717	2.360	0	4	9.41
JakW_13	4.20	-39.277	-8.105	3.668	5.907	-324	0.011	-4.456	7.632	0	2	9.69
JakW_17	4.00	-39.28	-8.131	3.668	5.907	-338	0.000	0.520	0.828	1	2	9.33
JakW_18	3.85	-39.296	-8.134	3.628	5.907	-323	0.001	0.194	0.797	-2	-11	9.54

JakW_19	3.48	-39.304	-8.081	3.634	5.896	-293	0.006	-0.568	8.673	3	1	9.84
McNish_14	3.75	-40.16	-8.604	5.555	5.535	-232	0.001	0.853	9.123	5	43	10.26
McNish_15	3.20	-40.158	-8.586	5.555	5.535	-190	0.000	0.355	0.714	0	4	10.58
McNish_16	4.80	-40.084	-8.561	5.555	5.564	-194	0.000	0.624	7.789	5	53	10.53
McNish_17	4.68	-40.072	-8.57	4.174	5.604	-249	0.002	0.001	12.940	1	57	10.21
Nightingale_71	2.67	-37.34	-12.5	4.607	5.695	-178	0.002	-1.026	6.764	0	46	10.76
RSA_33	3.40	-39.503	-6.791	15.303	5.716	-374	0.001	0.635	2.857	2	7	8.77
RSA_34	4.80	-39.489	-6.792	15.303	5.743	-423	0.001	-0.470	1.910	-1	14	7.97
RSA_36	4.30	-39.469	-6.813	15.303	5.743	-703	0.000	0.340	4.077	-7	-28	4.66
RSA_37	4.30	-39.491	-6.806	15.303	5.743	-531	0.002	-0.097	0.761	-7	-19	6.43

Table C. 4: SIMPROF clusters and territory for each transect (n=74).

Transect	Territory	SIMPROF Cluster
Asc_20	Ascension	t
Asc_21	Ascension	t
Asc_22	Ascension	u
Asc_23	Ascension	v
Asc_28	Ascension	a
Asc_29	Ascension	t
Asc_30	Ascension	v
Asc_31	Ascension	v
Asc_32	Ascension	t
Asc_33	Ascension	u
Asc_34	Ascension	t
Asc_35	Ascension	v
Asc_36	Ascension	t
Asc_37	Ascension	v
Asc_4	Ascension	u
Asc_5	Ascension	u
Asc_6	Ascension	t
Asc_7	Ascension	r
Grattan_143	Ascension	u
Grattan_144	Ascension	u
Grattan_39	Ascension	v
Grattan_40	Ascension	v
HS_7	Ascension	v
HS_8	Ascension	v
Unnamed_102	Ascension	t
Bon_87	St_Helena	v
Bon_91	St_Helena	t
Car_105	St_Helena	t
Car_106	St_Helena	u
Car_118	St_Helena	t
Car_120	St_Helena	v
SC_128	St_Helena	t
SC_129	St_Helena	t
STHGI_74	St_Helena	s
STHGI_75	St_Helena	s
STHLT_61	St_Helena	t
STHLT_62	St_Helena	v
STHSL_80	St_Helena	v
CrawE_48	Tristan_da_Cunha	q
CrawE_49	Tristan_da_Cunha	q
CrawE_50	Tristan_da_Cunha	q
CrawE_52	Tristan_da_Cunha	e
CrawE_53	Tristan_da_Cunha	q
CrawE_54	Tristan_da_Cunha	p
CrawE_55	Tristan_da_Cunha	q
CrawW_62	Tristan_da_Cunha	n
CrawW_63	Tristan_da_Cunha	n
CrawW_64	Tristan_da_Cunha	m
CrawW_65	Tristan_da_Cunha	m
CrawW_73	Tristan_da_Cunha	l
Gough_43	Tristan_da_Cunha	c
Gough_50	Tristan_da_Cunha	c
JakE_28	Tristan_da_Cunha	i
JakE_30	Tristan_da_Cunha	i
JakE_35	Tristan_da_Cunha	i
JakE_36	Tristan_da_Cunha	j

JakE_37	Tristan_da_Cunha	j
JakE_41	Tristan_da_Cunha	d
JakW_10	Tristan_da_Cunha	k
JakW_11	Tristan_da_Cunha	k
JakW_12	Tristan_da_Cunha	k
JakW_13	Tristan_da_Cunha	k
JakW_17	Tristan_da_Cunha	k
JakW_18	Tristan_da_Cunha	j
JakW_19	Tristan_da_Cunha	j
McNish_14	Tristan_da_Cunha	h
McNish_15	Tristan_da_Cunha	h
McNish_16	Tristan_da_Cunha	h
McNish_17	Tristan_da_Cunha	h
Nightingale_71	Tristan_da_Cunha	b
RSA_33	Tristan_da_Cunha	g
RSA_34	Tristan_da_Cunha	g
RSA_36	Tristan_da_Cunha	o
RSA_37	Tristan_da_Cunha	f

C.6 MDS

Non-metric multidimensional scaling allows for the collapsed SIMPROF clusters to be plotted in 2D in Figure C.3.

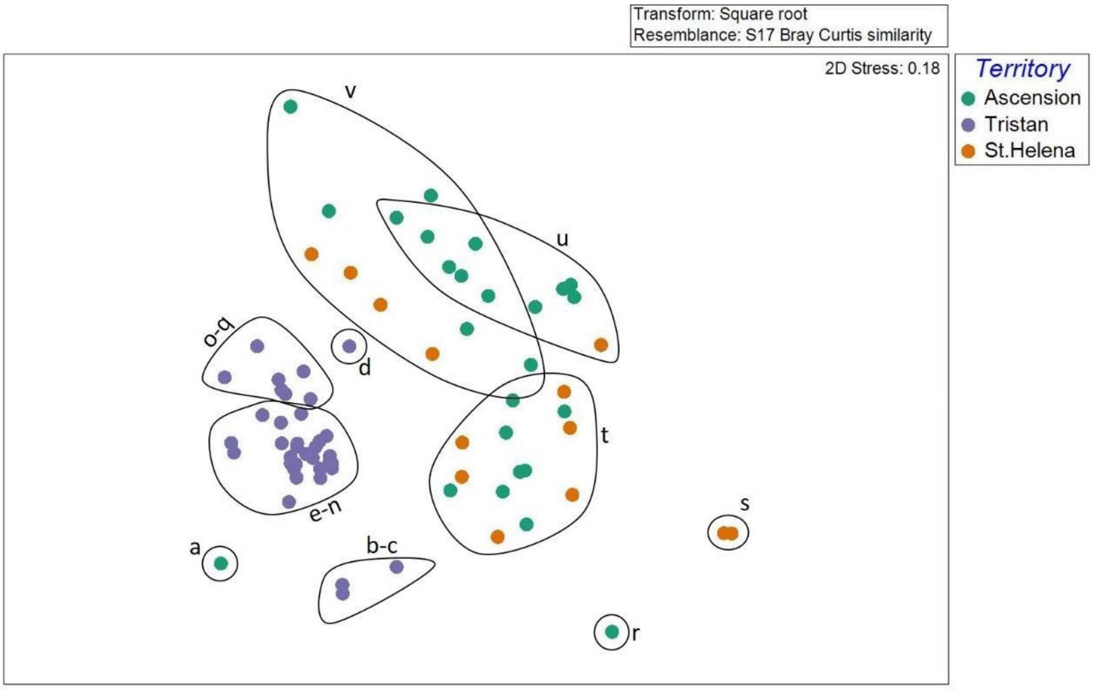


Figure C.3: Ordination of all 74 transects on a Bray-Curtis similarity matrix. Surrounding boxes represent the collapsed clusters displayed in the main text, with the letters depicting the individual clusters that fall within them.

C.7 Descriptions of clusters with example images

Cluster a

Description: The majority of this single-transect cluster from around Ascension Island shows hard substrate with a thin sediment veneer on top. Megafaunal species richness is low, with only few live taxa visible; serpulid worm casings are present on some rocks, but it is not clear whether they contain live organisms as no feeding appendages can be seen. Small *Desmophyllum pertusum* colonies are observed on some rocky outcrops but density is not high enough to be considered a coral garden. Figure C.4 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: No

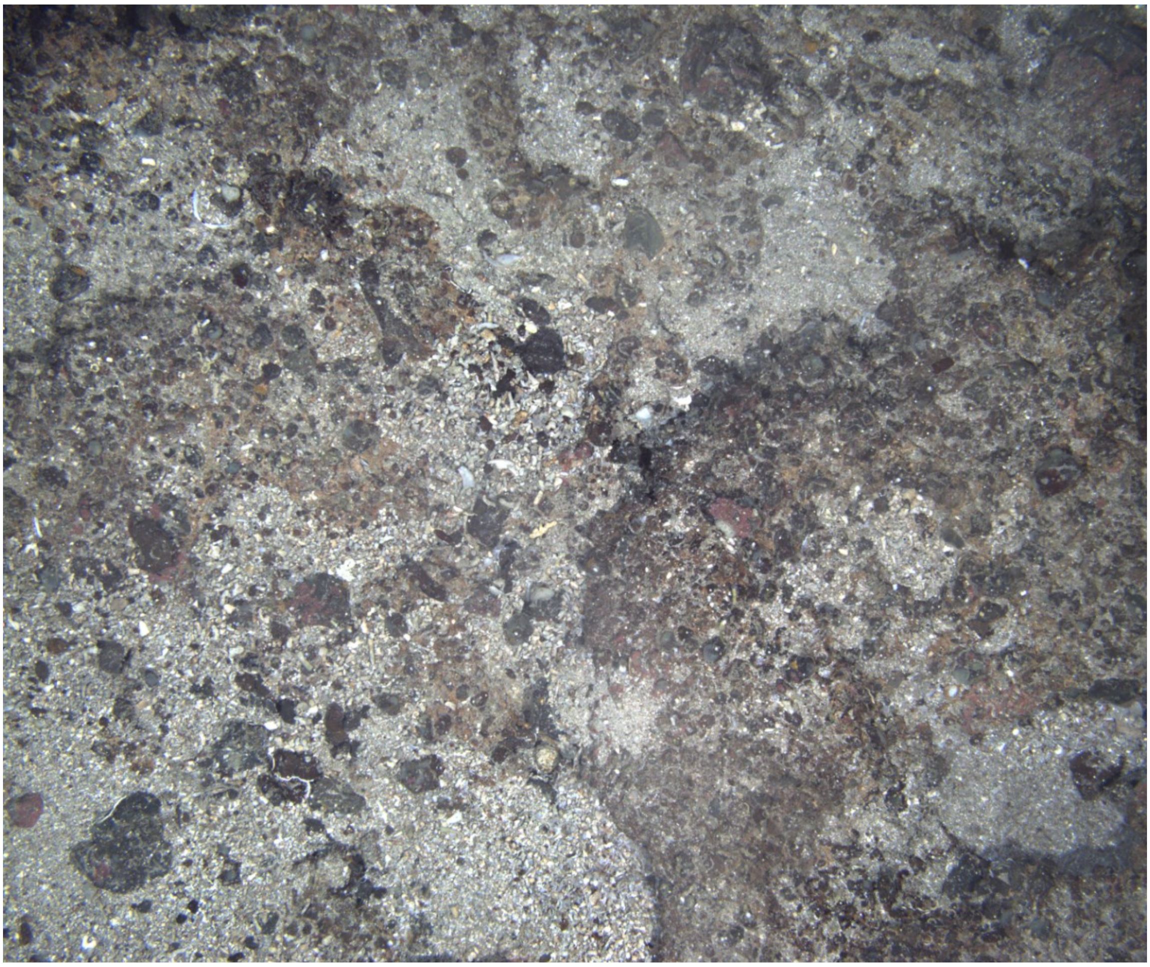


Figure C.4: Cluster a example image.

Cluster b

Description: This cluster contains a single transect from Nightingale Island (Tristan da Cunha archipelago); most images depict numerous pebbles and cobbles on coarse sand. Much of the hard substrate is colonised by Cnidarians, largely *Caryophyllia* spp. cup coral, *Thourella* spp. and stylasterids. Figure C.5 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: Mosaic of coral garden (dominated by gorgonians and stylasterids) and a hard-bottom cup coral field of *Caryophyllia* spp.

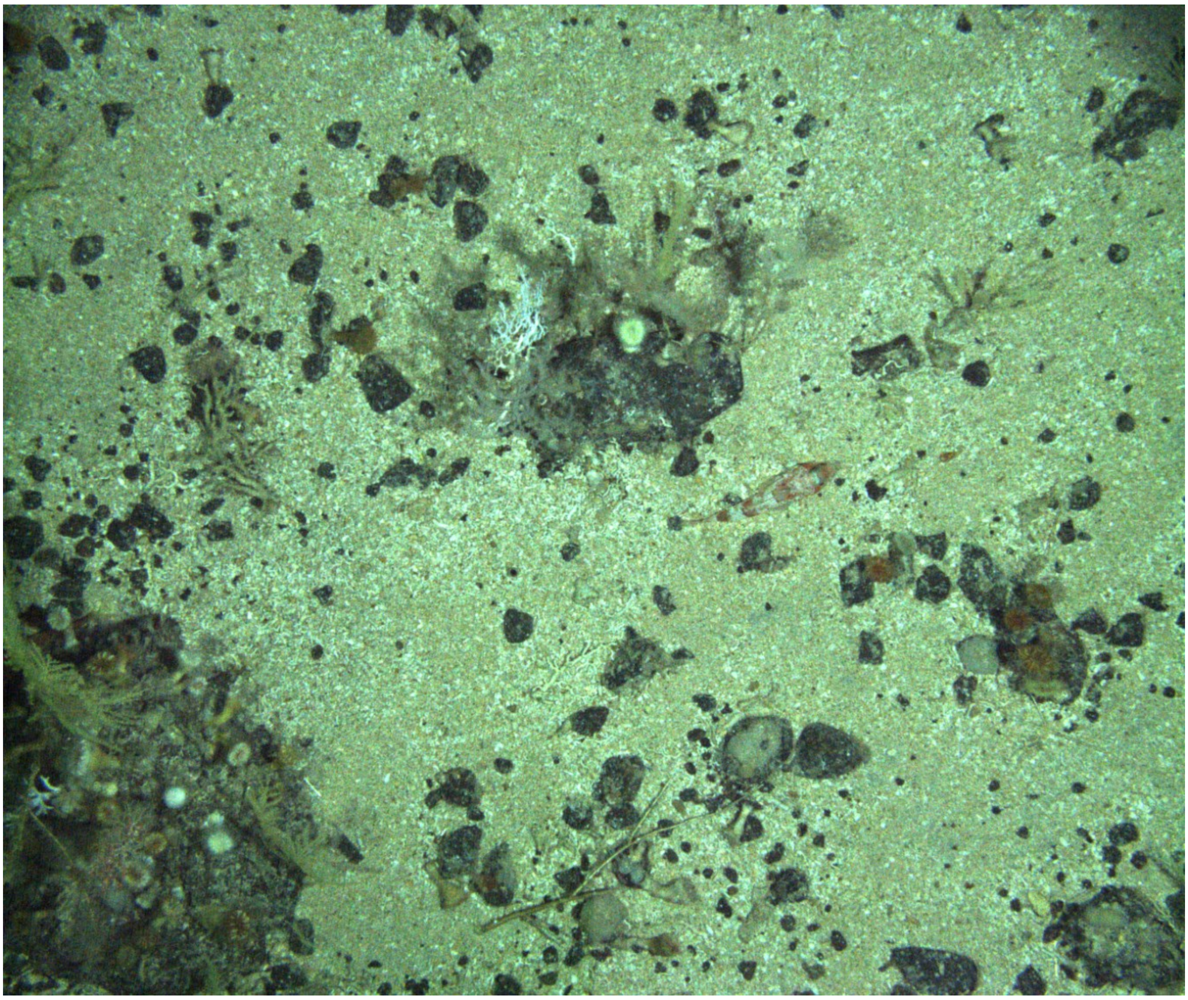


Figure C.5: Cluster b example image.

Cluster c

Description: This cluster contains images from Gough, the most southern island in the Tristan da Cunha archipelago. Substrate consists of pebbles and boulders situated on gravel. Large *Thourella* spp. as well as numerous *Caryophyllia* spp. cup corals colonise the larger hard substrate along with encrusting and structure-forming sponges. Figure C.6 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: Mosaic of coral garden (dominated by gorgonians and stylasterids) and a hard-bottom cup coral field of *Caryophyllia* spp.

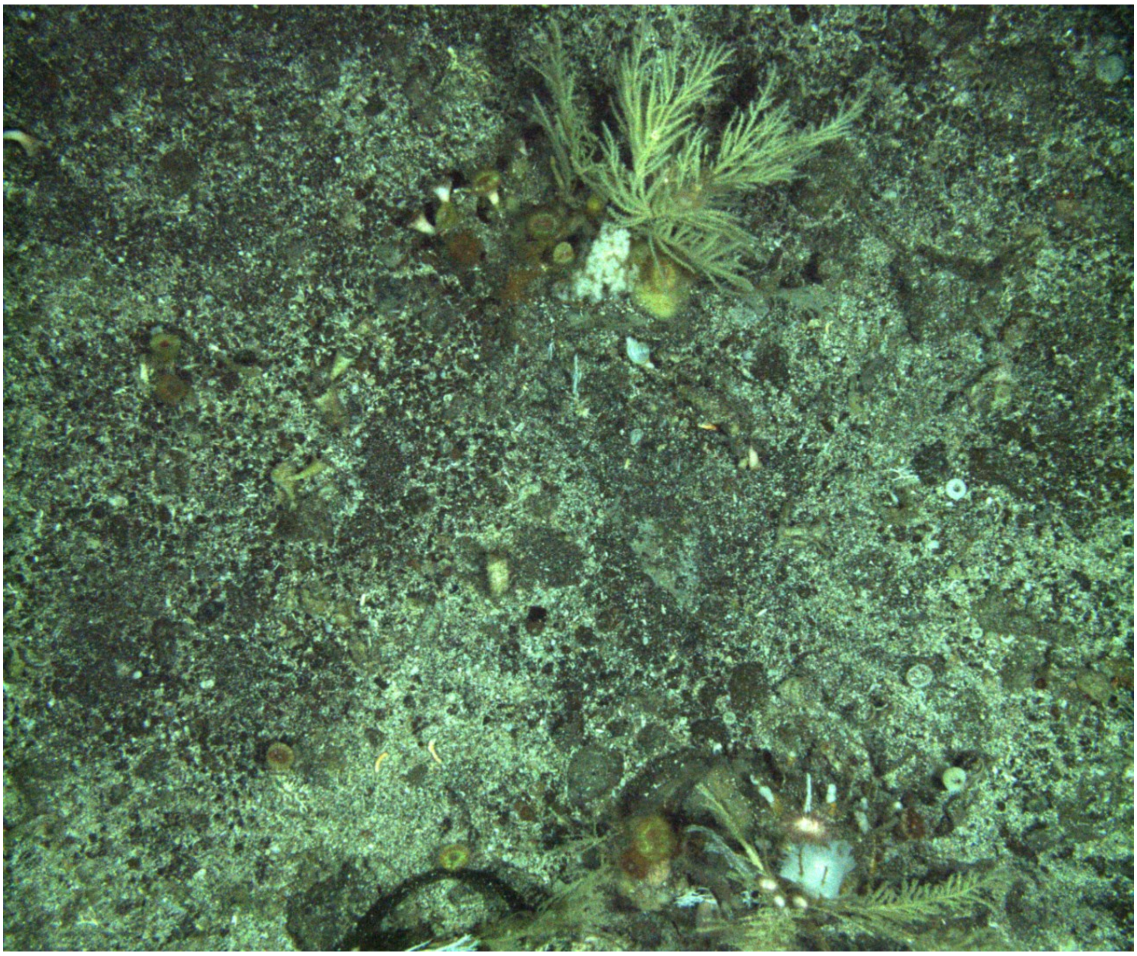


Figure C.6: Cluster c example image.

Cluster d

Description: Cluster d contains images from a single transect from Yakhont seamount in the Tristan da Cunha EEZ. The substrate consists of coral gravel with some exposed fine sand; there are a large amount of echinoid tests also present. The cluster is faunally sparse, with few brachiopods and Cnidarians (anemones and zoanthids). Small sea pens are present on some patches of exposed fine sediment, but this is not common enough for the transect to be considered a sea pen field. Figure C.7 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: No

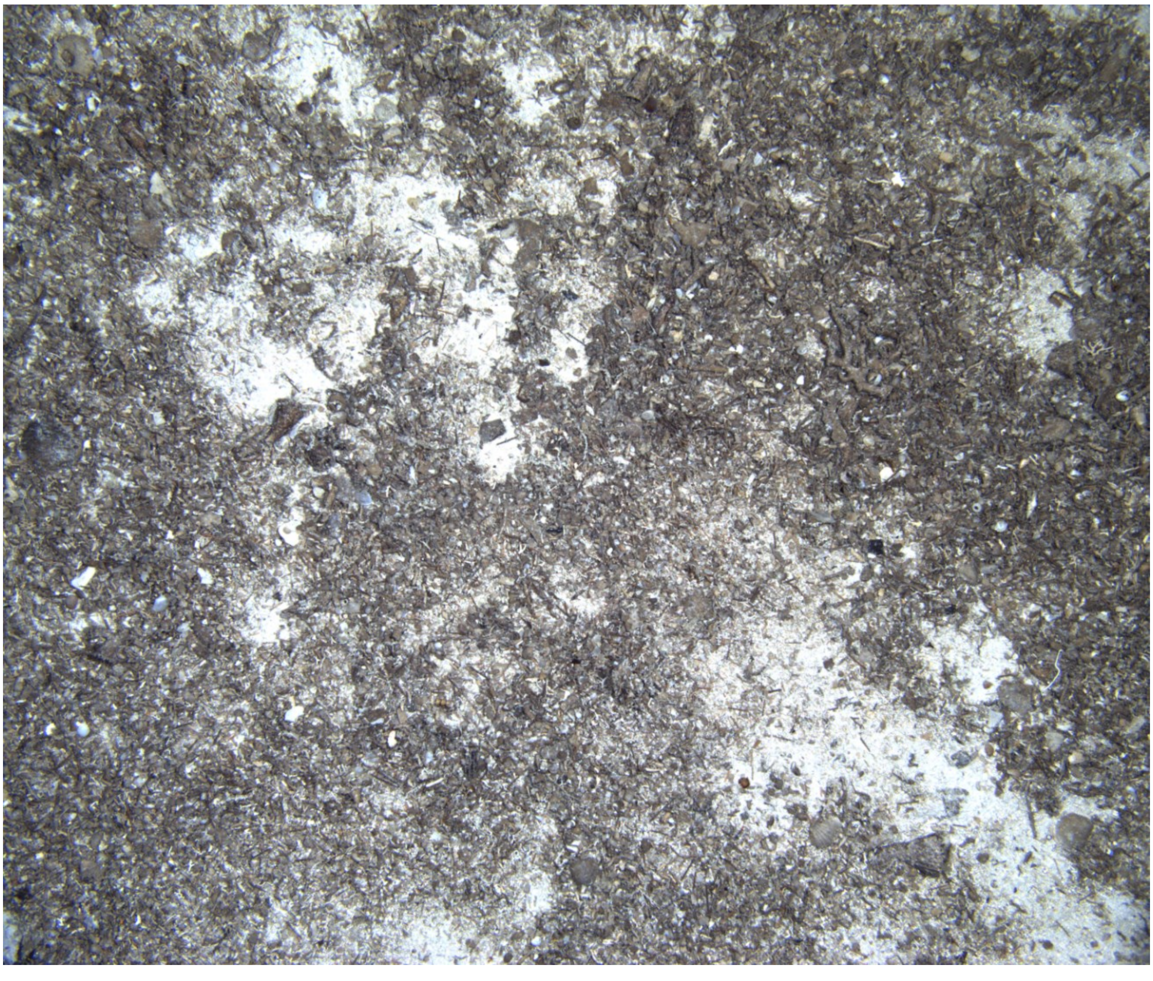


Figure C.7: Cluster d example image.

Cluster e

Description: This single-cluster transect from Crawford seamount in the Tristan da Cunha EEZ is characterised by exposed bedrock with infrequent boulders. Hard substrate is often colonised by encrusting species (largely sponges and serpulid worm casings). Large aggregations of an unidentified echinoid are present also. Figure C.8 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: No

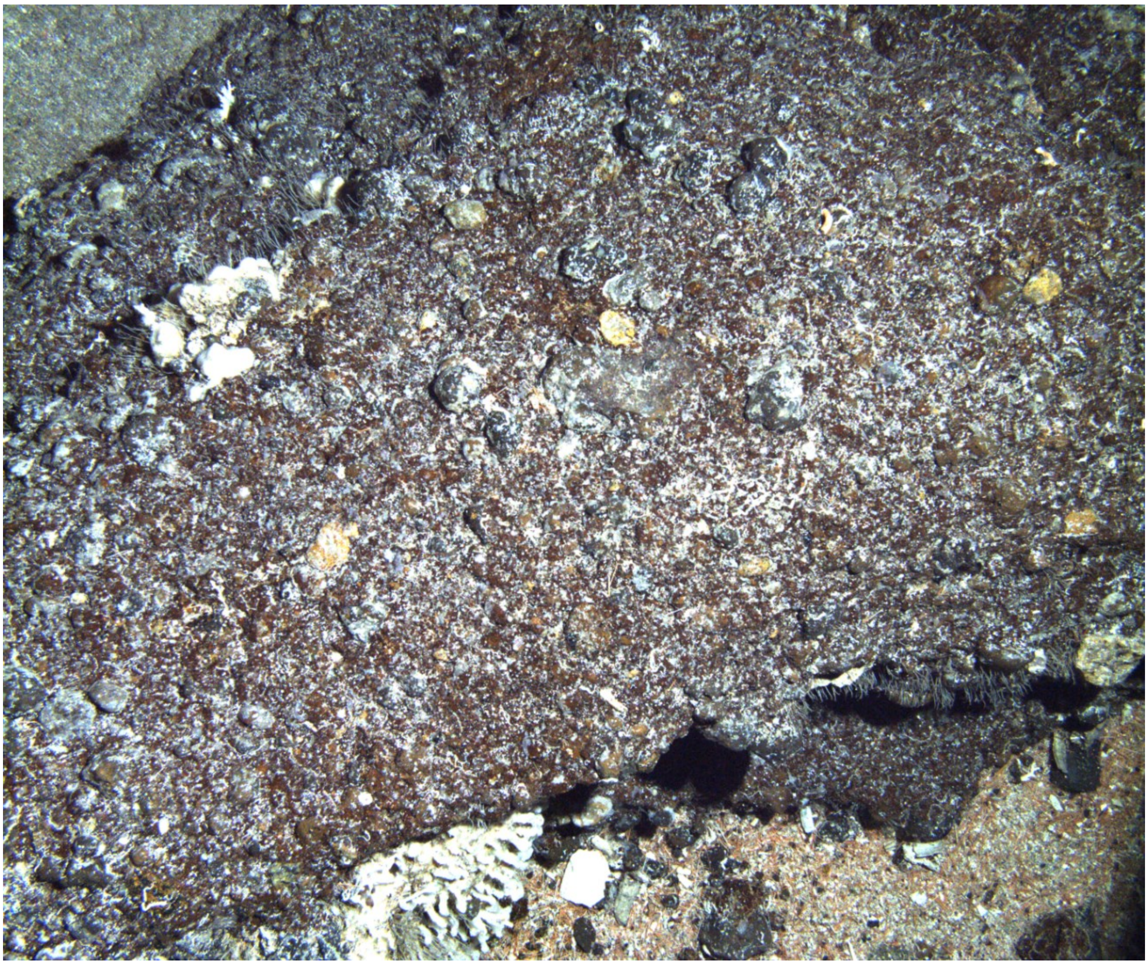


Figure C.8: Cluster e example image.

Cluster f

Description: Cluster f is a single-transect cluster from RSA seamount in the far southeast of the Tristan da Cunha EEZ. Images show a thin sediment veneer on rough bedrock with some infrequent pebbles, although two images show a cobble substrate similar to that of cluster h. There are infrequent aggregations of very small, structure-forming sponges however there is not enough evidence to class the area as a VME. Figure C.9 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: No

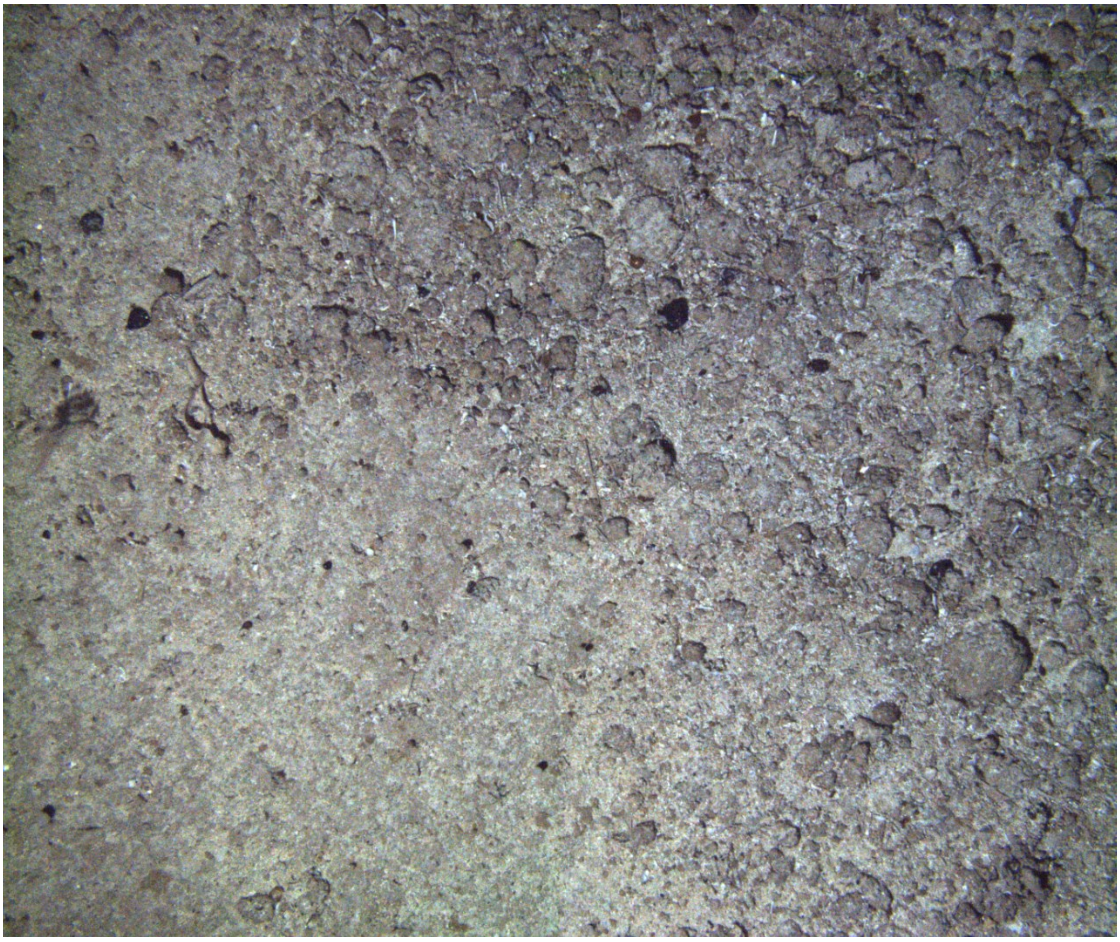


Figure C.9: Cluster f example image.

Cluster g

Description: Cluster g is composed of two transects from RSA seamount in the far southeast of the Tristan da Cunha EEZ. Images show a mix of substrates including bedrock, pebbles and sand. Most areas have low species richness, although some contain very small structure-forming sponges and small stylasterids. Figure C.10 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: No

Figure C.10: Cluster g example image.

Cluster h

Description: This cluster contains all transects from McNish seamount in the southeast portion of the Tristan da Cunha EEZ. Images show densely packed pebbles and cobbles with small soft substrate channels in between. Rock is typically colonised with encrusting and structure-forming sponges, an unidentified bivalve and *Caryophyllia* spp. cup corals; *Thourella* spp. are observed on the larger rocks. One of the four transects that make up the cluster contains larger areas of soft substrate and is consequently less species rich, although the same taxa colonise the less frequent patches of hard substrate as seen in the other transects. Figure C.11 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: Mosaic of coral garden (dominated by stylasterids) and a hard-bottom cup coral field of *Caryophyllia* spp.

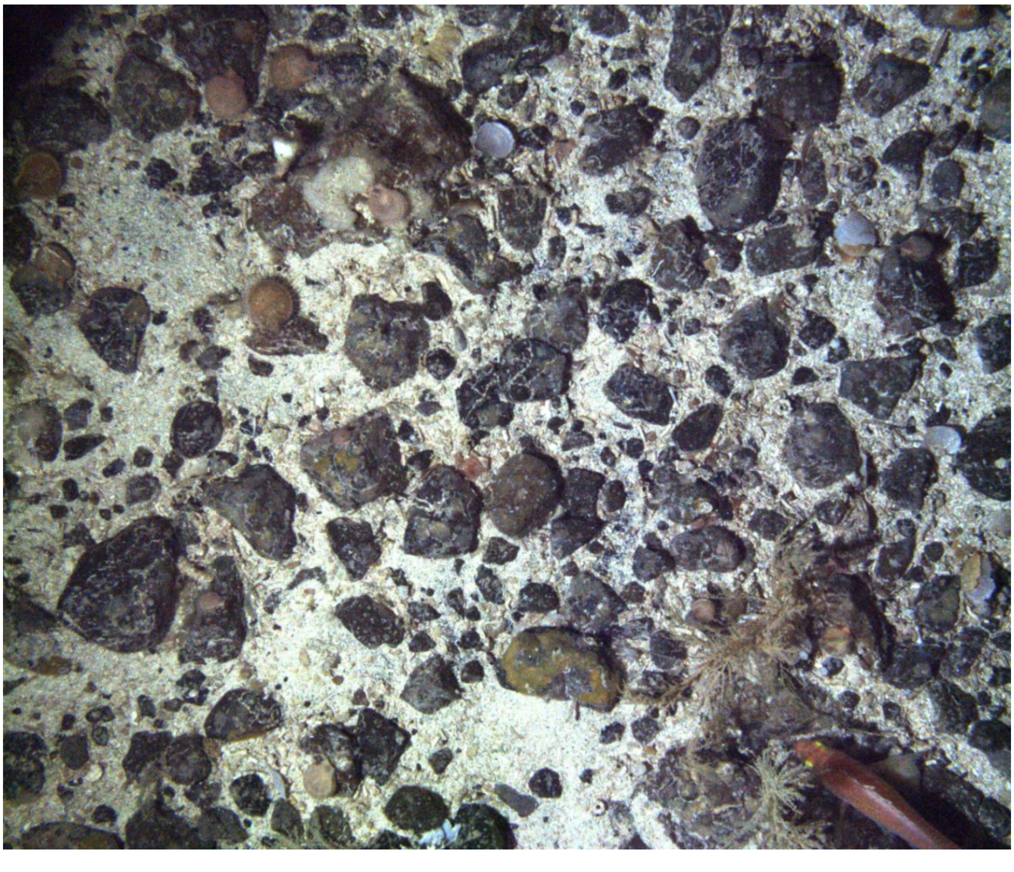


Figure C.11: Cluster h example image.

Cluster i

Description: Transects within cluster i are from Yakhont seamount. Similarly to cluster h, they show pebbles and cobbles densely packed with small soft substrate channels in between. Hard substrate is typically colonised by sponges, hydroids, with many large ophiuroids also present. There are occasional stylasterids, antipatharians and large anemones (possible *Bolocera tuediae*) present. Figure C.12 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: No

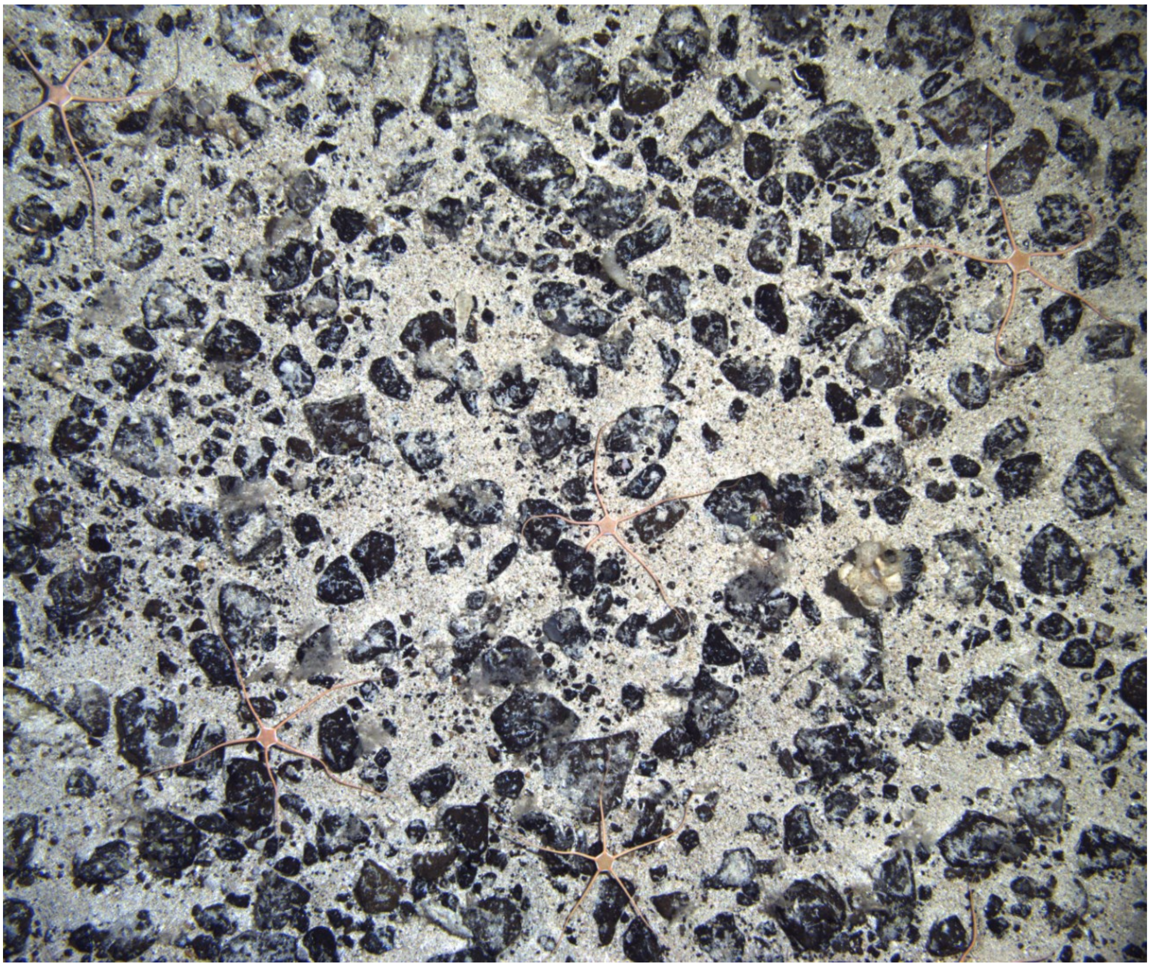


Figure C.12: Cluster i example image.

Cluster j

Description: Cluster j comprises four transects from Yakhont seamount in the Tristan da Cunha EEZ. The substrate type is characterised by pebbles and cobbles (with a large size range of both) on fine sand. Hard-bottom *Caryophyllia* spp. cup corals are the most dominant taxa along with ophiuroids and sponges. There are also occasional gorgonians (family: Chrysogorgidae) and stylasterids. One of the four transects was not considered a VME on its own, although this was only by a small margin. Figure C.13 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: Mosaic of hard-bottom cup coral field of *Caryophyllia* spp. and a coral garden (dominated by gorgonians and stylasterids)

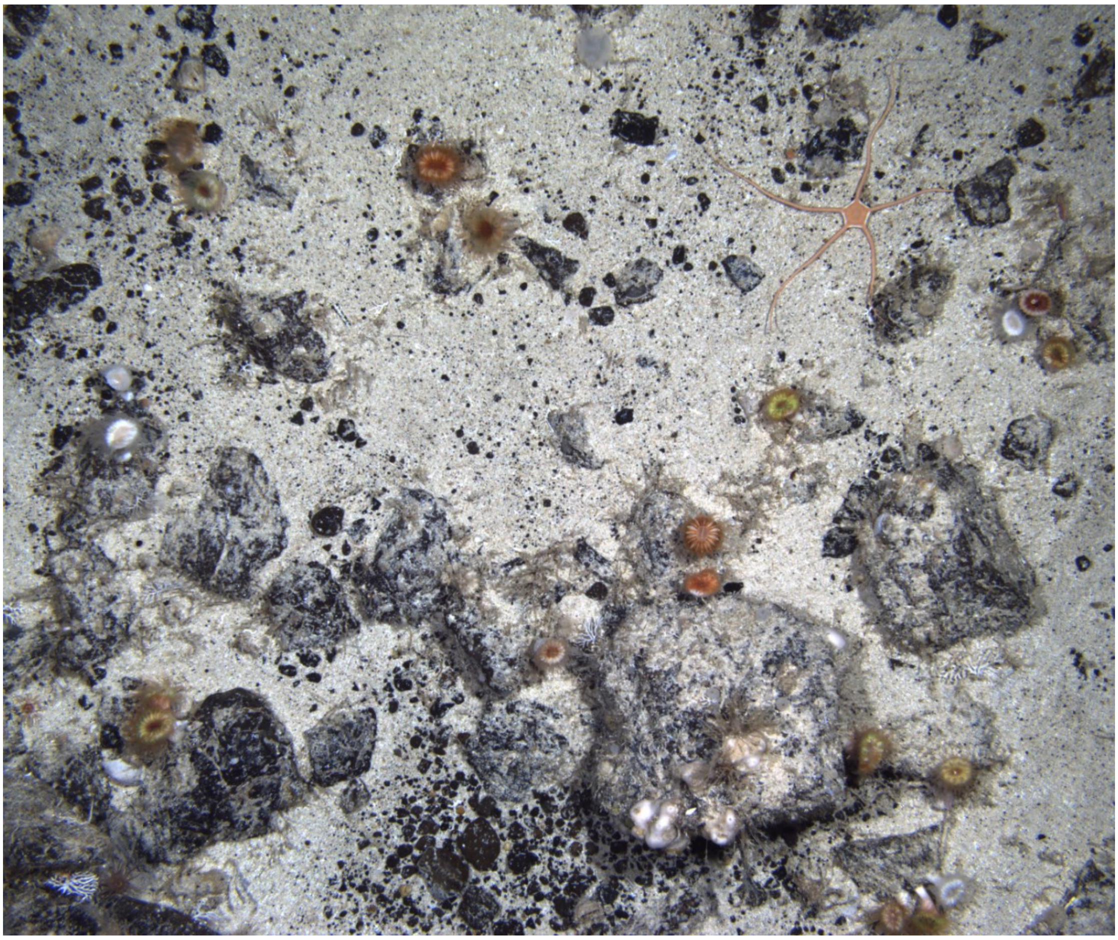


Figure C.13: Cluster j example image.

Cluster k

Description: This cluster contains five transects from Yakhont seamount in the Tristan da Cunha EEZ. Substrate type is variable with fine sand being covered by small pebbles to large cobbles, often supporting hydroid and ophiuroid communities. One of the five transects shows dense *Desmophyllum pertusum* reef (Figure C.14) with a small epifaunal community comprised largely of ophiuroids, decapods, and some *Lepidoperca coatsii*. Areas with hard substrate shows VME taxa including antipatharians, stylasterids and *Caryophyllia* spp. cup corals, but these do not characterise the cluster overall. Figure C.15 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: Partial *Desmophyllum pertusum* reef

Figure C.14: Desmophyllum pertusum reef in cluster k.

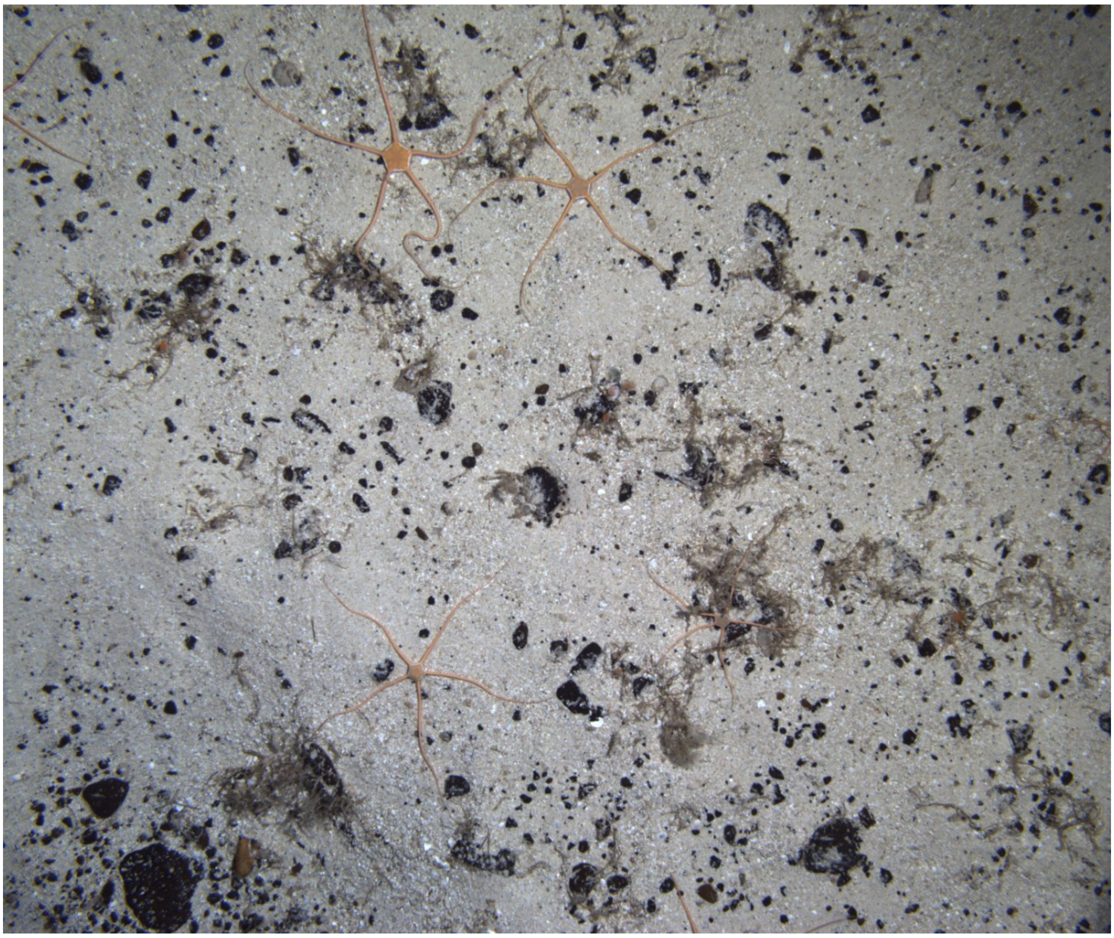


Figure C.15: Cluster k example image.

Cluster l

Description: This single-transect cluster comes from Crawford seamount in the central region of the Tristan da Cunha EEZ. Substrate consists largely of coral rubble and/or gravel with few pebbles. There is little live taxa in view, although there is an encrusting sponge on some hard substrate. Figure C.16 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: No

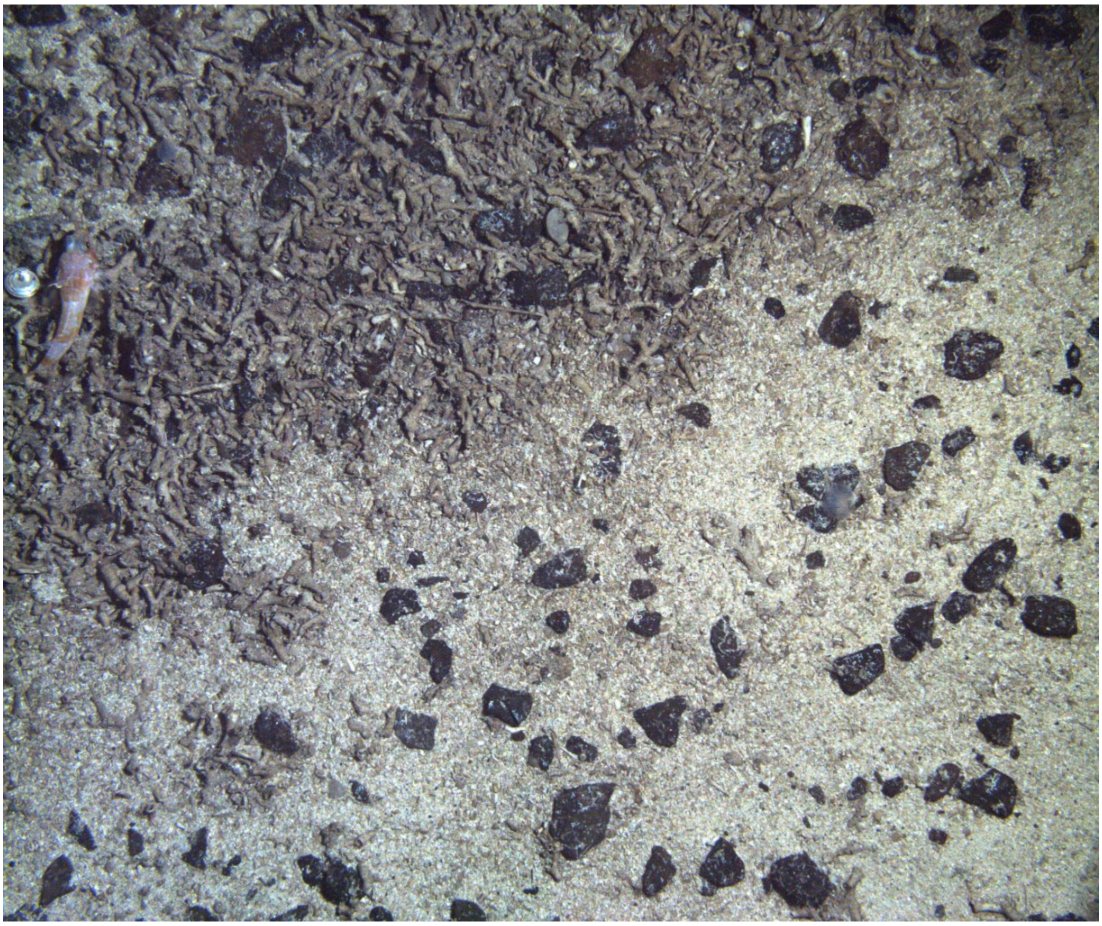


Figure C.16: Cluster l example image.

Cluster m

Description: Cluster m is comprised of two transects from Crawford seamount in the central region of the Tristan da Cunha EEZ. Fine sand makes up the majority of the substrate of one transect, whilst the other has more hard substrate in the form of pebbles and cobbles upon which there are structure-forming sponges and *Caryophyllia* spp. cup corals. This transects constitutes a mosaic VME of hard-bottom cup coral field and coral garden, however the cluster overall cannot be described as a VME. Figure C.17 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: No

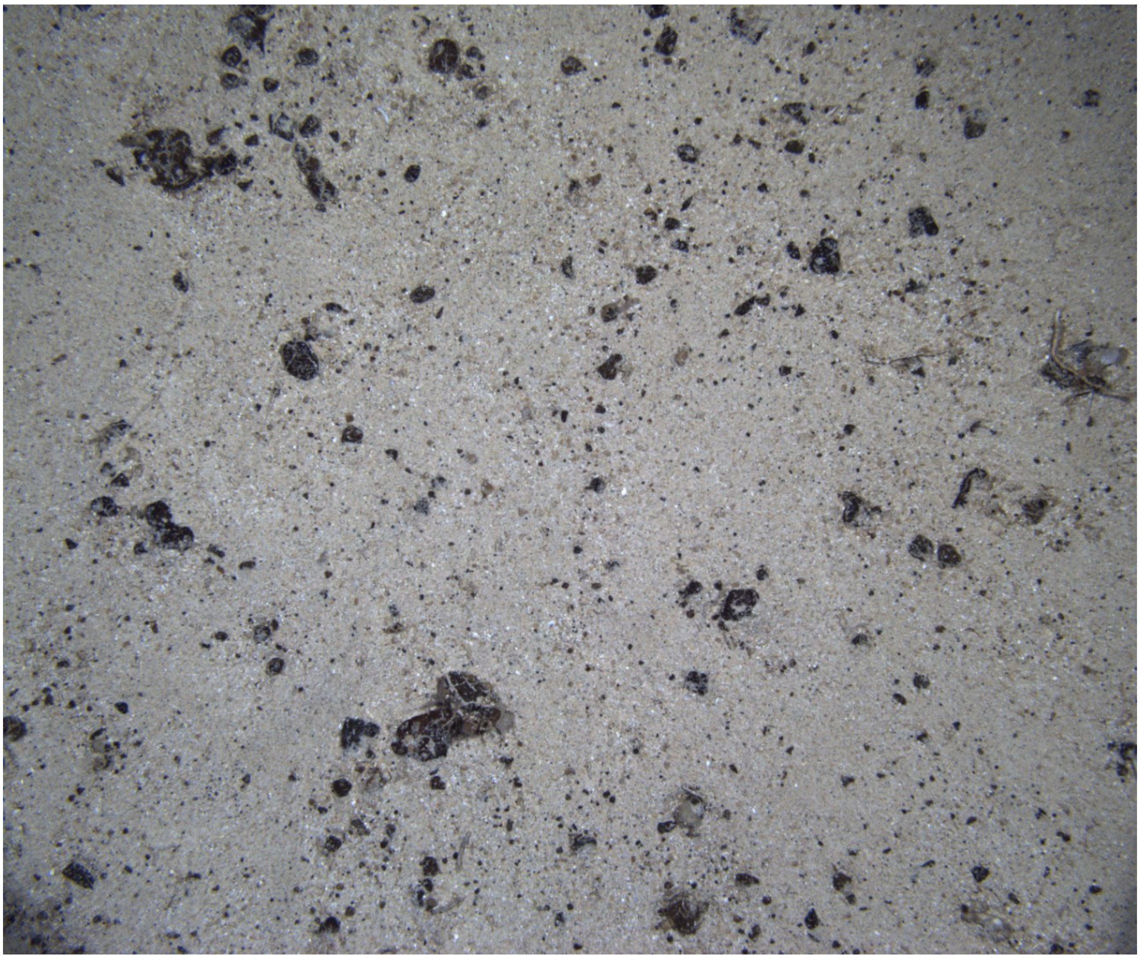


Figure C.17: Cluster m example image.

Cluster n

Description: Cluster n is comprised of two transects from Crawford seamount in the central region of the Tristan da Cunha EEZ. Dominant substrate types are pebbles and cobbles on fine sand. Where there is hard substrate, faunal communities are species rich and dominated by hard-bottom *Caryophyllia* spp. cup corals (Figure C.18) and structure-forming sponges; larger rocks support some antipatharians. Figure C.19 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: Mosaic of hard-bottom cup coral field of *Caryophyllia* spp. and a coral garden (dominated by antipatharians)

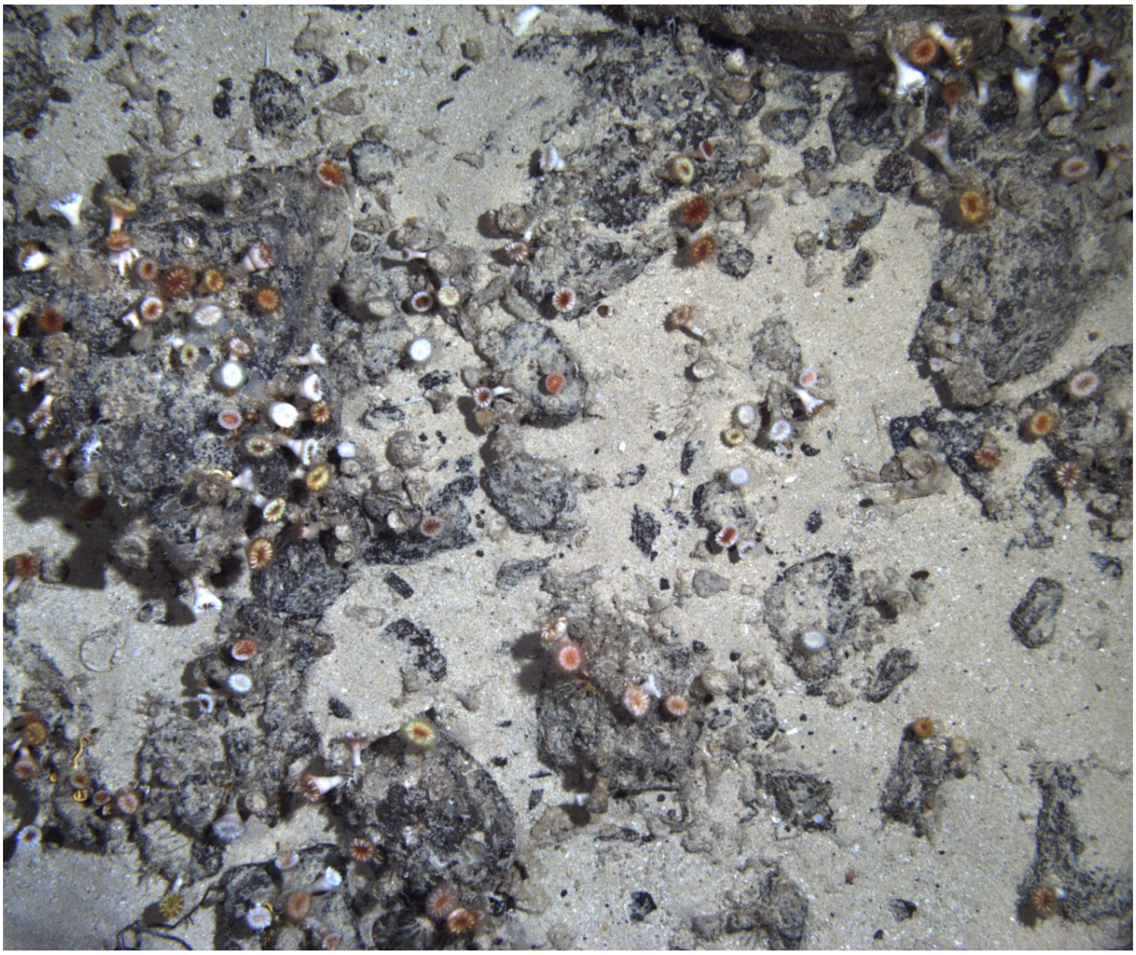


Figure C.18: Hard-bottom cup coral field VME example from cluster n.

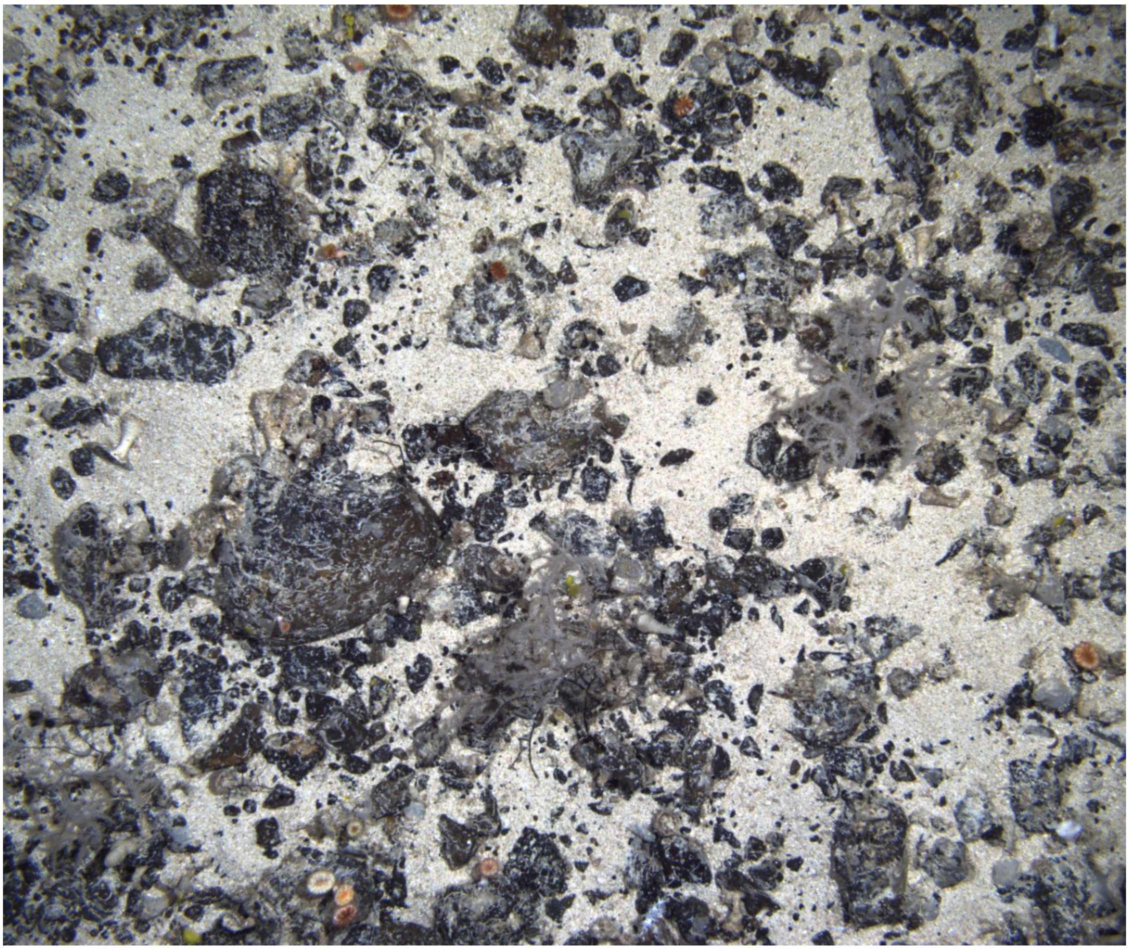


Figure C.19: Cluster n example image.

Cluster o

Description: Dominant substrate types are variable including coral rubble and exposed bedrock, the latter of which is often covered by a thin sediment veneer. The faunal community seems linked to substrate type with large ophiuroids dominating the coral rubble areas, and structure-forming sponges and gorgonians on the bedrock/sediment veneer. Numerous images show aggregations of antipatharians (likely *Bathypathes* spp.), hence its classification as a hard-bottom coral garden. Figure C.20 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: Hard-bottom coral garden dominated by antipatharians

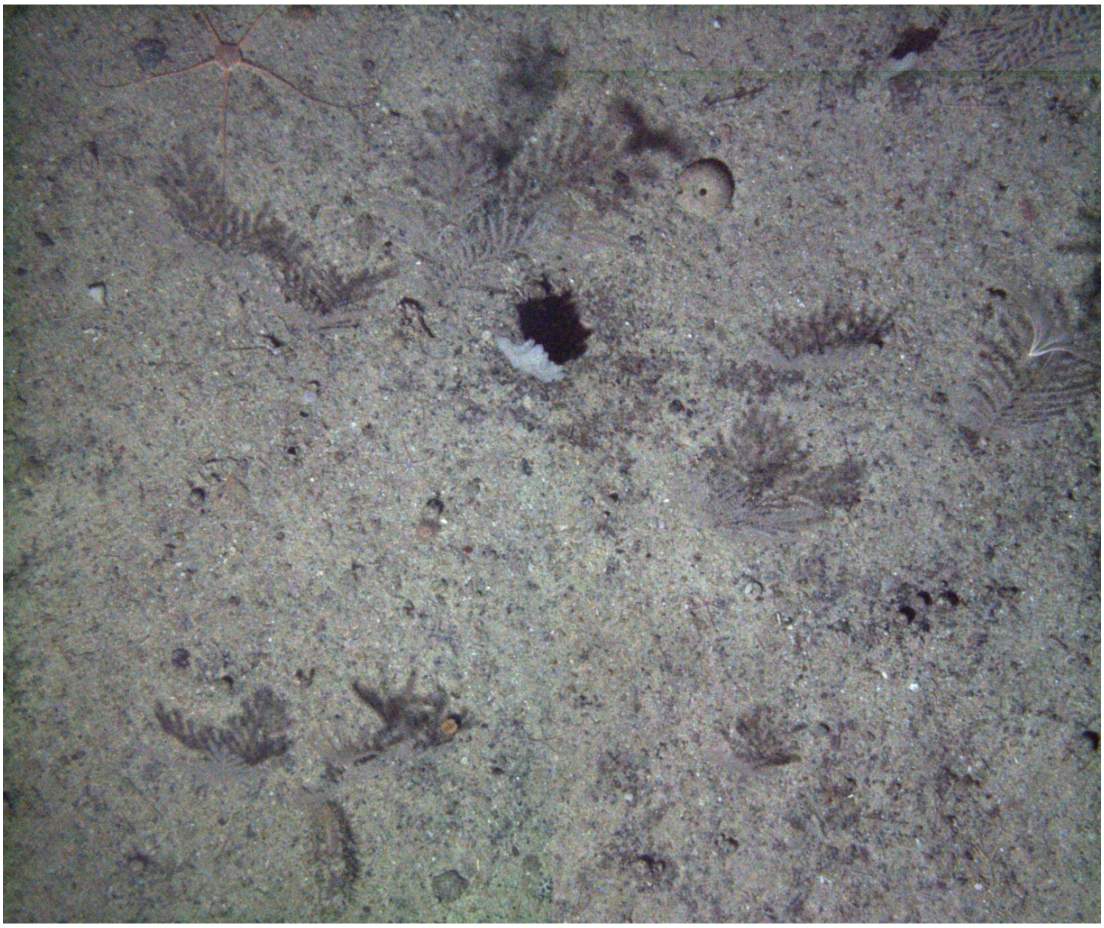


Figure C.20: Cluster o example image depicting an antipatharian-dominated hard-bottom coral garden VME.

Cluster p

Description: Cluster p consists of a single transect from Crawford seamount in the central region of the Tristan da Cunha EEZ. Substrate is typically bedrock and/or coral rubble. One the hard substrate, communities of stylasterids are present, along with some sponge taxa. The coral rubble appears dominated by hydroids and hermit crabs with a commensal anemone. Figure C.21 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: No

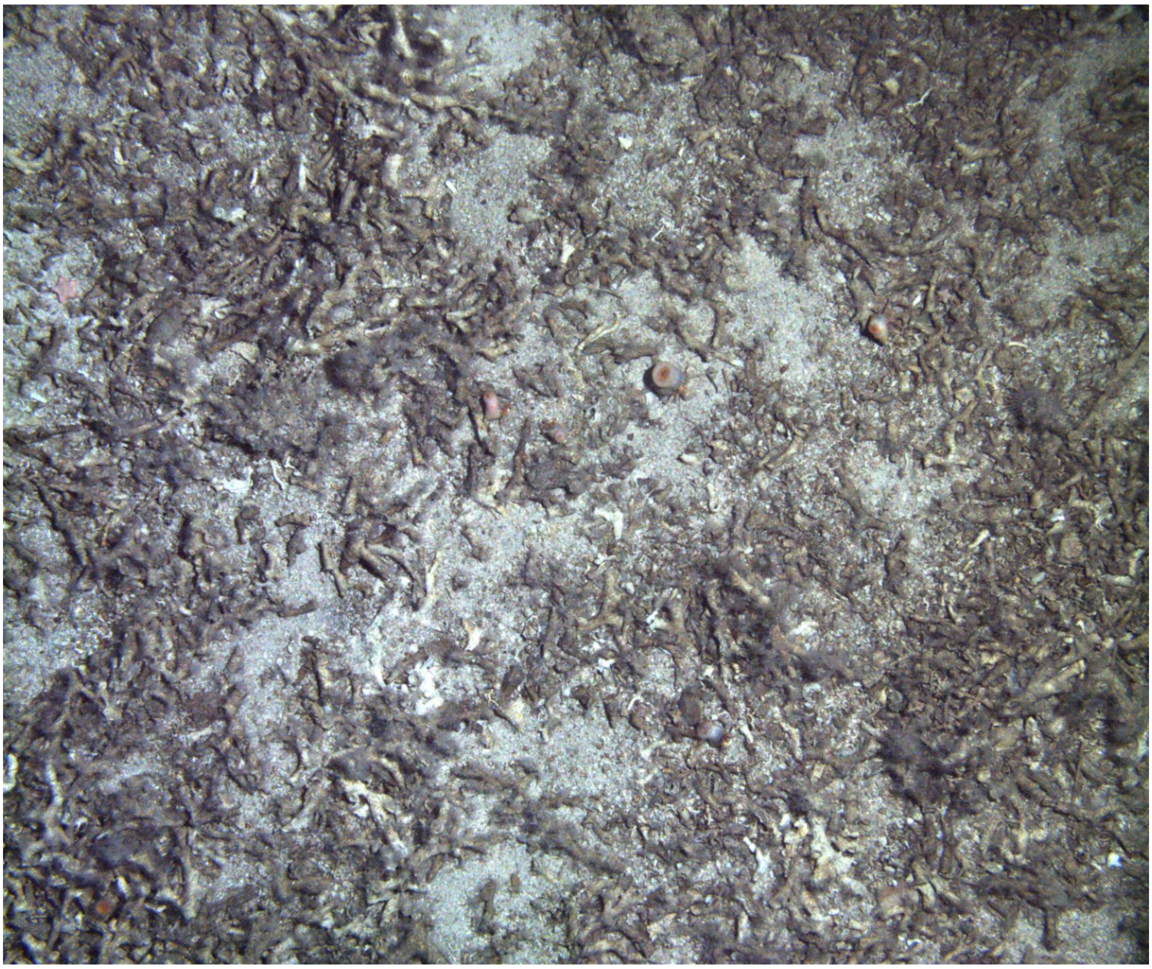


Figure C.21: Cluster p example image.

Cluster q

Description: Cluster q contains of five transects from Crawford seamount in the central region of the Tristan da Cunha EEZ. Substrate type is mixed across the cluster, although there is a dominance of coral-related substrate including *Solenosmilia variabilis* reef framework and rubble. Reef framework supports an epifaunal community consisting largely of ophiuroids, encrusting sponges, squat lobsters and hydroids, whilst the rubble provides substrate for brachiopods. Two transects support a stylasterid-dominated coral garden VME (Figure C.22) and this is characterised by bedrock with a thin sediment veneer. Figure C.23 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: *Solenosmilia variabilis* reef (largely dead framework) and stylasterid-dominated coral garden

Figure C.22: Stylasterid-dominated hard-bottom coral garden VME in cluster q.

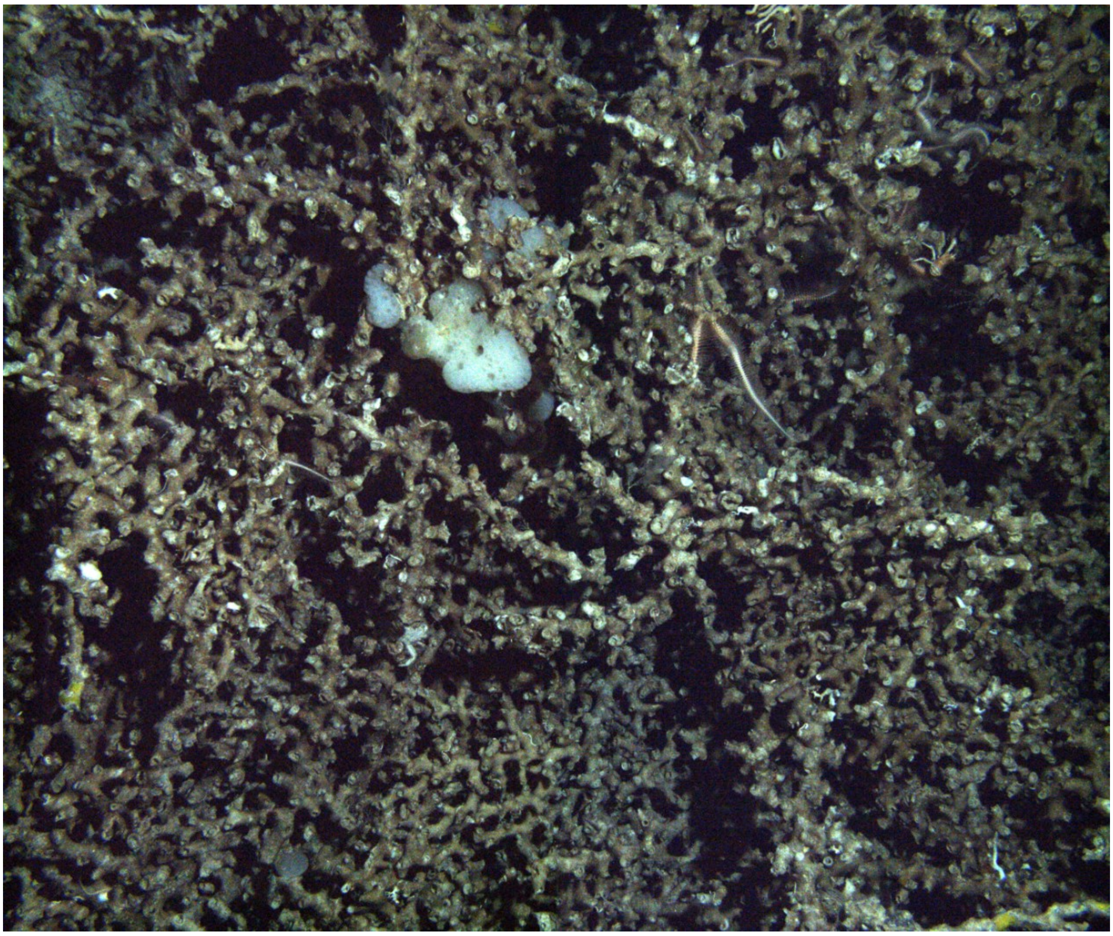


Figure C.23: Cluster q example image.

Cluster r

Description: Cluster r contains a single transect from around Ascension Island. The dominant substrate type is course sand with some occasional gravel. Mobile taxa are observed in almost all images, often showing multiple fish species. There appears to be no sessile, benthic epifaunal community in most instances. Figure C.24 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: No

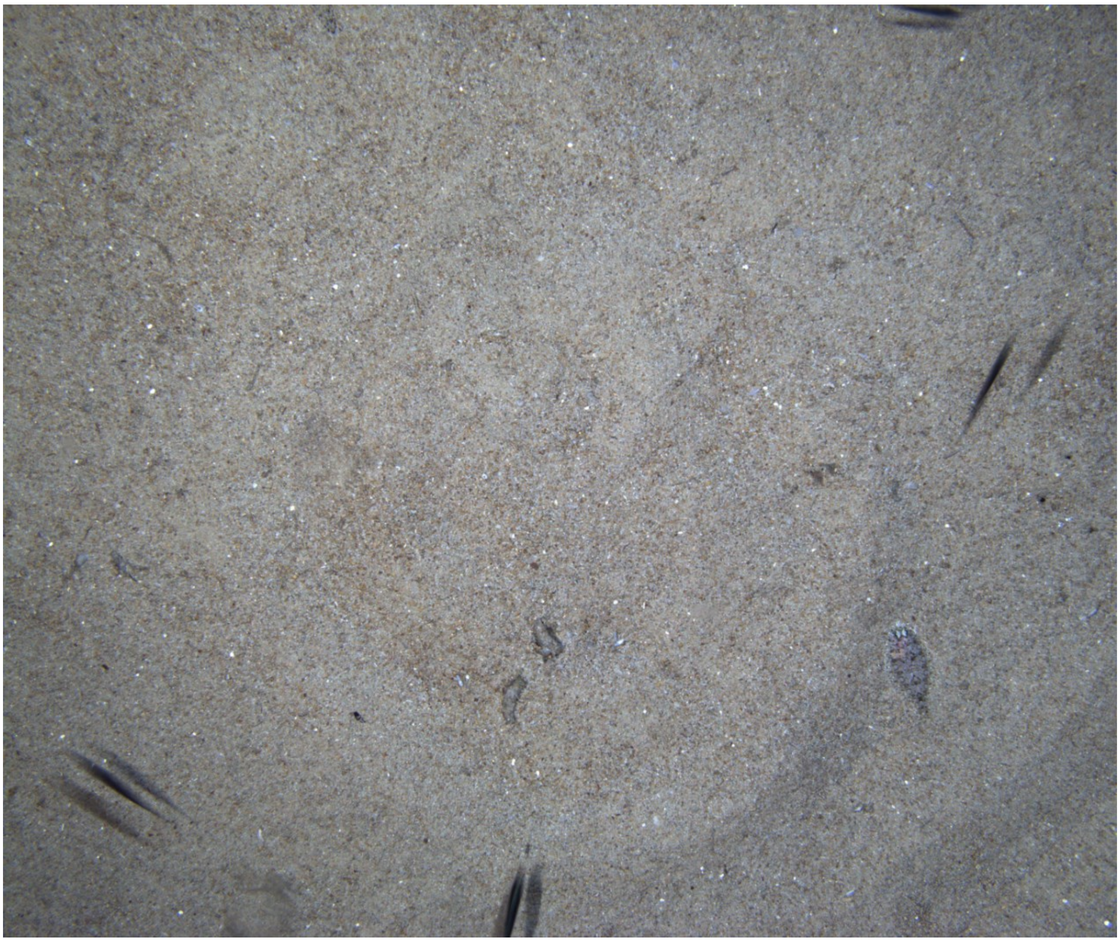


Figure C.24: Cluster r example image.

Cluster s

Description: Cluster s consists of two transects from around the island of Saint Helena. The dominant substrate type in all images is sand although the grain sizes vary. Very few fauna are present with the exception of cerianthids and the occasional cidarid urchin. Figure C.25 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: No

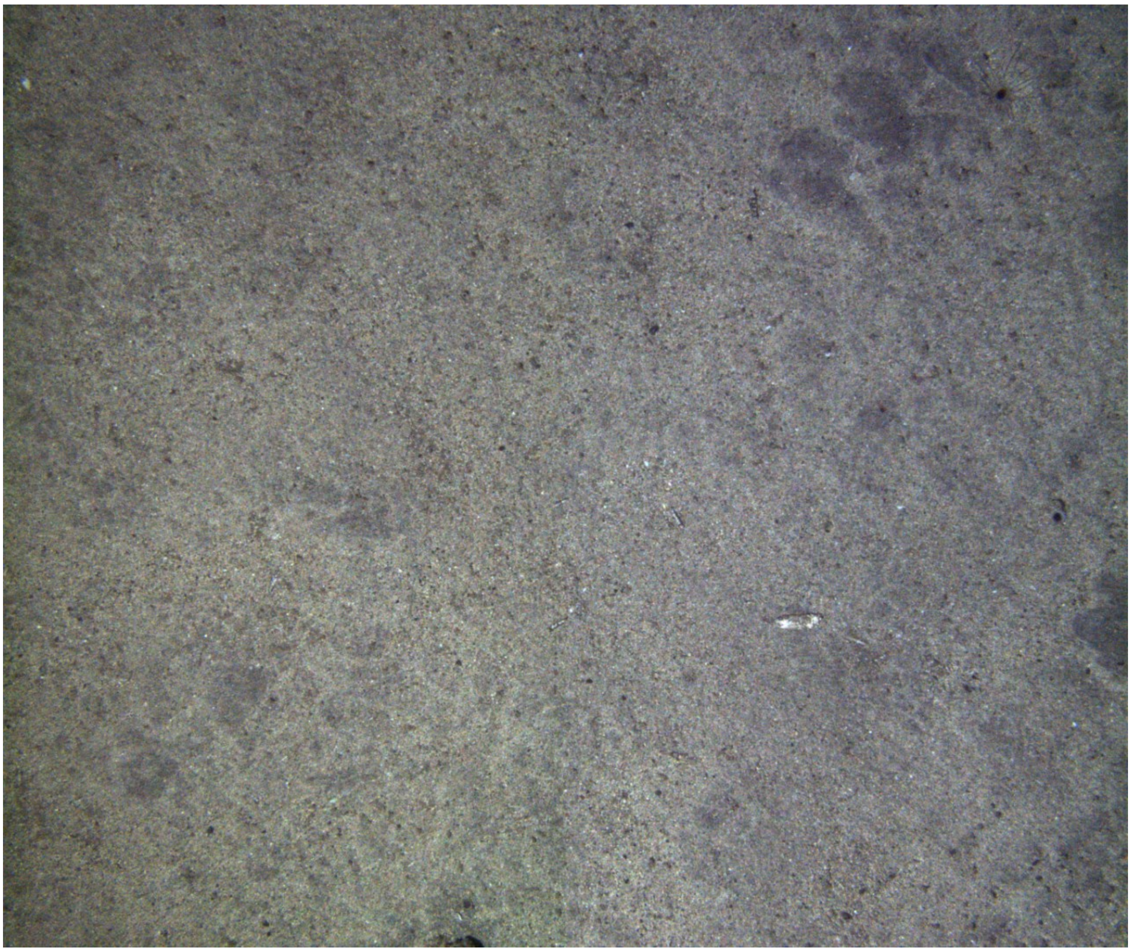


Figure C.25: Cluster s example image.

Cluster t

Description: Cluster t comprises 14 transects from 5 locations across the EEZs of both Ascension and Saint Helena. This cluster includes a range of habitat types including *Desmophyllum pertusum* reef (Figure C.26) and a sea pen field (Figure C.27), both of which are classed as VMEs. Substrates vary dependent on transect, with soft sediment areas, reef framework and bedrock all represented in the images. Soft sediment areas are typically dominated by cidarid urchins and soft-bottom cup corals, and in one area by multiple species of sea pen (sometimes of the *Protoptilum* genus). Reef framework is often dominated by ophiuroid mats, but large, filter feeding *Aphrocallistes* spp. are also present along with anemones. Whilst this cluster seems less coherent than others, there is a strong presence of cidarid urchins in all transects. Figure C.26 and Figure C.27 provide example images and full environmental information is supplied in the electronic supplementary material.

VME: Partial *Desmophyllum pertusum* reef and sea pen field

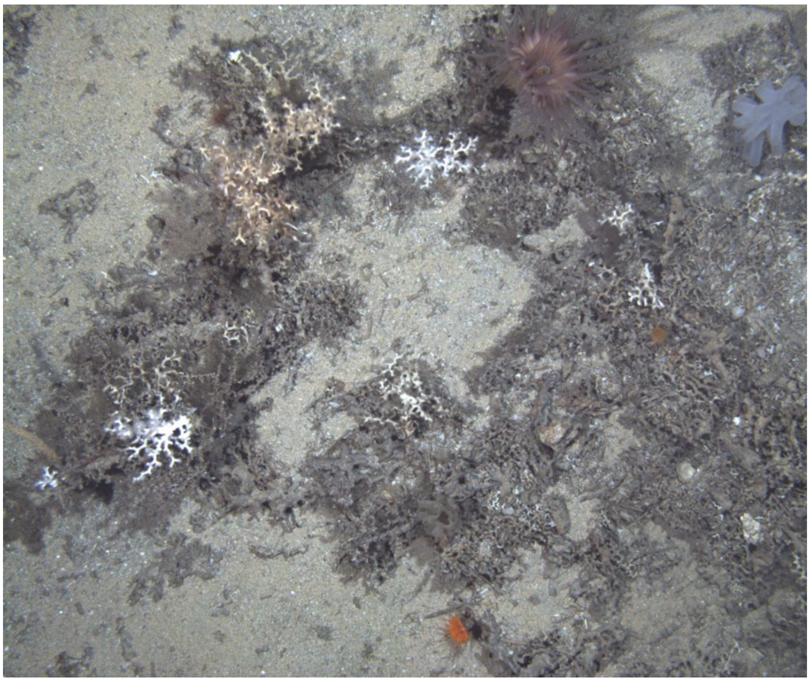


Figure C.26: Desmophyllum pertusum reef VME from cluster t.

Figure C.27: Sea pen field VME from cluster t.

Cluster u

Description: Whilst species richness is low, there are occasional soft-bottom fauna observed including gastropods, sea pens, cerinathids and soft-bottom cup corals. The hard substrate that is present has a low species richness also. Figure C.28 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: No

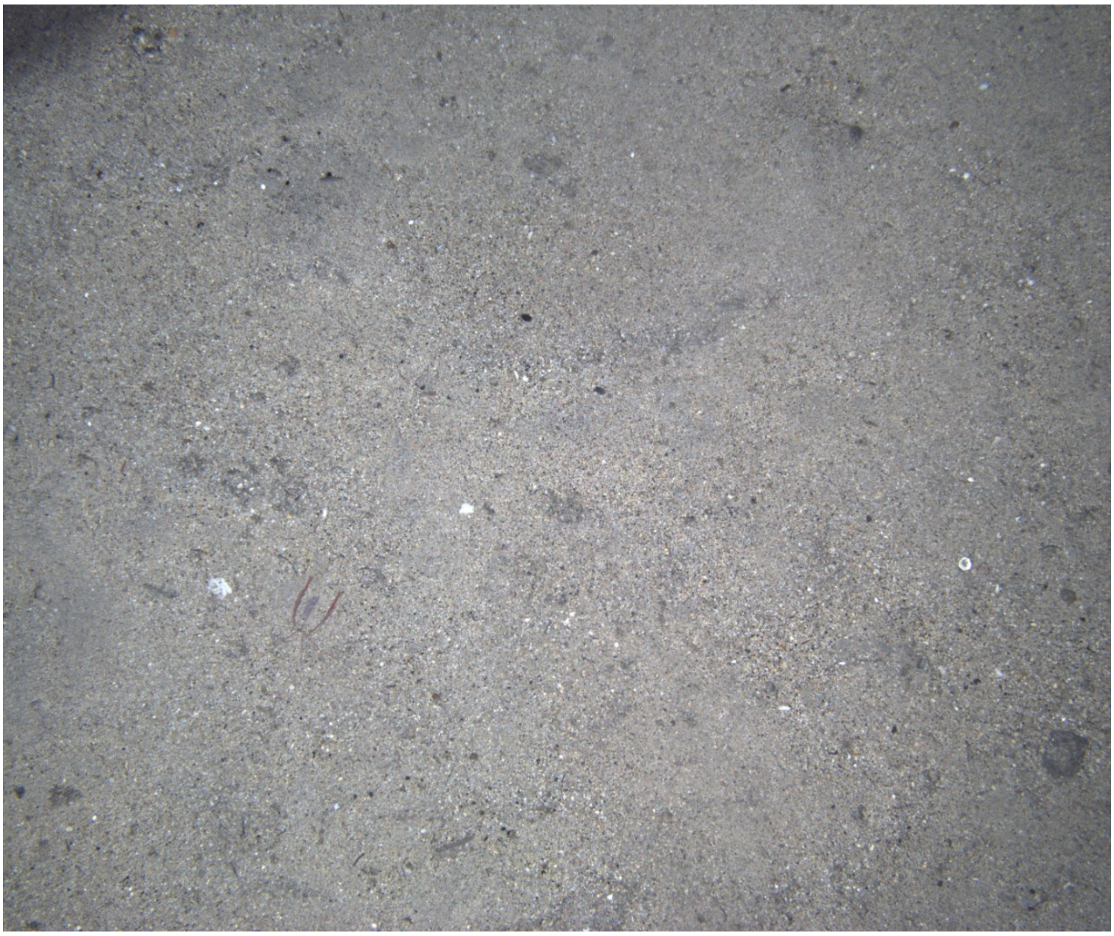


Figure C.28: Cluster u example image.

Cluster v

Description: The 13 transects that make up cluster v are from 6 sites across the EEZs of Ascension and Saint Helena. This cluster is typically characterised by hard substrates including reef framework and boulders, however some images show soft substrates including sand (these typically show sediment around the base of rocky outcrops). Rock is often encrusted with serpulid worms. There are small patches of live *Solenosmilia variabilis* on reef framework (Figure C.29) as well as epifaunal crinoids and encrusting sponges. Figure C.29 provides an example image and full environmental information is supplied in the electronic supplementary material.

VME: Partial *Solenosmilia variabilis* reef

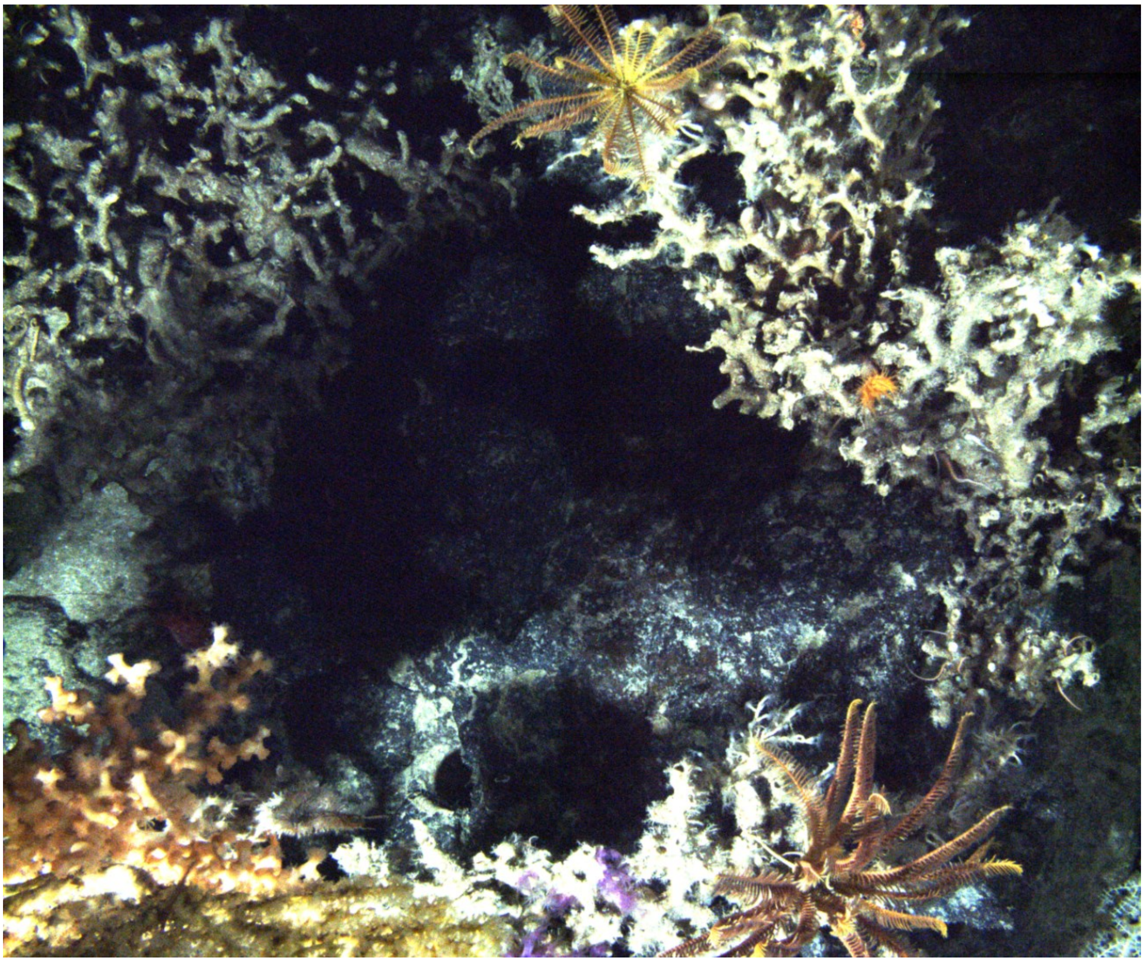
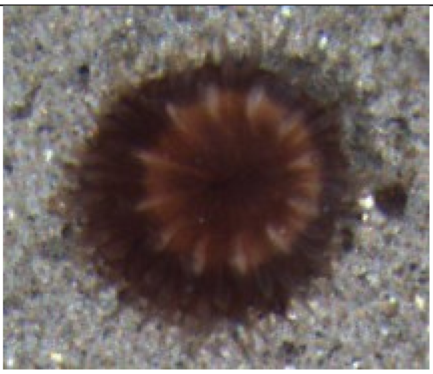
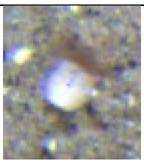
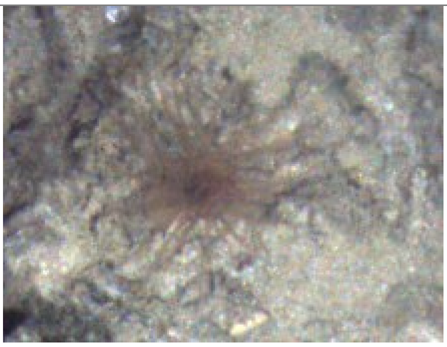
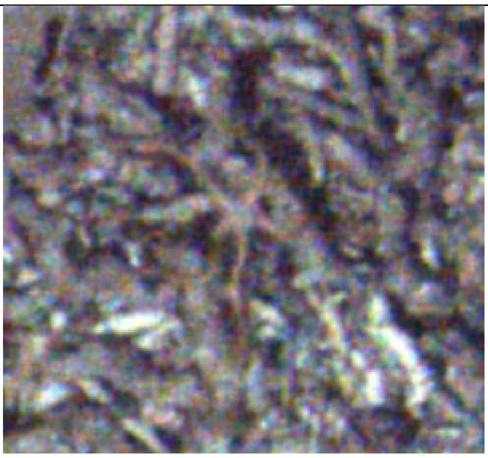
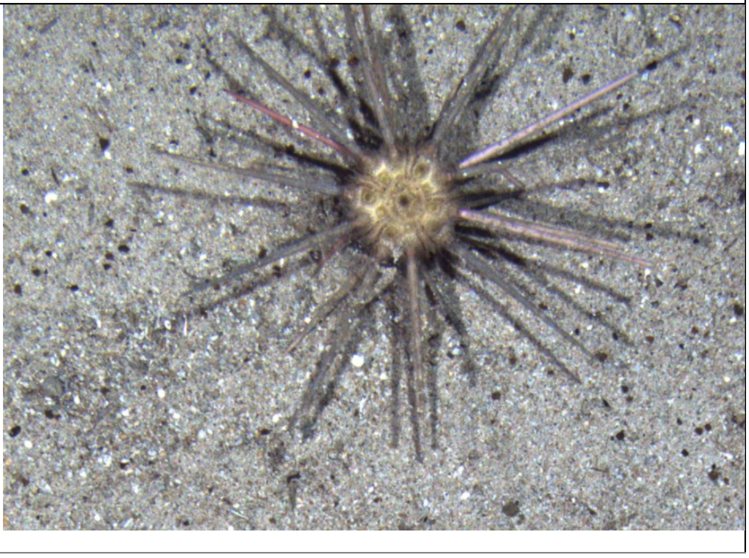


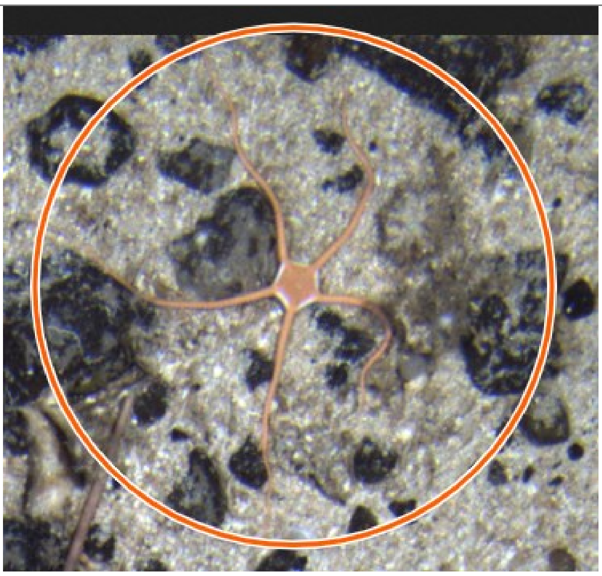
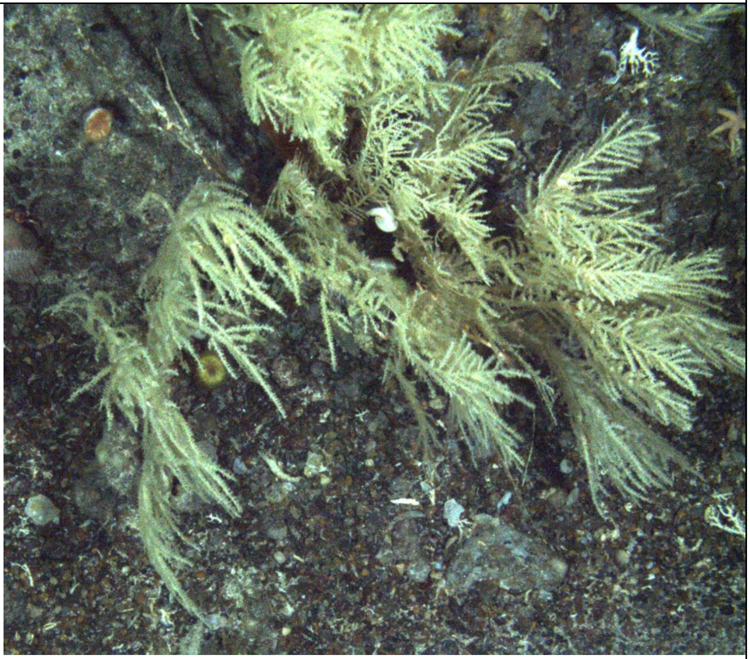
Figure C.29: Solenosmilia variabilis reef VME in cluster v.

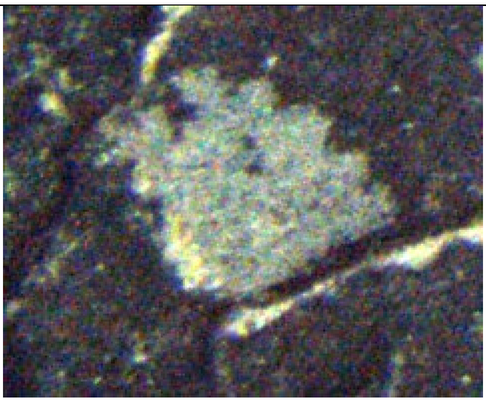
C.8 Characterising taxa images

Table C.5: Images, Operational Taxonomic Unit (OTU) codes and descriptions of the characterising taxa identified by the SIMPER.

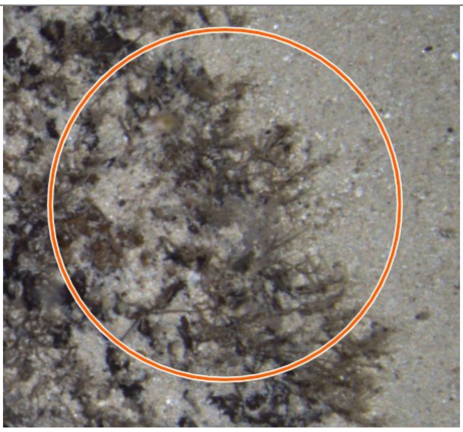
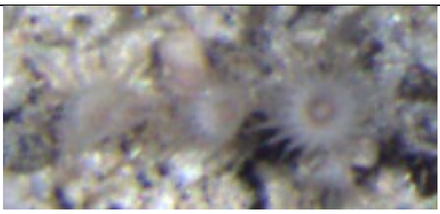
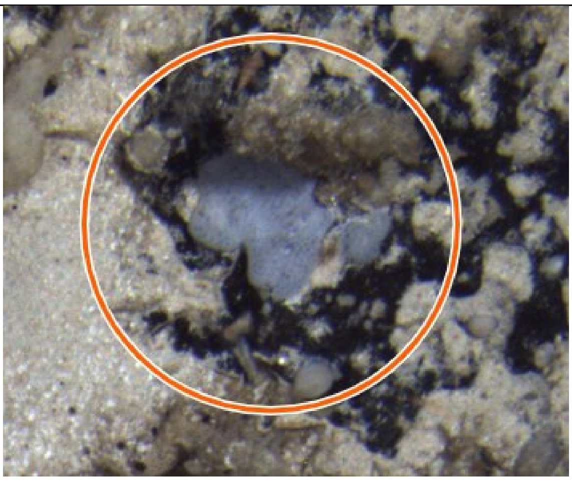
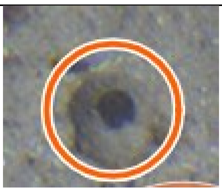
OTU Code	**Description in SIMPER table(s)**	**Image**
AB01	Hard-bottom *Caryophyllia* spp.	
AB114	Soft-bottom Caryophyllidae	
AB174	Actiniaria 4	

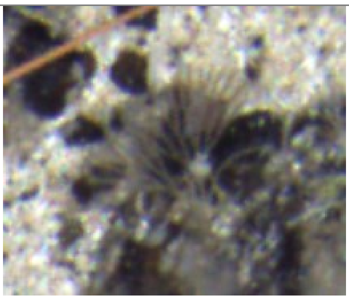
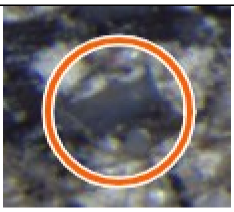
AB198	Actiniaria 3	
AB199	Reef-associated Ophiuroidea	
AB205	Cidaroida	

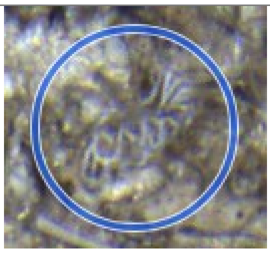
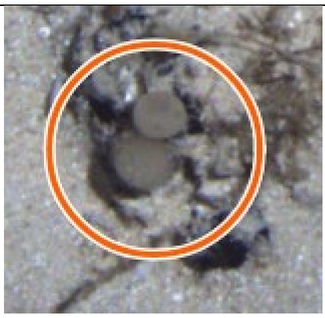
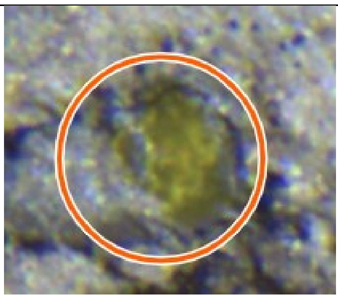
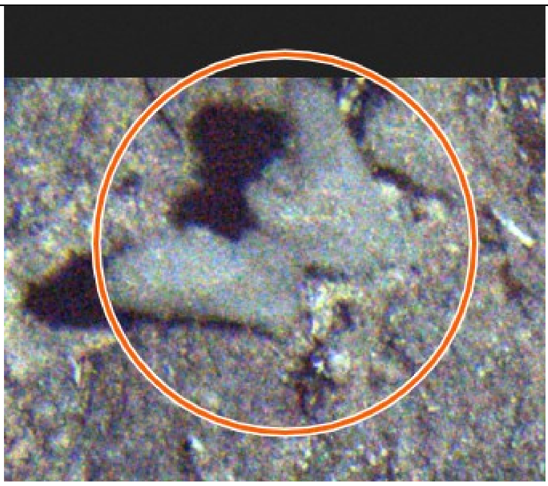
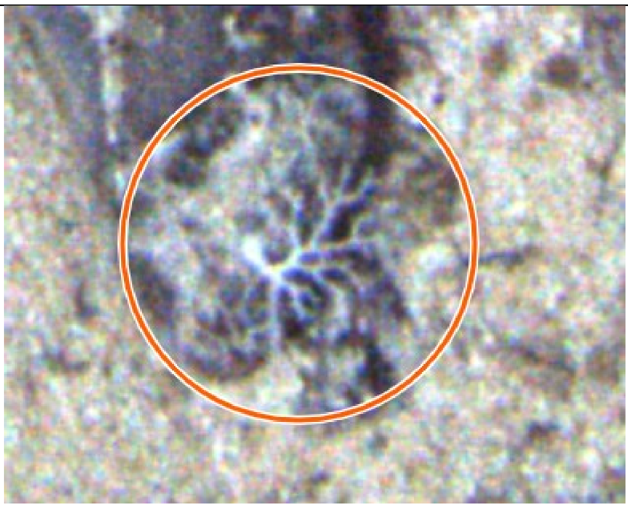
AB235	*Ophiomusium* sp.	
AB24	*Thouarella* spp.	
AB287	Gastropoda 2	

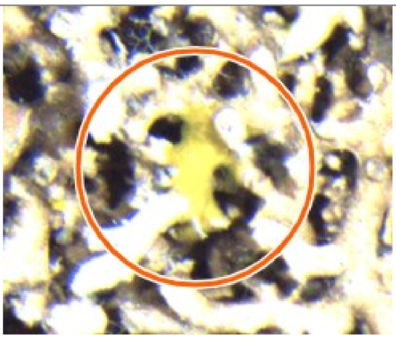
AB294	Serpulidae	
AB298	Bryozoan 2	
AB300/179 (merged)	Decapoda	

AB315	SF sponge 5	
AB346	Galatheoidea	
AB418	Brachiopoda	
AB433	Gastropoda 1	
AB48	Hydroid 2	

AB567	Hydroid 1	
AB568	Zoantharia	
AB569	Actiniaria 1	
AB571	EC sponge 2	
AB579	SF sponge 4	

AB582	Hydroid 3	
AB583	EC sponge 1	
AB585	Bivalvia 1	
AB586	SF sponge 3	
AB587	Hormathiidae	

AB591	Bryozoan 1	
AB596	SF sponge 1	
AB62	EC sponge 3	
AB633	SF sponge 2	
AB696	Stylasteridae 1	

AB726	EC sponge 4	

APPENDIX D

D.1 North Atlantic temperature layers

Generalised Additive Models (GAMs) were used to create bottom temperature and bottom salinity raster grids, at a resolution of 200 m. The temperature and salinity models were built using data obtained from ROV and drop-frame CTD probes, as well as additional CTD profiles obtained from the British Oceanographic Data Centre (BODC).

The geographic extent of the bathymetry encompasses two distinct water masses; North Atlantic and Arctic Bottom Water. These two water masses are geographically separated by the Wyville Thomson Ridge (WTR) at the northern end of the Rockall Trough basin, with the two water masses interacting and mixing periodically over the WTR. For the purpose of building more accurate temperature and salinity models, each water mass (and consequently north and south of the ridge) was modelled separately.

Table D. 1: Data used to build bottom temperature and salinity models. CTD data obtained from cruises marked with an asterisk (*) were not owned by the authors but obtained from the British Oceanographic Data Centre (BODC) archive. Model refers to the response (temperature or salinity) and geographic location (north or south of the Wyville Thomson Rudge).

Data Source/Cruise	No. of points	Type	Location
Model: Temperature South			
2009/03-JNCC	38,727	Drop-frame CTD probe	Anton Dohrn Seamount
Cruise 01-07-01	852	ROV CTD probe	Canyons MCZ
Cruise: D183* CTD: 118707	561	CTD profile	Rockall Plateau (-20.0645, 56.016)
Cruise: D184* CTD: 11892#3	271	CTD profile	Edoras Bank (-20.6495, 55.7023)
Cruise: D233* CTD: 13493	547	CTD profile	Lórien Knoll (-19.9977, 54.4995)
Cruise: CD62* CTD: 62016	571	CTD profile	Fangorn Bank (-20.0025, 55.2018)
Cruise: CD62* CTD: 62017	689	CTD profile	Fangorn Bank (-19.9825, 55.7787)
Cruise: CD62* CTD: 62018	587	CTD profile	Rockall Plateau (-20.0117, 56.3562)
Cruise: CD62* CTD: 62084	450	CTD profile	Rockall Plateau (-17.992, 57.0275)
Deep Links (JC136) – points south of the WTR.	968,208	ROV CTD probe	George Bligh Bank, North of Rockall Bank, Anton Dohrn Seamount
Eurofleets (CE15011)	135,385	ROV CTD probe	George Bligh Bank, North of Rockall Bank, Porcupine Bank, Porcupine Seabight, Rockall Plateau
SEA/SAC Survey 2007	275,156	ROV CTD probe	George Bligh Bank, Hatton Bank, Rosemary Bank
JC060	31,083	ROV CTD probe	North Rockall Bank, Hatton-Rockall Basin, Darwin Mounds
SeaRovers 2017 (CE17009)	1,412,129	ROV CTD probe	Porcupine Bank
Model: Temperature North			

SEA/SAC Survey 2007	38,251	ROV CTD probe	West Shetland Channel (WSC)
Model: Salinity South			
Deep Links (JC136) – points south of the WTR.	994,234	ROV CTD probe	George Bligh Bank, North of Rockall Bank, Anton Dohrn Seamount
Eurofleets (CE15011)	139,443	ROV CTD probe	George Bligh Bank, North of Rockall Bank, Porcupine Bank, Porcupine Seabight, Rockall Plateau
SeaRovers 2017 (CE17009)	191,903	ROV CTD probe	Porcupine Bank
Model: Salinity North			
Cruise: 0511S*	1441	CTD Profile	61.9005, -05.7545 60.4167, -04.3132
Cruise: 0610S*	1053	CTD Profile	60.218, -5.9535
Cruise: 0709S*	1089	CTD Profile	60.7170, -5.1005 60.2998, -4.0765
Cruise: 0811S*	214	CTD Profile	60.676, -2.8803
Cruise: 1096S*	1400	CTD Profile	61.7345, -3.2652
Cruise: 1211S*	261	CTD Profile	61.0327, -5.9483
Cruise: 1309S*	3036	CTD Profile	60.0437, -5.384
Cruise: 1312S*	1220	CTD Profile	61.3848, -3.7018
Cruise: 1402S*	1631	CTD Profile	61.1878, -3.0985
Cruise: 1609S*	969	CTD Profile	61.585, -04.2505
Cruise: 1611S*	165	CTD Profile	61.8153, -5.3537
Cruise: 2302H*	507	CTD Profile	60.6632, -4.6747

For each region, multiple bottom temperature and salinity GAMs were constructed using the "gam" function from the "mgcv" package. Different combinations of variables (depth, latitude, longitude) and parameters (knots) were trailed to identify the best performing model. Model performance was evaluated by assessing the GCV score and deviance explained. The best performing GAMs were selected (Table D.2) and used to predict onto the bathymetry raster, gridded at 200 m. The north and south temperature and salinity models were then merged, creating final bottom temperature and salinity raster grids.

Table D.2: Metrics of the final GAMs selected for each region. K values indicate the number of knots applied to a model term by the smoothing term.

Model	**Formula**	**GCV Score**	**Deviance Explained (%)**	**Degrees of Freedom**
Temperature North	temp ~ s(depth, k=5)	0.050008	99.30	4, 29
Temperature South	temp ~ s(depth, k = 4) + s(lat, long)	0.05328	97.60	4, 29
Salinity North	sal ~ s(depth) + s(lat, long)	0.00054605	96.30	9, 29
Salinity South	sal ~ s(depth) + s(lat, long)	0.00054605	96.30	9, 29

D.2 North Atlantic biological data

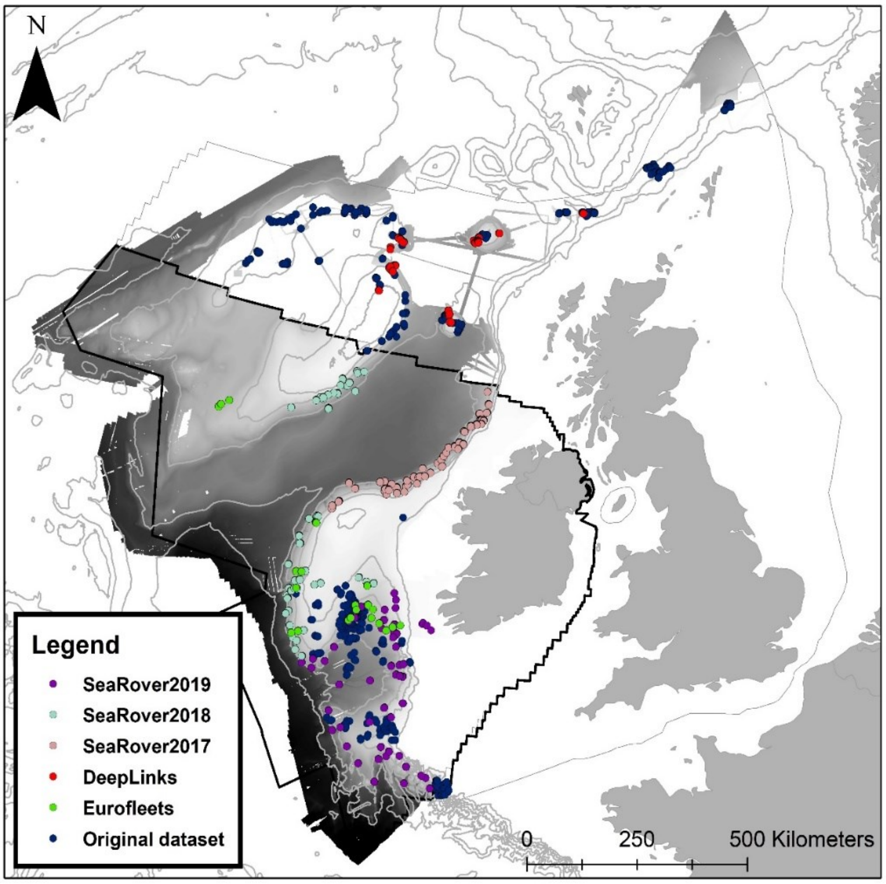


Figure D.1: Map of the UK and Ireland's Extended Continental Shelf claim limits showing the full dataset used to build the model described in Chapter 4. Original dataset refers to data described in Ross & Howell (2013) and Ross et al. (2015). Data is plotted by presence-absence in Chapter 4. High-resolution bathymetry shown is described in the Chapter text.

D.3 Individual generalised additive models (GAMs)

To determine their explanatory power and whether environmental variables were individually significant, binomial GAMs were fitted, using four knots and a gamma of 1.4 to reduce the over-fitting (Kim & Gu, 2004). All variables were individually significant in explaining deviance in the presence-absence data (Table D.3), with bathymetry (depth) and temperature explaining the most. Confidence intervals for individual GAMs are plotted in Figure D.2.

Table D.3: Metrics for individual GAMs fitted to presence-absence data.

Variables	**p-value**	**Adj. R^2**	**Deviance Explained (%)**	**UBRE**
Bathymetry	<0.001	0.091	20.1	-0.59610
BBPI	<0.001	0.021	3.74	-0.51353
Curvature	<0.001	0.036	5.54	-0.52253
FBPI	<0.001	0.053	7.79	-0.53379
Plan Curve	<0.001	0.047	6.16	-0.52564
Profile Curve	<0.001	0.019	3.16	-0.51093
Rugosity	<0.001	0.051	9.46	-0.54225
Salinity	<0.001	0.013	3.71	-0.51350
Slope	<0.001	0.012	3.43	-0.51190
Temperature	<0.001	0.074	18.4	-0.58750

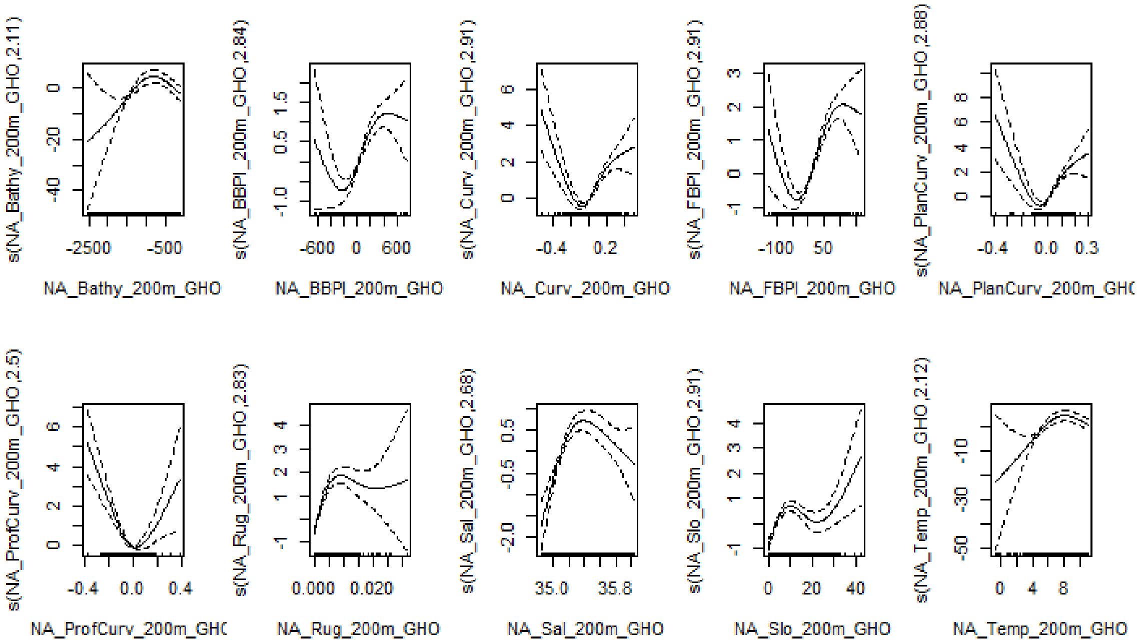


Figure D.2: Confidence intervals for individual GAMs fitted to the presence-absence data.

D.4 Correlation of variables

Pearson's correlation matrices were calculated, and where pairs of environmental variables scored coefficients ≥±0.7, one correlate was removed to reduce collinearity within the data (Table D.4). Decisions regarding which variable to remove was based on the individual significance of the variable and ecological relevance of one correlate over the other, based on expert opinion. Where this was not clear cut, the correlate to be removed was decided in the proceeding stepwise selection step.

Table D.4: Correlation matrix for habitat suitability model variables calculated in R. Coefficients ≥±0.7 are shown in bold

	Depth	BBPI	Curvature	FBPI	Plan Curvature	Profile Curvature	Rugosity	Salinity	Slope	Temperature
Depth	-	-	-	-	-	-	-	-	-	-
BBPI	0.336	-	-	-	-	-	-	-	-	-
Curvature	0.041	0.223	-	-	-	-	-	-	-	-
FBPI	0.120	0.511	**0.742**	-	-	-	-	-	-	-
Plan Curvature	0.019	0.114	**0.818**	0.554	-	-	-	-	-	-
Profile Curvature	-0.048	-0.253	**-0.897**	**-0.707**	-0.480	-	-	-	-	-
Rugosity	-0.074	0.117	0.285	0.323	0.287	-0.213	-	-	-	-
Salinity	0.462	0.140	0.075	0.096	0.045	-0.080	0.122	-	-	-
Slope	-0.262	0.028	0.054	0.059	0.061	-0.035	0.453	0.015	-	-
Temperature	0.636	0.336	0.070	0.134	0.048	-0.070	0.053	**0.707**	-0.084	-

D.5 Stepwise selection of variables

The combination of variables selected for the final habitat suitability model was determined using forward and backward stepwise selection of variables to construct the best performing model. For forward-stepwise selection, variables were systematically added to a GAM in the order of best ranking un-biased risk estimator (UBRE) score as determined by individual GAMs. The final model was determined when the addition of variables did not significantly improve the UBRE score, or when variables within the model were no longer statistically significant terms. Conversely, although a significant increase in UBRE score is desirable after the addition of a new model term, a smaller increase in UBRE does not mean that a variable is not important. Therefore, author's expert knowledge of the species, model extent and prior HSMs meant fine-scale bathymetric position index (FBPI) was also selected as a variable in the final model, despite it not significantly improving the UBRE score when added as a term. Where a variable of a highly correlated pairing – if not removed in the previous step – is first selected as a GAM term, its opposing correlate is rejected from any further analysis.

Backward-stepwise selection was carried out by firstly creating a GAM incorporating all non-correlated environmental variables. Non-significant model terms ($p > 0.05$) and terms with the lowest individual UBRE scores were systematically removed from the model. This continued until all variables within the model were statistically significant, or where overall model performance was significantly reduced by eliminating further variables. These selections were also confirmed as the best performing combination of variables using the "dredge" function from the MuMIn package (Barton, 2020).

Forward and backwards stepwise processes selected depth, temperature, rugosity and plan curvature as final variables (Table D.5); this selection was also confirmed using the “dredge” function. As discussed in the chapter, after initial trials depth was manually removed from the stepwise selection process to improve transferability of the final model across ocean basins with different water mass structures. Table D.5 outlines the minor drop in performance when depth is removed as an environmental variable.

Table D.5: Difference in GAM performance at the pre-selection stage when bathymetry (depth) is removed as a variables.

Variables	**UBRE**	**R^2**	**D%**
Bathymetry + Temperature + Rugosity + Plan Curvature + FBPI	-0.66197	0.229	34.6%
Temperature + Rugosity + Plan Curvature + FBPI	-0.64992	0.201	32.1%

D.6 Environmental comparison between the North and South Atlantic

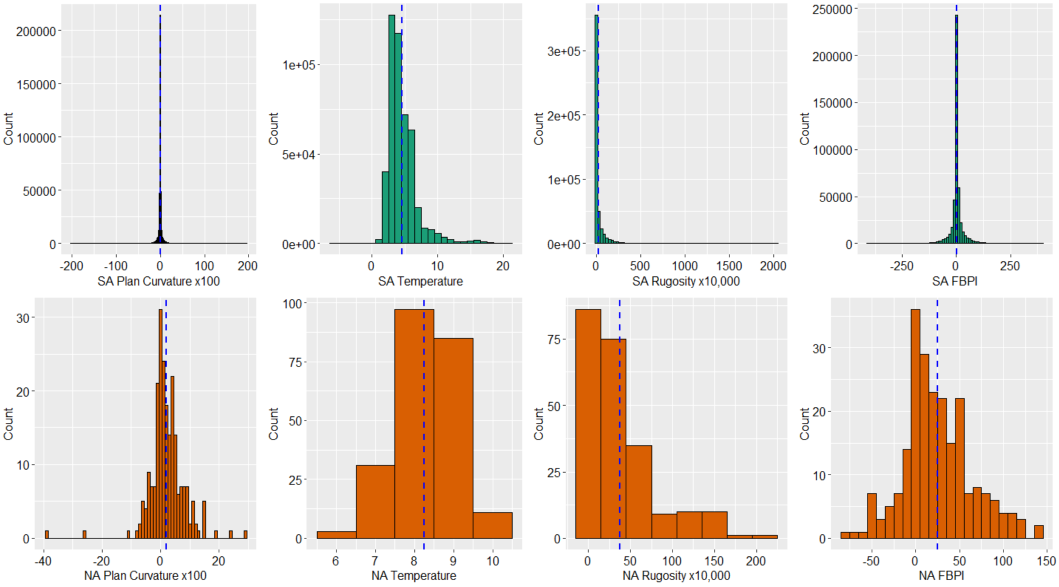


Figure D.3: Model variable histograms for North Atlantic (NA) presence data and South Atlantic (SA) model (presence, absence and masked areas) data.

D.7 South Atlantic temperature layers

Data from the British Oceanographic Data Centre (BODC) for the total area in Figure D.4 were combined with CTD data collected aboard cruises to the UKOT of Ascension Island, Saint Helena and Tristan da Cunha (JR287, JR684, JR-NG, JR17004 and DY100; Figure D.5). The area in question was split into six tiles to reduce computational power required to build the temperature models (Figure D.4). Initially, Tile D2 and E were combined, but Tile E was later separated because the Algulhas current represents a different biogeographic region from the rest of Tile D2.

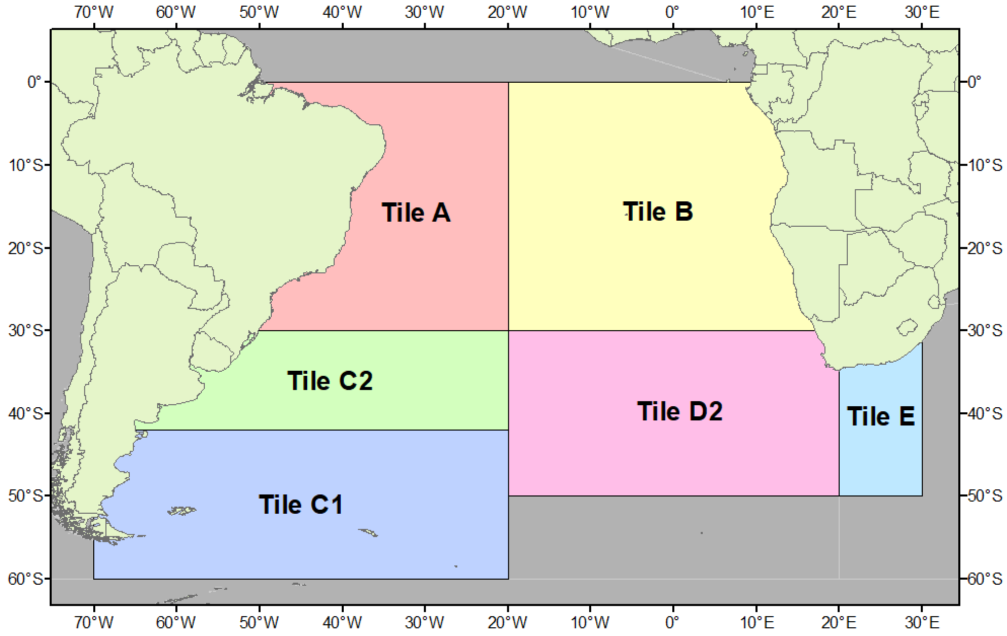


Figure D.4: Methodology used to split the South Atlantic Ocean into six tiles.

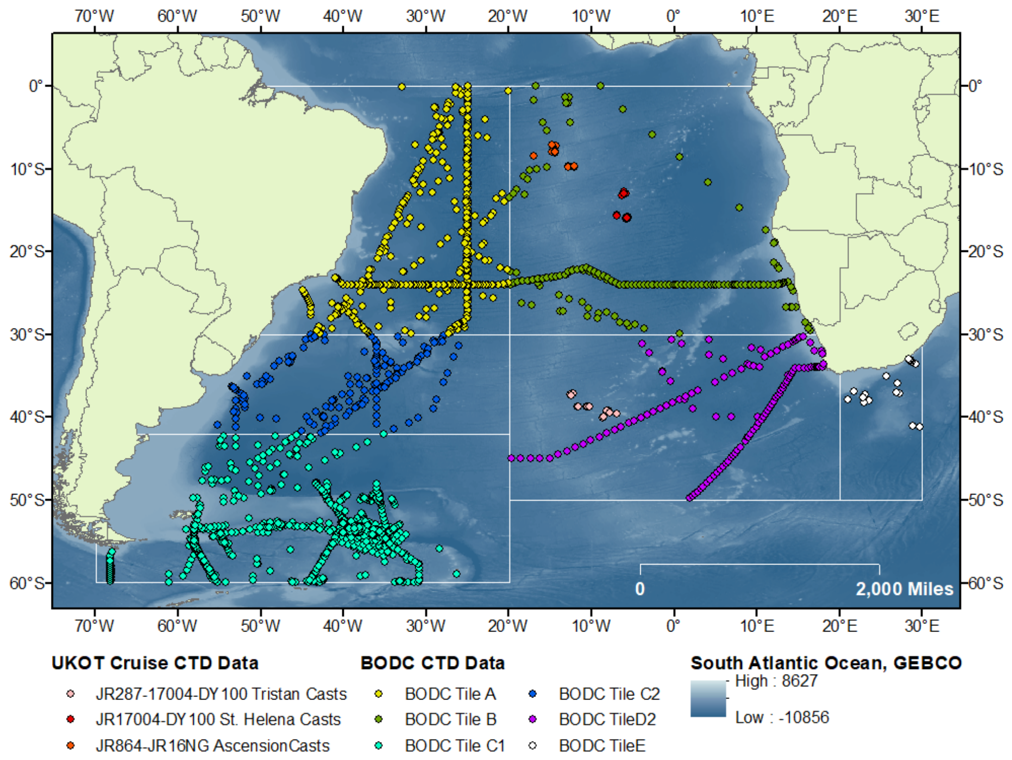


Figure D.5: CTD data from the UKOT cruises and BODC database plotted on the South Atlantic Ocean. White lines show Tie outlines from Figure D.4.

For each tile, *in-situ* temperature data were partitioned into training and test datasets at an 80/20% split, respectively. Using the 'mgcv' R package (Wood, 2011), depth, latitude and longitude were each tested individually to ascertain whether they were significant predictors of temperature. Combinations of predictors were trialled for each tile, and for five (Tiles A, B, C1, C2 and D2) final models, depth, latitude and longitude were used as predictors. For the model within Tile E, only depth and longitude were used as predictors of temperature. Confidence intervals for all models plot tightly suggesting a reliable model (Figure D.6 – Figure D.11).

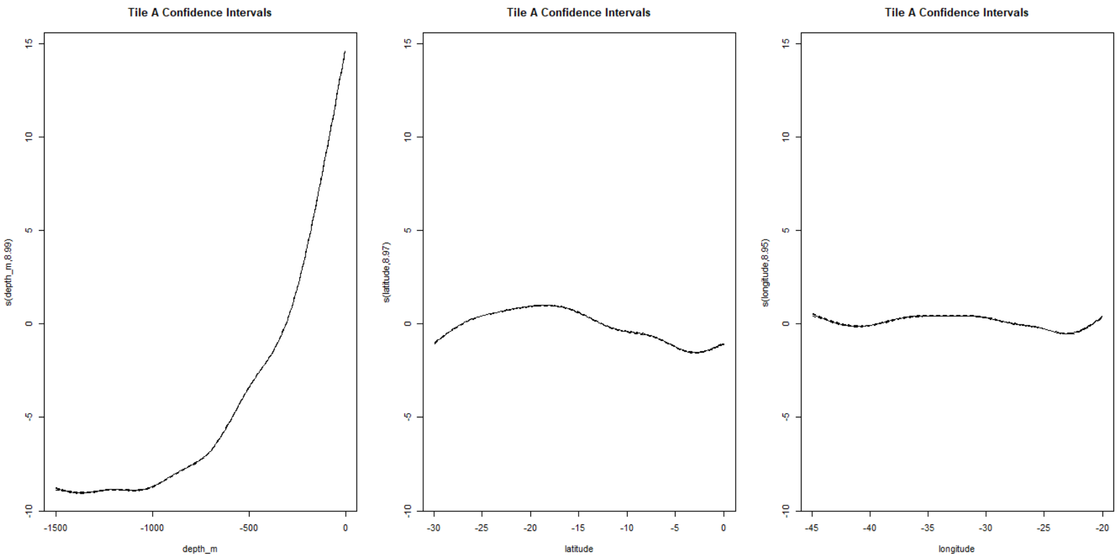


Figure D.6: Confidence intervals for (L-R) depth, latitude and longitude for tile A.

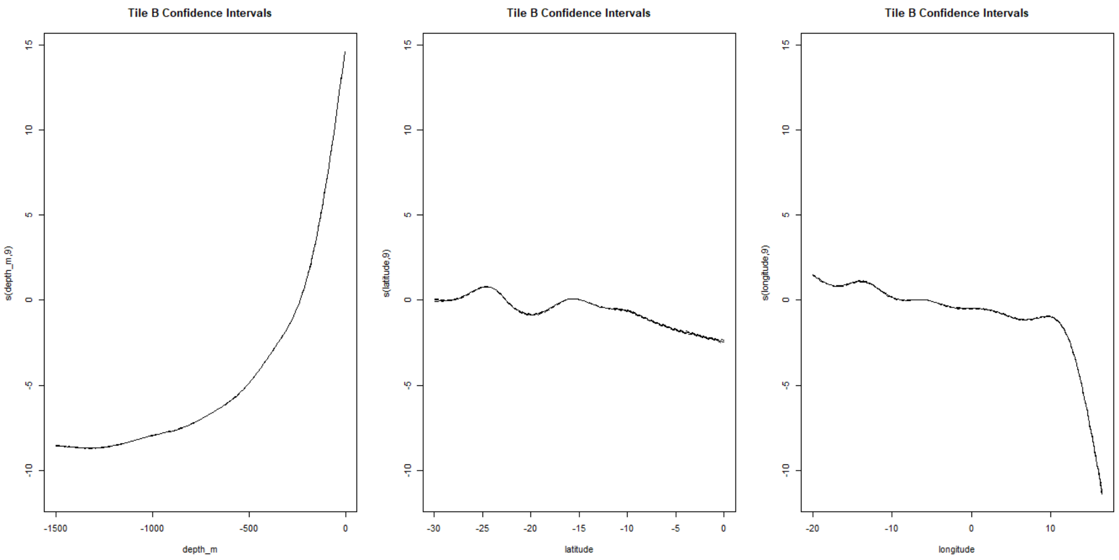


Figure D.7: Confidence intervals for (L-R) depth, latitude and longitude for tile B.

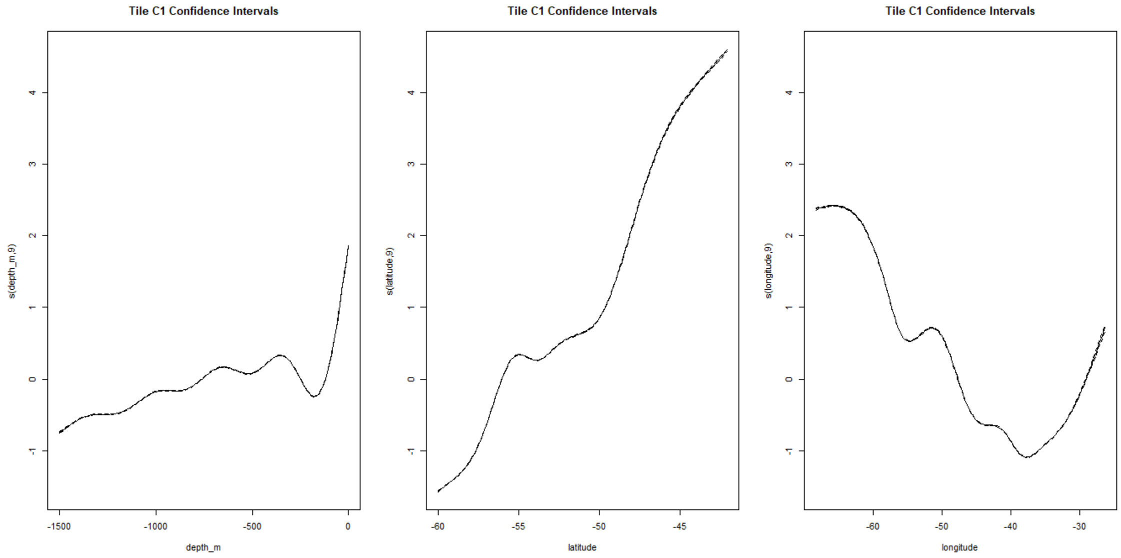


Figure D.8: Confidence intervals for (L-R) depth, latitude and longitude for tile C1.

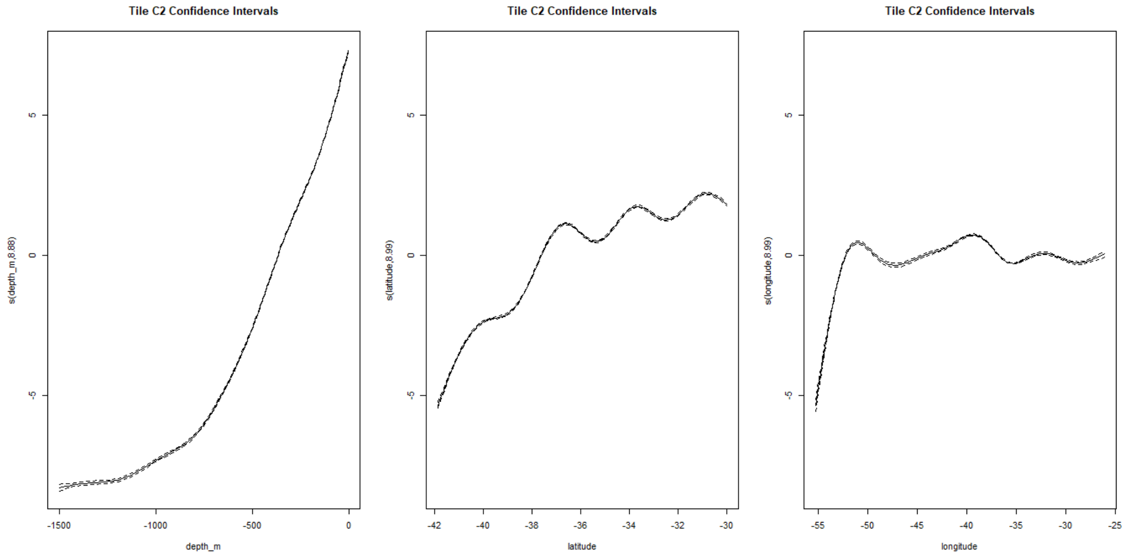


Figure D.9: Confidence intervals for (L-R) depth, latitude and longitude for tile C2.

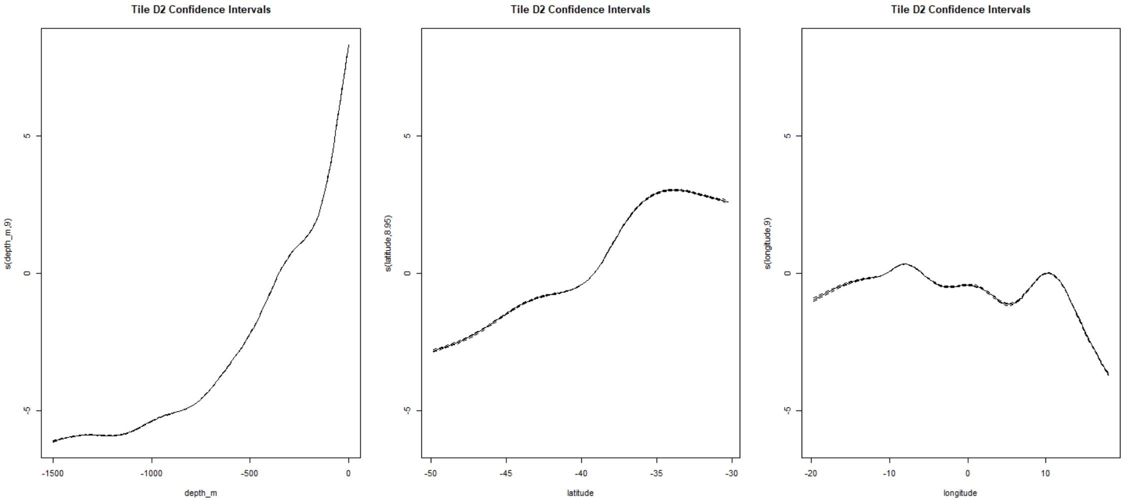


Figure D.10: Confidence intervals for (L-R) depth, latitude and longitude for tile D2.

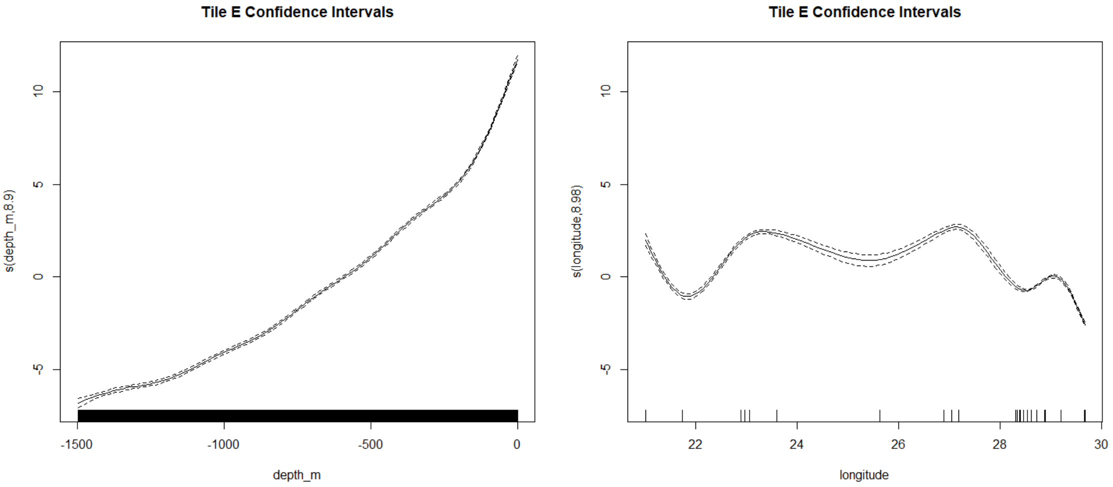


Figure D.11: Confidence intervals depth (left) and longitude (right) for tile E.

When the predicted values of each model built with the 80% training dataset are compared against the reserved 20% test *in-situ* values, strong Pearson's correlations are reported (Table D.6). Predicted vs. observed predictions are represented graphically in Figure D.12 – Figure D.17.

Table D.6: Pearson's correlation coefficients for each temperature tile. Correlations calculated between randomly selected training (80%) and test (20%) data.

Tile code	**Pearson's correlation coefficient between training and test datasets (2 d.p.)**
A	0.97
B	0.99
C1	0.82
C2	0.95
D2	0.98
E	0.95

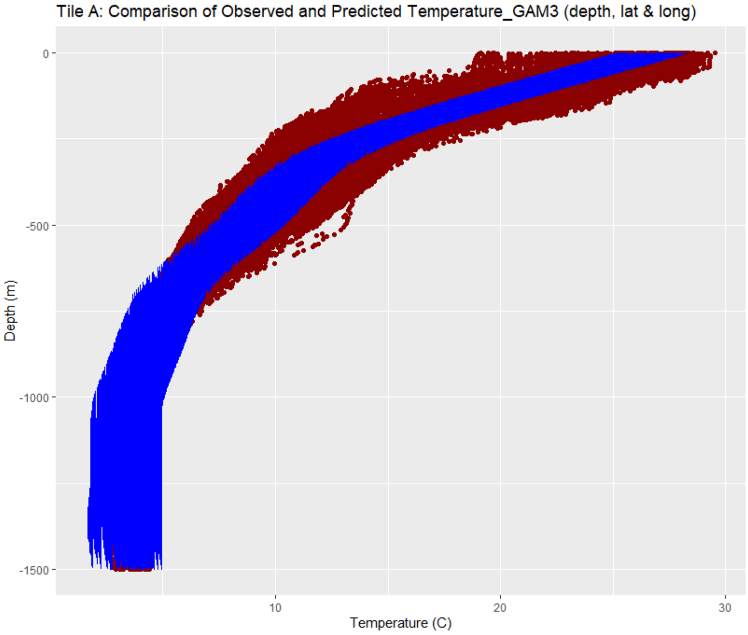


Figure D.12: Observed temperatures from CTD casts in tile A are plotted in red and the corresponding temperatures as predicted by the GAM are represented by the blue line.

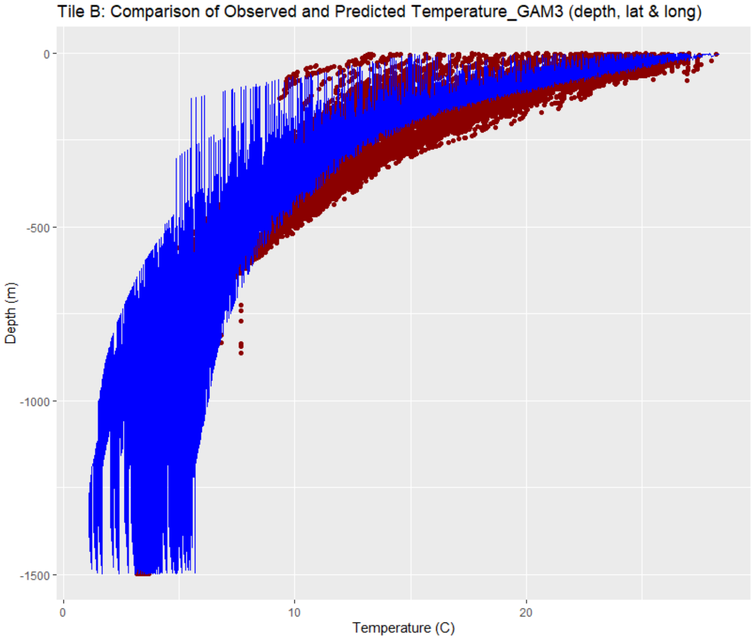


Figure D.13: Observed temperatures from CTD casts in tile B are plotted in red and the corresponding temperatures as predicted by the GAM are represented by the blue line.

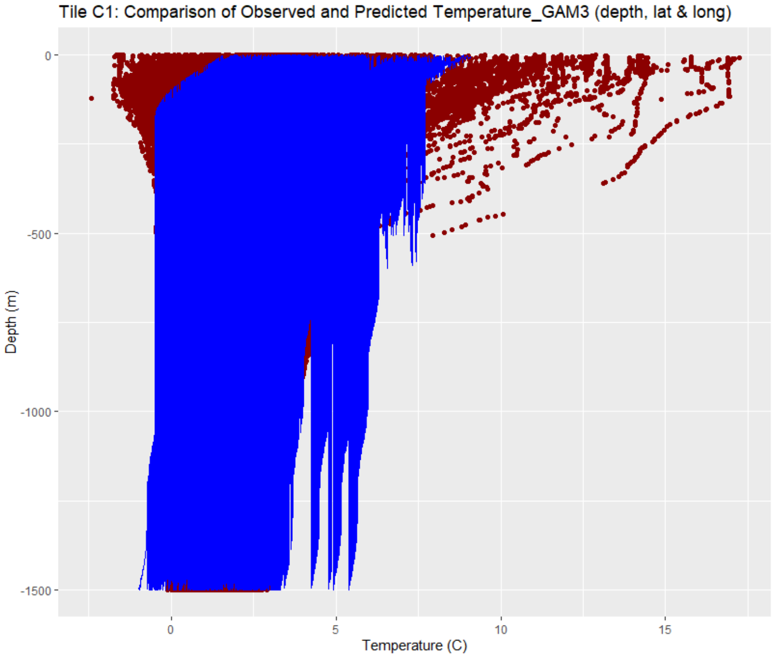


Figure D.14: Observed temperatures from CTD casts in tile C1 are plotted in red and the corresponding temperatures as predicted by the GAM are represented by the blue line.

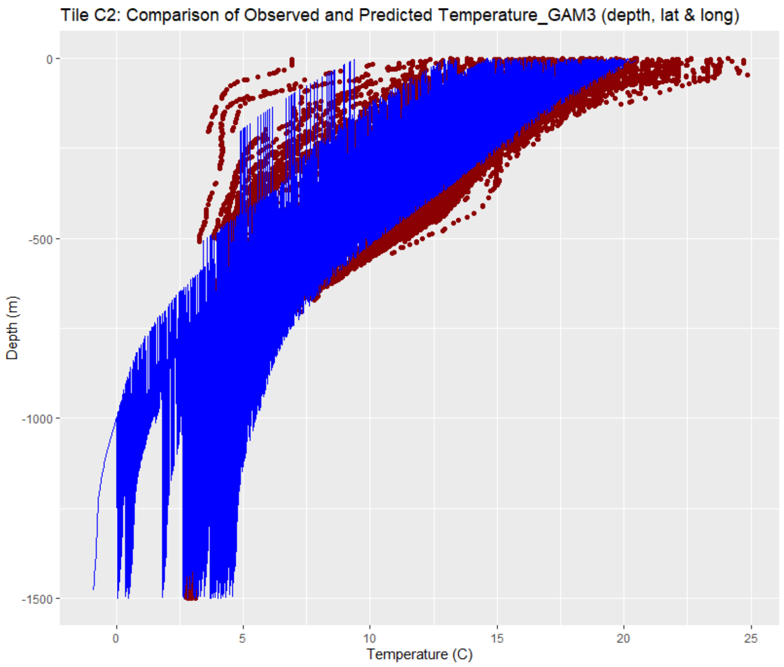


Figure D.15: Observed temperatures from CTD casts in tile C2 are plotted in red and the corresponding temperatures as predicted by the GAM are represented by the blue line.

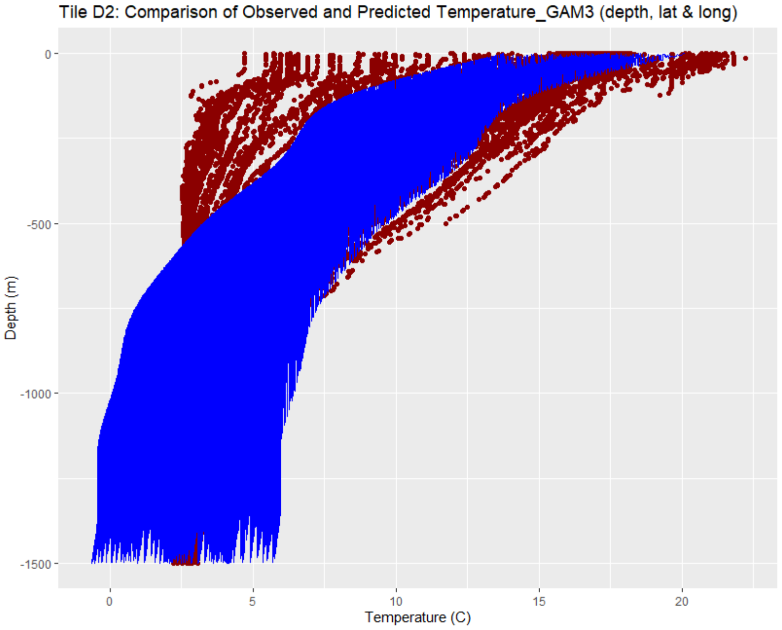


Figure D.16: Observed temperatures from CTD casts in tile D2 are plotted in red and the corresponding temperatures as predicted by the GAM are represented by the blue line.

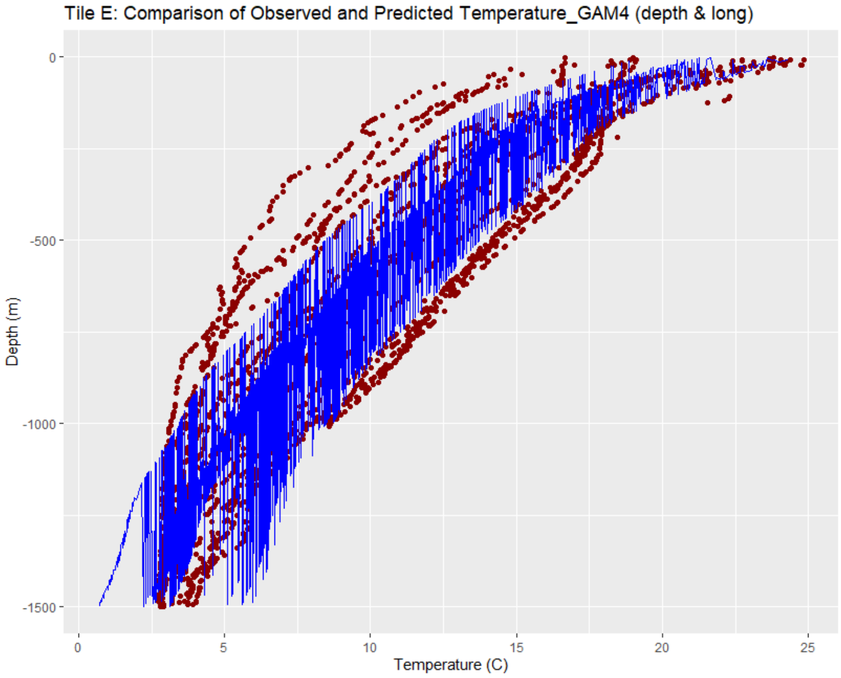


Figure D.17: Observed temperatures from CTD casts in tile E are plotted in red and the corresponding temperatures as predicted by the GAM are represented by the blue line.

D.8 Splitting of basin for bathymetric calculations

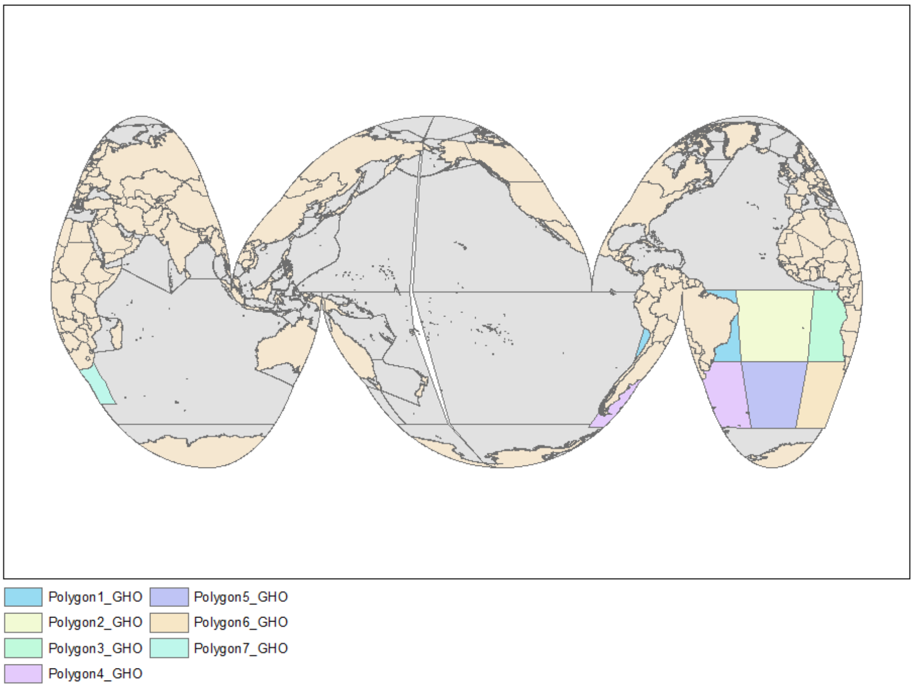


Figure D.18: Splitting of basin for bathymetric calculations.

D.9 MaxEnt jackknife plots and response curves

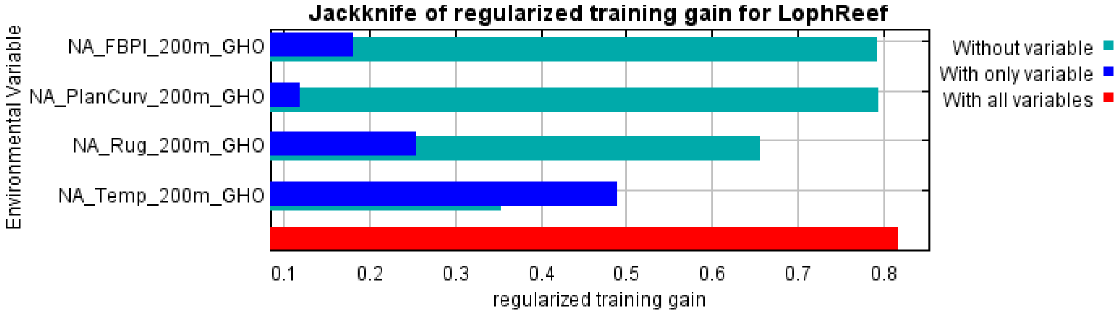


Figure D.19: MaxEnt jackknife plots for the final model showing relative importance of each variable in the model.

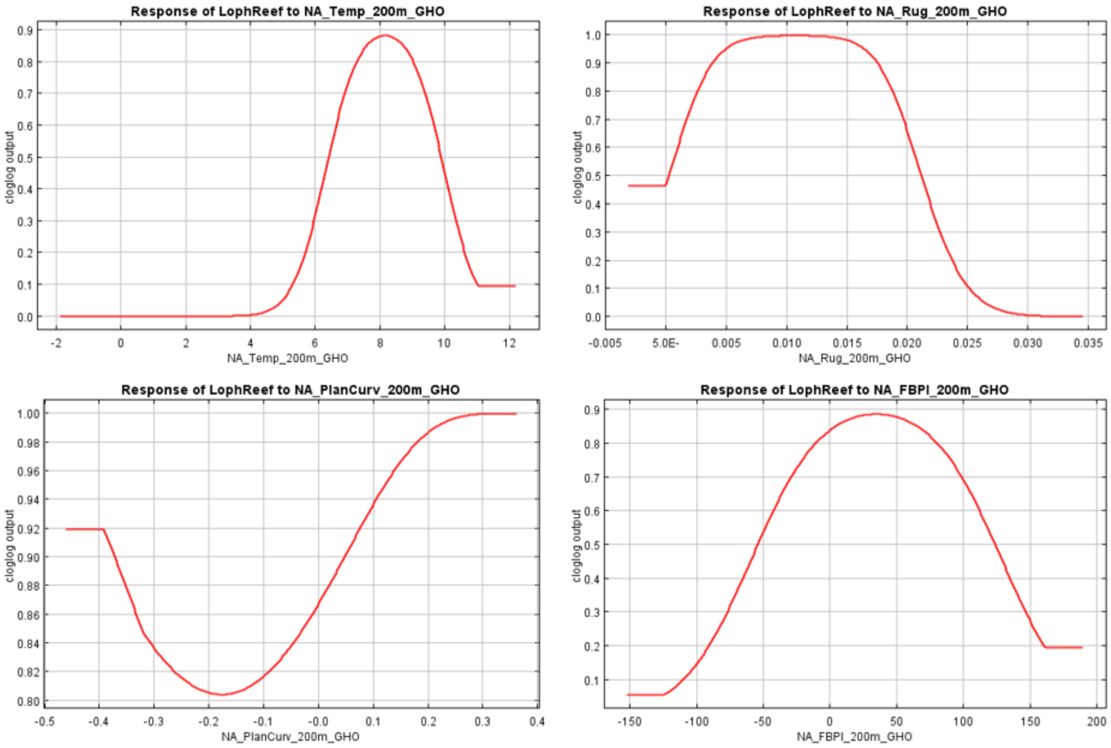


Figure D.20: Response curves for each environmental variable from the final MaxEnt model.

D.10 Presence histograms for each variable

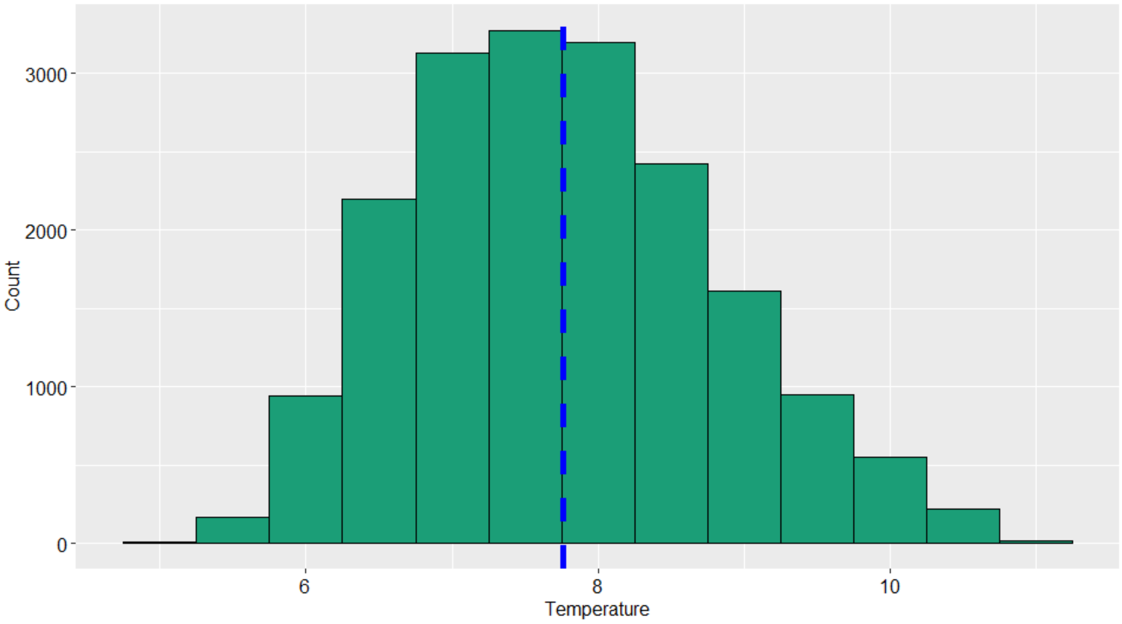


Figure D.21: Histogram of temperature for predicted presences in the South Atlantic. The blue dashed line represents the mean at 7.76 °C.

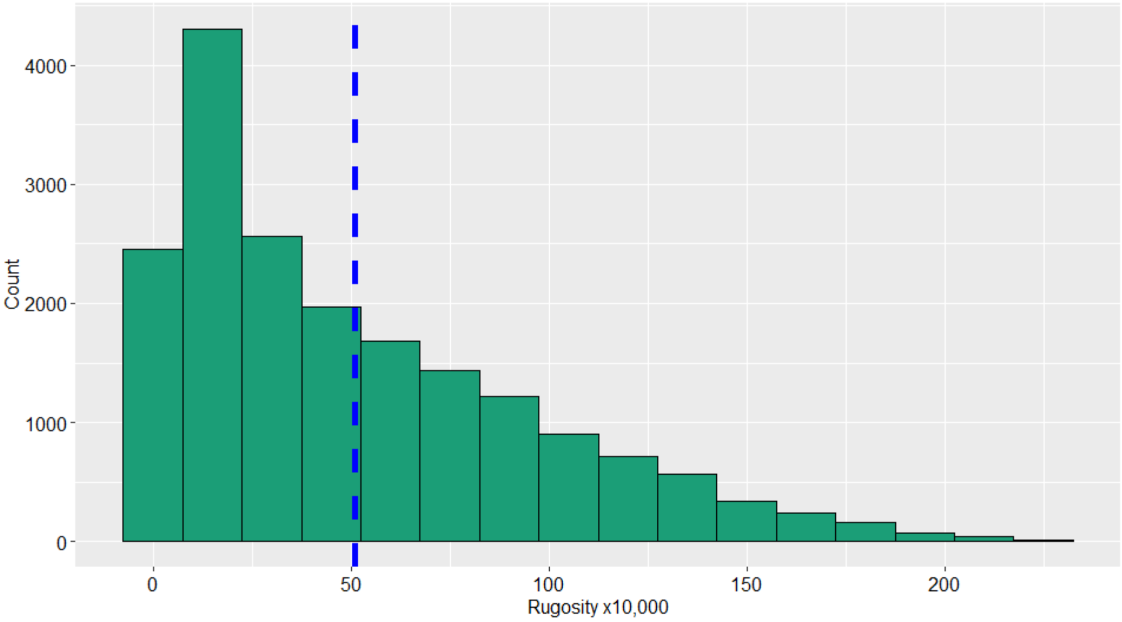


Figure D.22: Histogram of rugosity x10,000 for predicted presences in the South Atlantic. The blue dashed line represents the mean at 51.03 (therefore real mean is 0.005103).

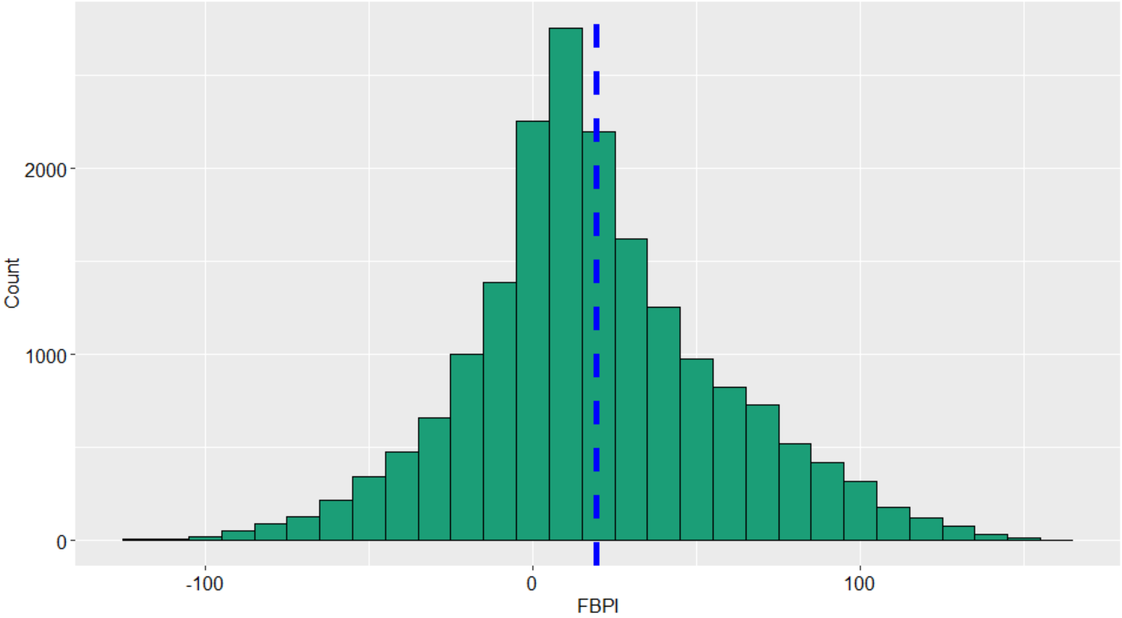


Figure D.23: Histogram of fine-scale bathymetric position index (FBPI) for predicted presences in the South Atlantic. The blue dashed line represents the mean at 19.50.

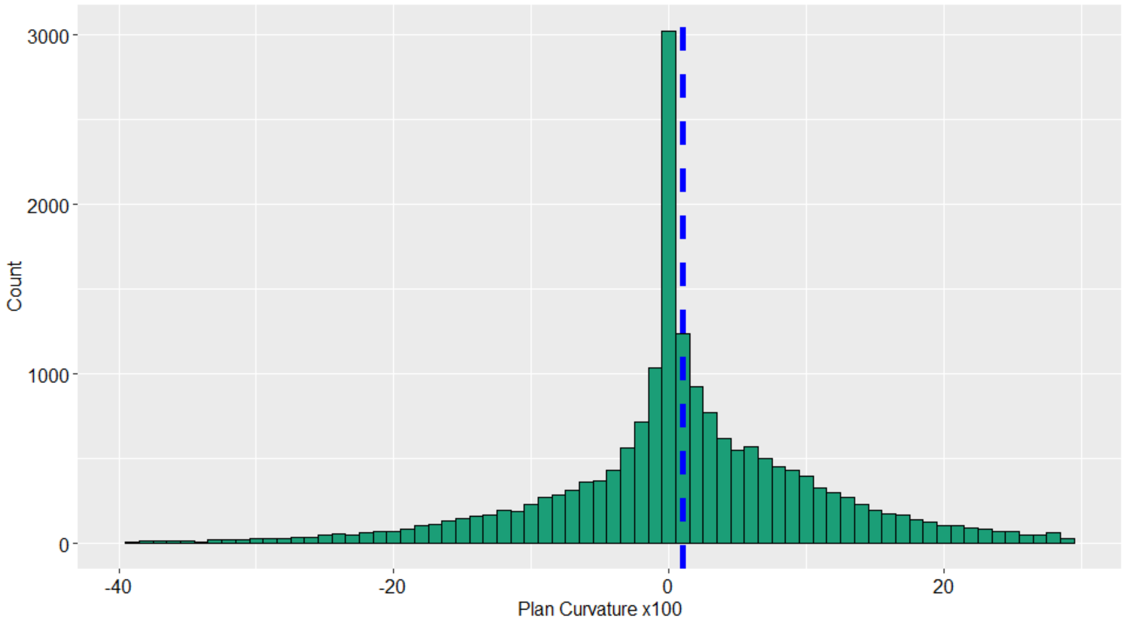


Figure D.24: Histogram of plan curvature x100 for predicted presences in the South Atlantic. The blue dashed line represents the mean at 0.99 (therefore real mean is 0.0099).

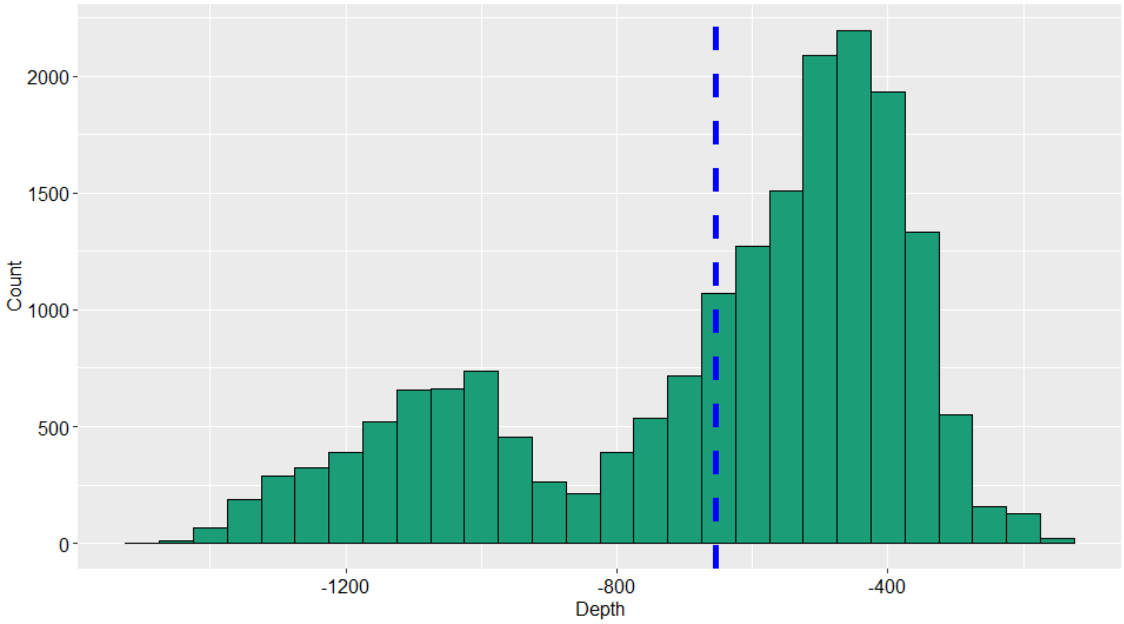


Figure D.25: Histogram of depth for predicted presences in the South Atlantic. The blue dashed line represents the mean at 654.48 m

APPENDIX E

E.1 Calinski-Harabasz Index

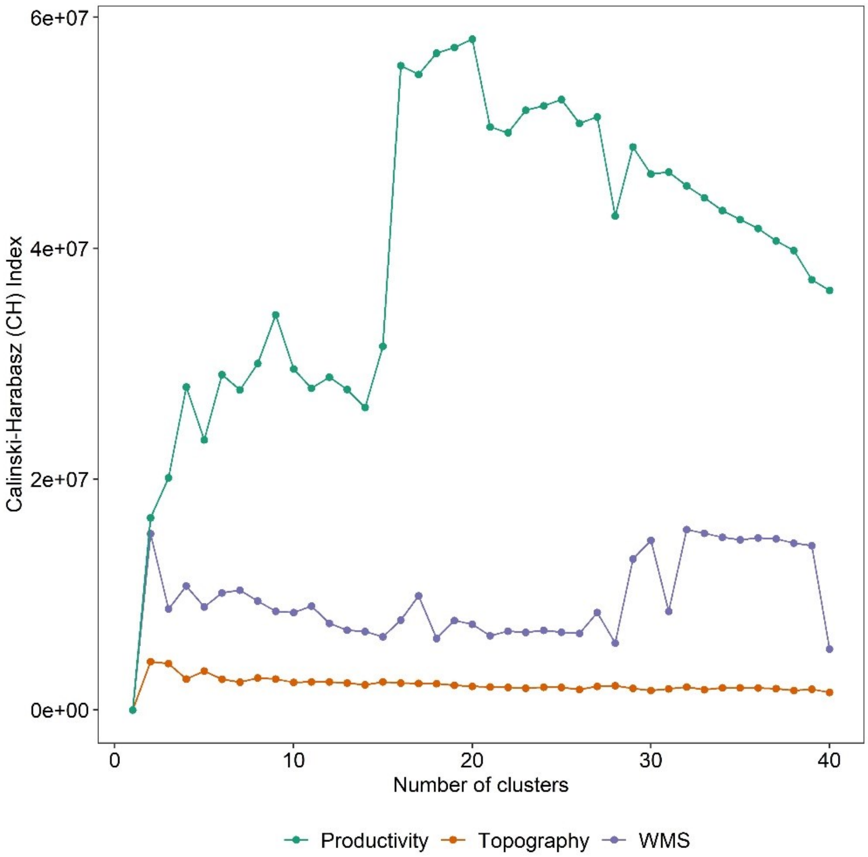


Figure E.1: Calinski-Harabasz (CH) index for each variable/class of variables.

E.2 Water mass structure details

Table E.1: Temperature and salinity summary values for each water mass structure cluster.

Variable	**Min**	**Max**	**Mean**	**Description**
Temperature	-1.8	-0.5	-0.8	1, offshore
Salinity	32.2	35.0	34.8	1, offshore
Temperature	-1.2	0.37	-0.1	2, offshore
Salinity	31.9	35.1	34.6	2, offshore
Temperature	0.3	1.0	0.7	3, offshore
Salinity	31.7	35.1	34.7	3, offshore
Temperature	-1.7	10.1	0.3	4, offshore
Salinity	5.0	32.2	25.8	4, offshore
Temperature	1.0	2.5	1.3	5, offshore
Salinity	31.0	35.1	34.7	5, offshore
Temperature	1.6	2.6	2.0	6, offshore
Salinity	32.0	35.2	34.8	6, offshore
Temperature	2.4	5.3	3.4	7, offshore
Salinity	29.1	35.6	34.6	7, offshore
Temperature	4.9	9.9	6.9	8, inshore
Salinity	29.2	36.7	34.4	8, inshore
Temperature	7.0	17.3	10.6	9, inshore
Salinity	13.0	36.8	32.6	9, inshore
Temperature	12.3	20.1	15.4	10, inshore
Salinity	23.5	40.7	36.4	10, inshore
Temperature	20.1	31.4	26.1	11, inshore
Salinity	9.9	40.4	34.5	11, inshore
Temperature	20.1	30.2	25.0	12, inshore
Salinity	35.8	40.8	39.4	12, inshore

E.3 Topography comparison

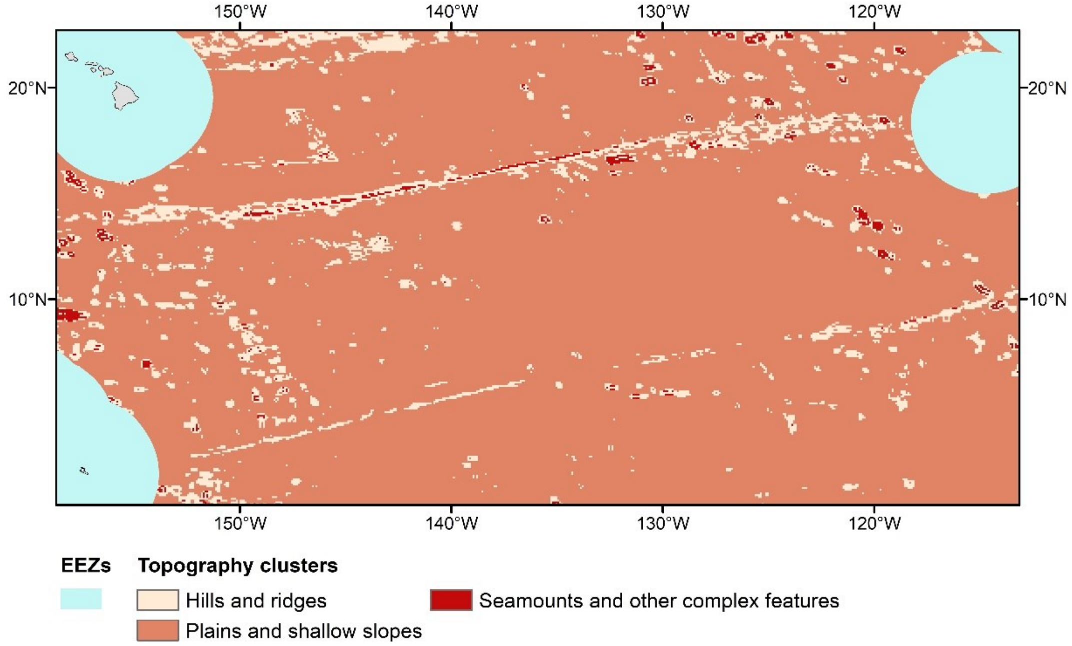


Figure E.2: Topography input layer from this study for extent of McQuaid *et al.*'s (2020) *classification of the CCZ.*

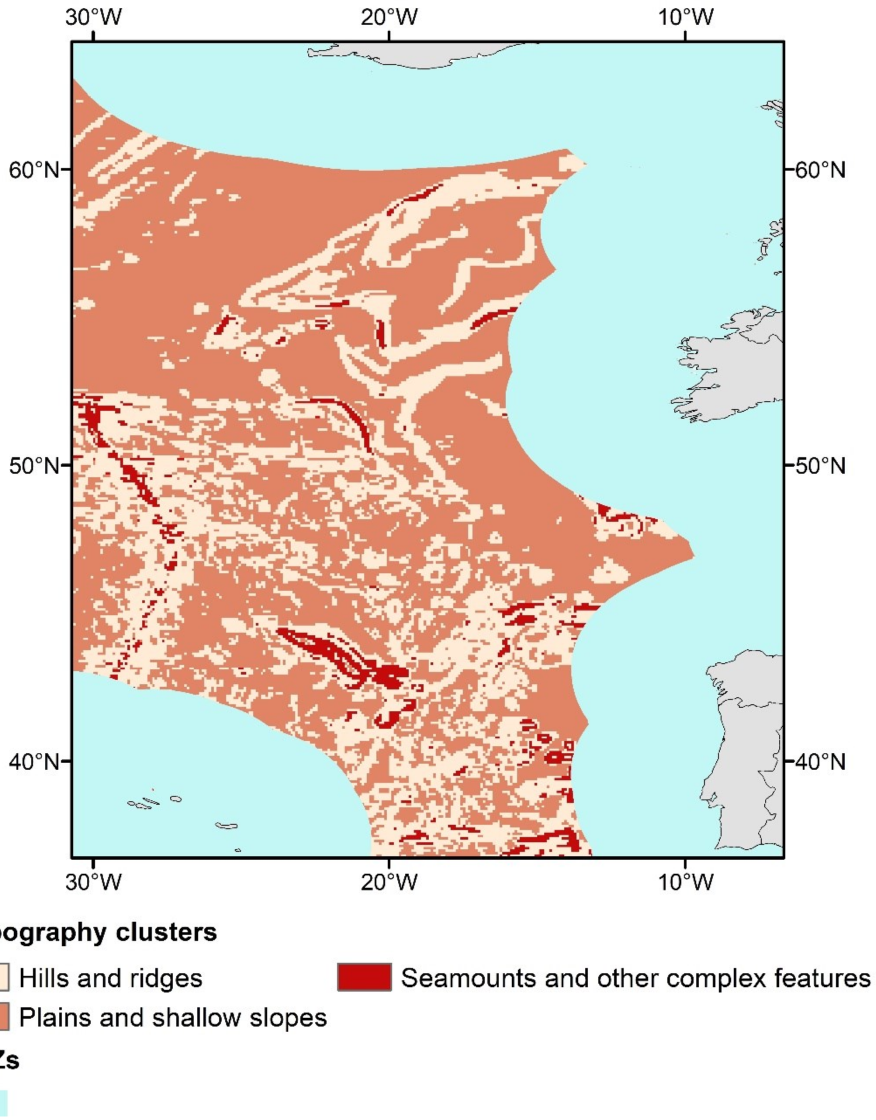


Figure E.3: Topography input layer from this study for extent of Evans *et al.'s* (2015) *classification of the northeast Atlantic.*

E.4 Porcupine Seabight

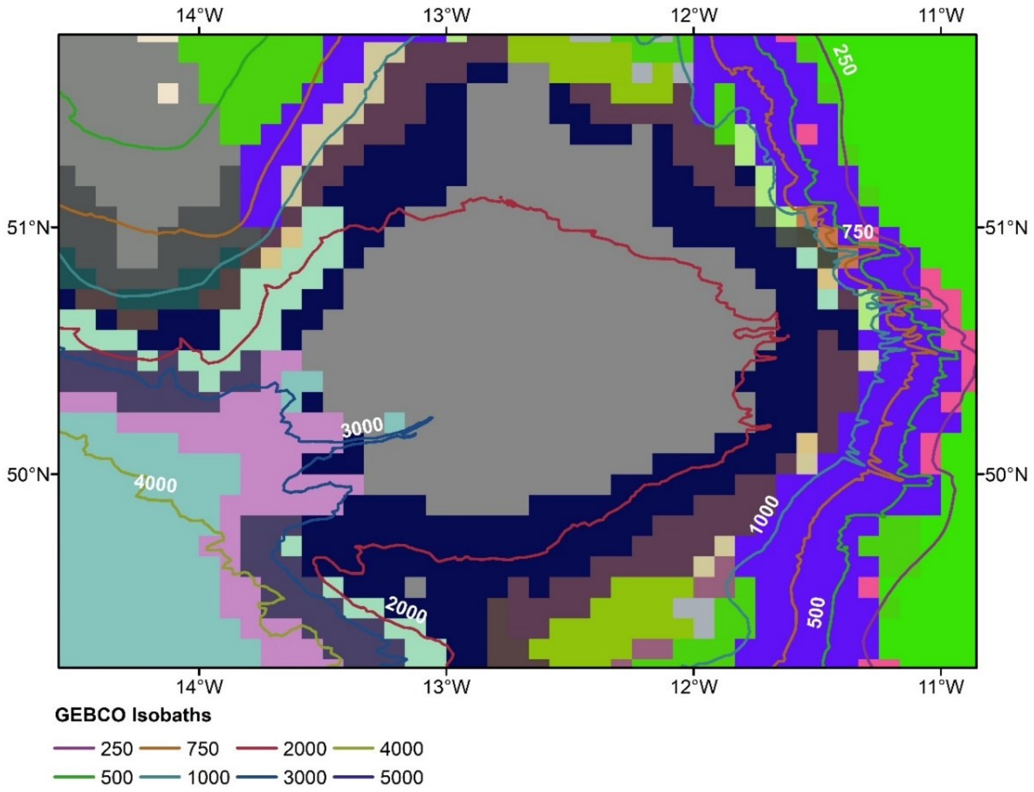


Figure E.4: Habitat classes for the PSB, northeast Atlantic. The upper slope zone is represented by the purple and pink band between the 250 and 750 m isobaths; the zone of rapid faunal change is represented by the quick succession of different habitat classes between the 750 and 1500 m isobaths; the large area represented by the single grey habitat class is considered the beginning of the lower bathyal zone just above the 2000 m isobath; the shift in communities just above the 3000 m isobath is considered the bathyal-abyssal overlap.

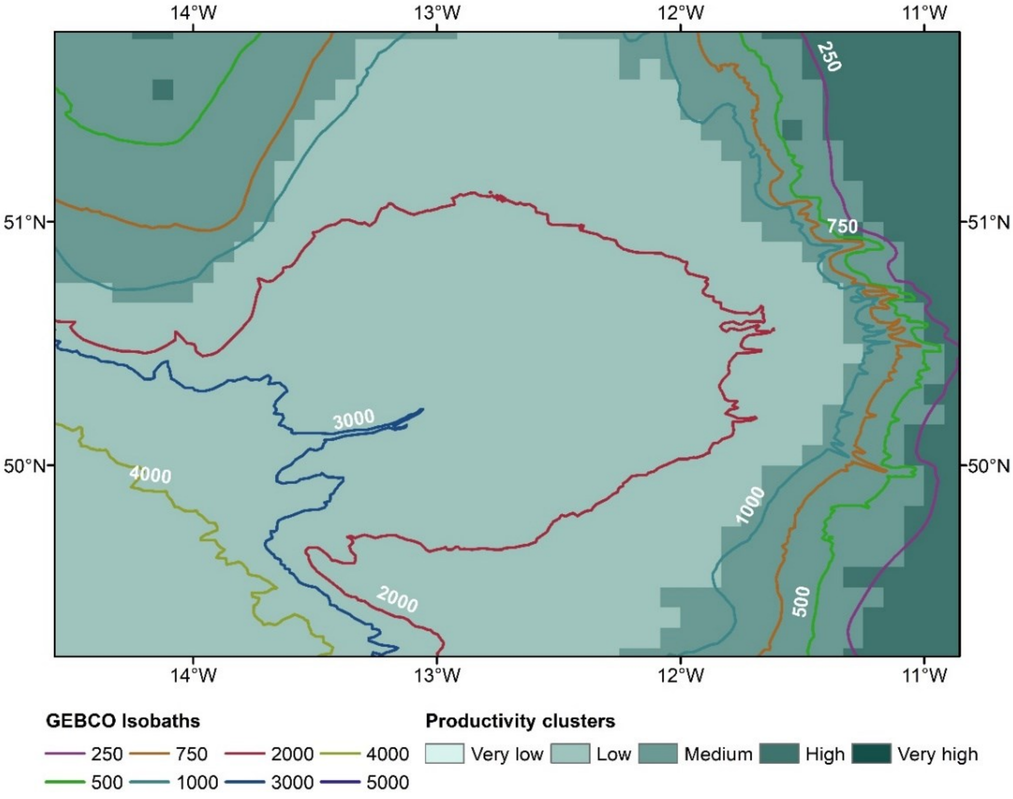


Figure E.5: Productivity classes for the Porcupine Seabight.

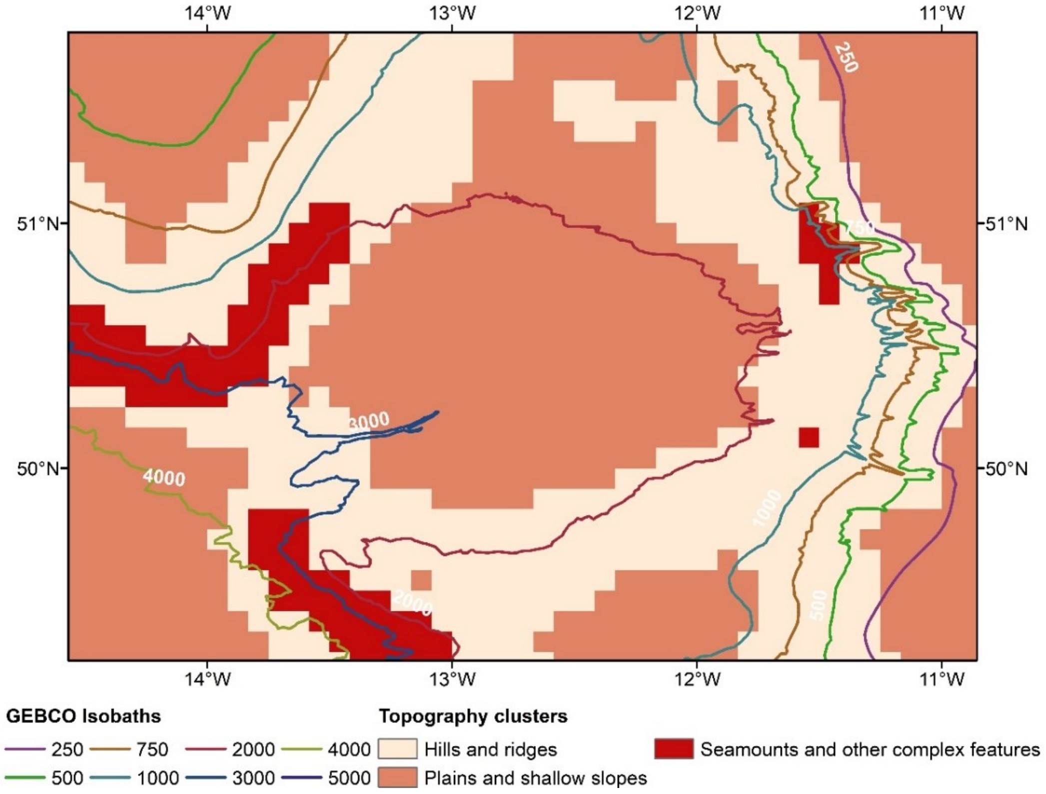


Figure E.6: Topography classes for the Porcupine Seabight.

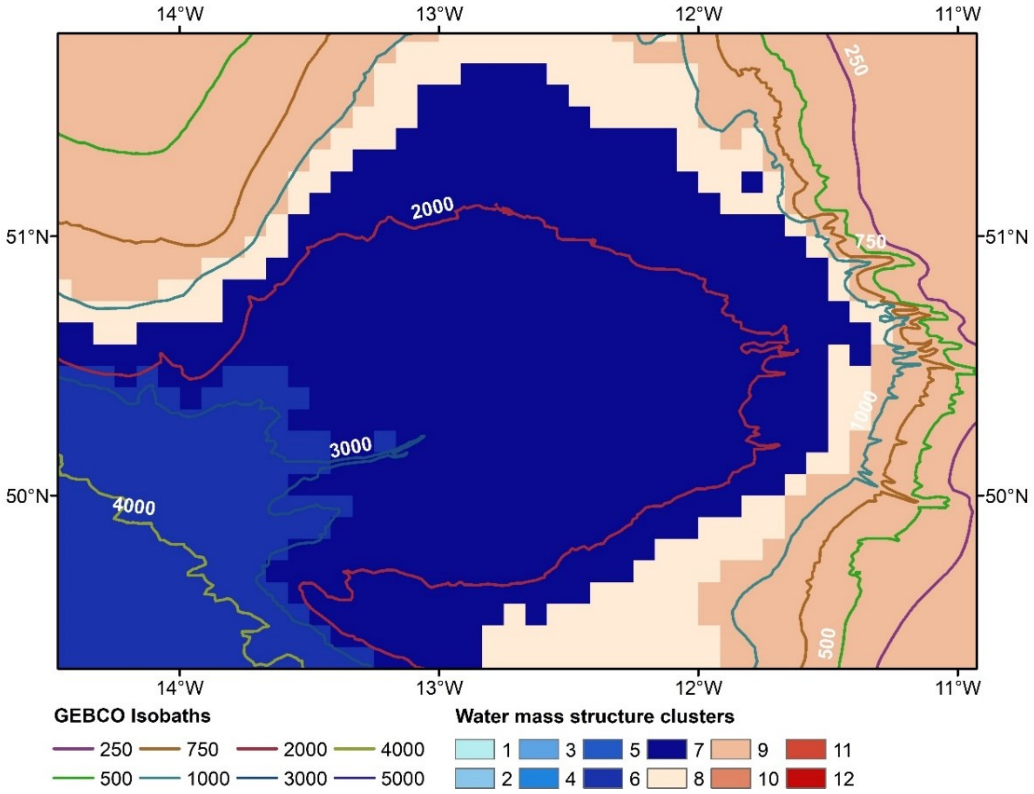


Figure E.7: Water mass structure classes for the Porcupine Seabight.

E.5 Gulf of Mexico

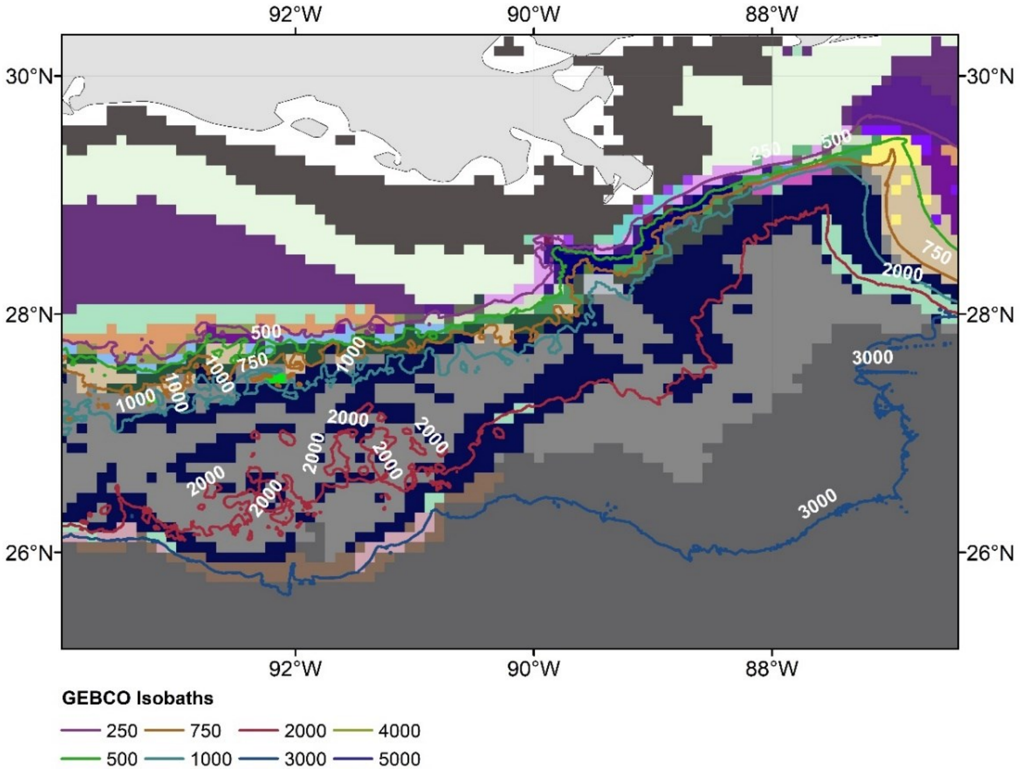


Figure E.8: Habitat classes for the Gulf of Mexico. Following boundaries are based on the ocean off the peninsula at ~ 89 °W, 29° N where data are comparable to most previous studies. The lower boundary of shelf fauna is observed around the 100 m isobath where the purple habitat classes begin; the rapid turnover zone is considered to be between the 100 and 1000 m isobaths on the slope; the 1000 m faunal break is represented by the beginning of the light grey and navy blue habitat classes; the upper boundary of the true abyssal zone is located between the 2000 and 3000 m isobaths represented by the change in habitat classes from lighter to darker grey.

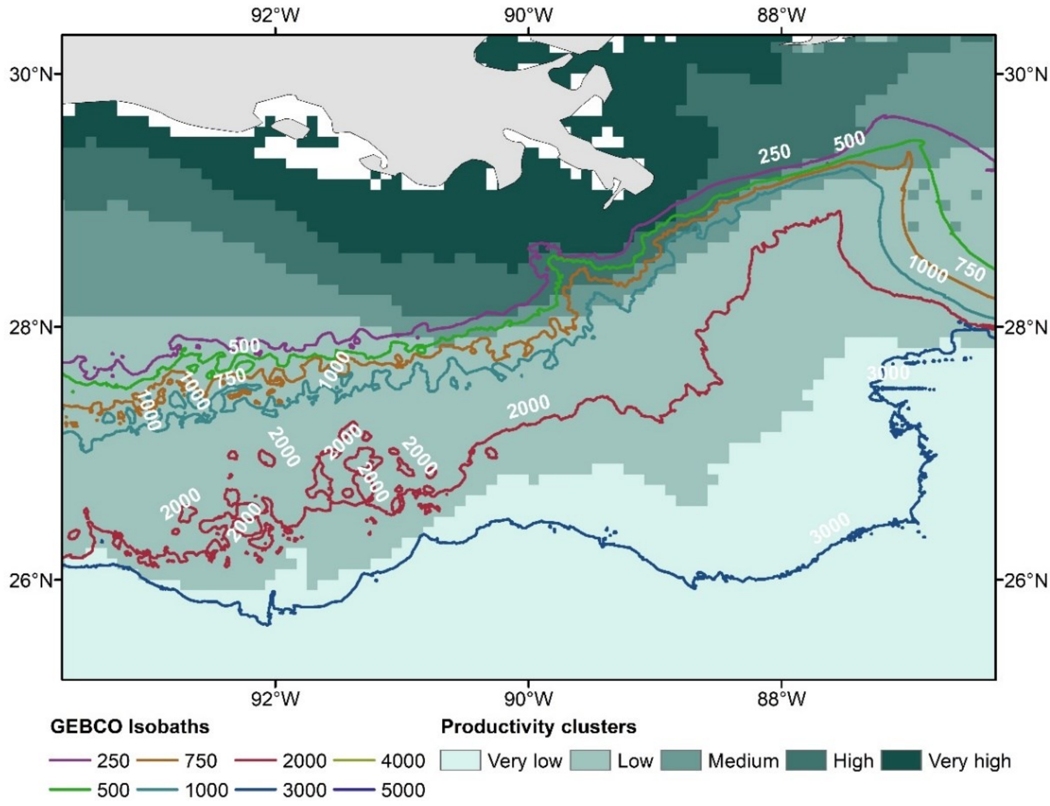


Figure E.9: Productivity classes for the Gulf of Mexico.

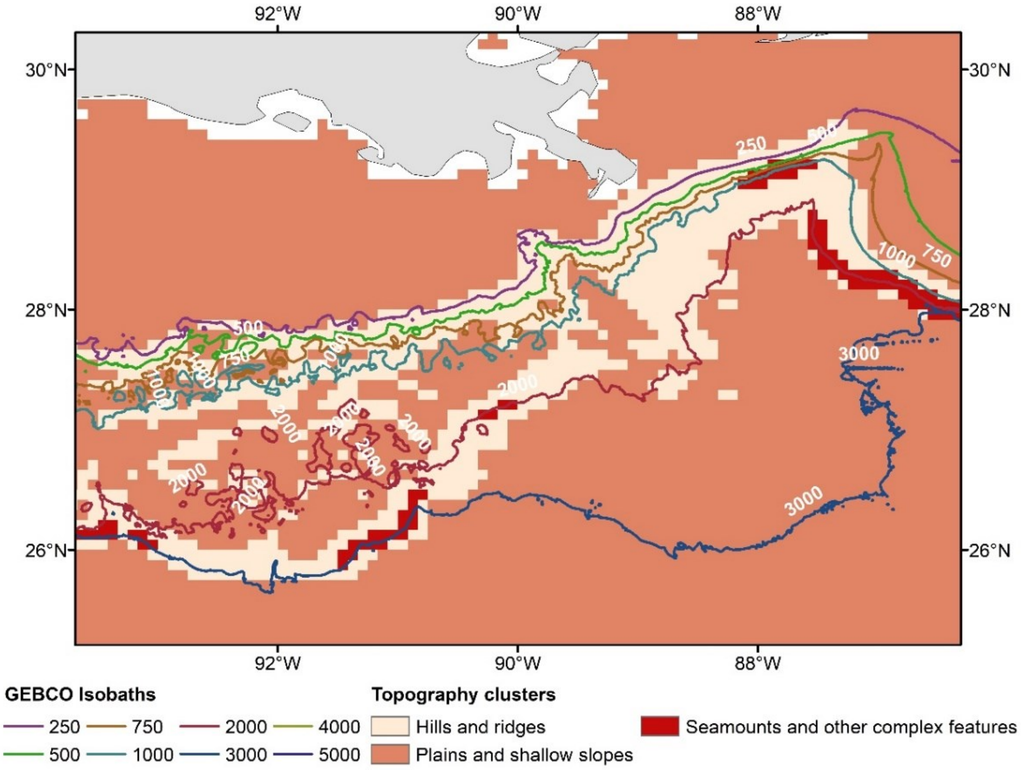


Figure E.10: Topography classes for the Gulf of Mexico.

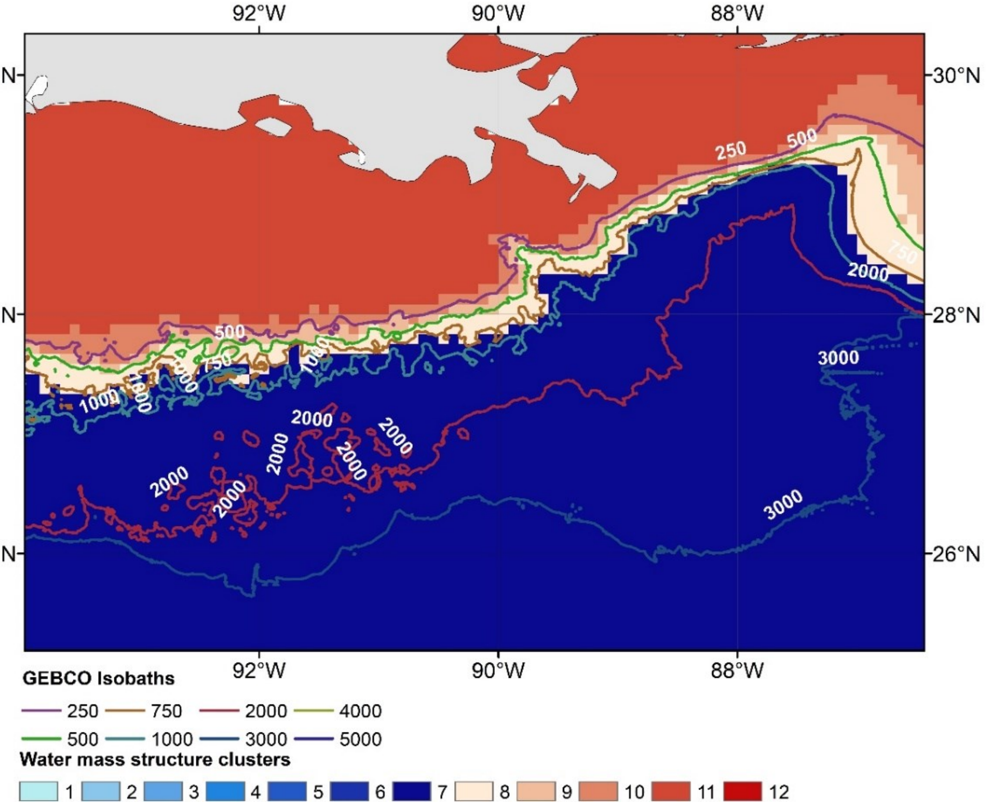


Figure E.11: Water mass structure classes for the Gulf of Mexico.

E.6 Central Pacific

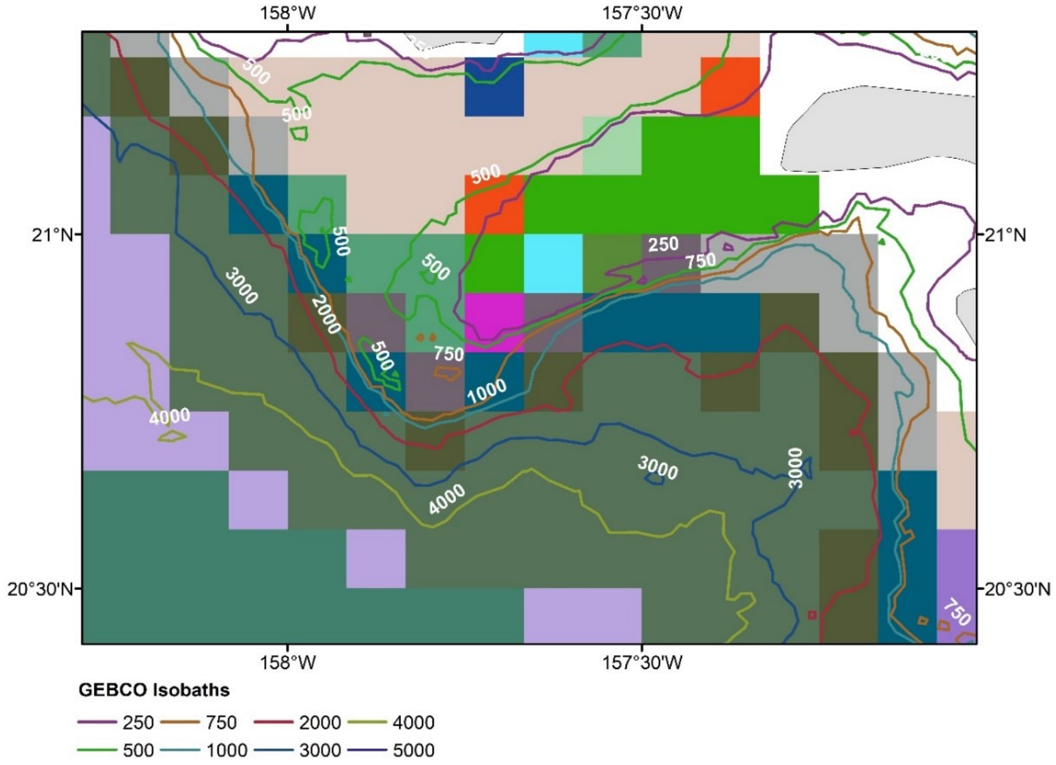


Figure E.12: Habitat classes for the Hawaii. The lower boundary of shelf fauna is observed around the 500 m isobath where the light green habitat class ends; after this point, steep terrain prevents description of habitat classes relationships to particular depth bands.