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An Integrated Ecological and Geophysical Approach to Habitat Mapping and its Application in Marine Conservation

By

Oliver Thomas Hogg

Thesis for the degree of Doctor of Philosophy

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ABSTRACT

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Global biodiversity is in decline, with the marine environment experiencing significant and increasing anthropogenic pressures. As a response, very large (10^5–10^6 km^2) marine protected areas (MPAs) have become the dominant form of environmental protection in the marine environment. At present, however, paucity in scientific sampling makes prioritising which regions of the ocean to protect, especially over such large spatial scales, particularly problematic. One such very large MPA, covering an area of over 1 million Km^2, is located at the sub-Antarctic South Georgia and South Sandwich Islands (SGSSI). This study uses the SGSSI MPA as a model system to assess the application of benthic habitat mapping as an evidence-based framework for the spatial prioritisation of marine conservation.

This study presents an interdisciplinary methodology to marine landscape mapping, as a top-down, objective statistical approach to hierarchically partition and map the benthic environment into physical habitats types. Ordination analysis demonstrates a statistically significant relationship between environmentally-derived landscape mapping clusters and the composition of benthic species data from the region, thus attributing ecological relevance to the marine landscape map. Furthermore, this study adopts a bottom-up approach to habitat mapping, using an ensemble of habitat suitability models. Potential distributions are modelled for a range of benthic faunal attributes relevant to marine management, based on taxonomic classification, functional traits and vulnerability to disturbance. These modelled distributions are used to describe, for the first time, the bio-physical characteristics of SGSSI's benthic environment. Synthesising both top-down and bottom-up approaches to habitat mapping, this study assesses the physical landscape clusters and modelled distribution results in relation to the spatial protection currently enforced at SGSSI. This synthesis addresses, (i) whether marine spatial planning in the region is representative in terms of the habitats and fauna it protects; and (ii) whether this interdisciplinary methodology at SGSSI can inform on MPA design and designation more universally, in what is an increasingly exploited, yet still poorly understood marine environment.

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Academic Thesis: Declaration of Authorship

I, **Oliver Thomas Hogg** declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

An Integrated Ecological and Geophysical Approach to Habitat Mapping and its Application in Marine Conservation

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
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   Hogg, O.T., Huvenne, V., Griffiths, H.J., Dorschel, B., Linse, K. (2016) Landscape mapping at sub-Antarctic South Georgia provides a protocol for underpinning large-scale marine protected areas. Scientific Reports, 6. 10.1038/srep33163.

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Date:

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Chapter 1: Introduction

1.1 State of the marine environment

Global biodiversity is in decline, with the rate of species extinctions far exceeding that of speciation (Hooper et al., 2012; McCauley et al., 2015). Human activities are exerting increasing pressures on the marine environment (Halpern et al., 2008; Butchart et al., 2010) through activities such as fishing (Jackson et al., 2001; Pauly et al., 2005), mining (Wedding et al., 2015), chemical contamination by hazardous substances (e.g. plastics - Brennecke et al., 2016), inputs of nutrients (Andersen et al., 2015) and modification to habitats (Dafforn et al., 2015) including the propagation of invasive species (Bax et al., 2003). Furthermore the world's oceans are becoming warmer and more acidic (Stocker et al., 2013), driving changes in the distributions of marine species (Burrows et al., 2014) and impinging on ecosystem processes, functions and services (Worm et al., 2006), on which current societal and economic standards depend (Millennium Ecosystem Assessment, 2005; Cardinale et al., 2012; Mulder et al., 2015). This anthropogenic driven change to the natural world has led to the adoption of the term Anthropocene to describe the current epoch (Crutzen, 2006).

Anthropogenic impact, whilst increasing ubiquitous in the marine environment, is not uniform in its intensity, with the greatest pressures associated with coastal ecosystems of the North Sea, Japan and the Eastern Caribbean (Halpern et al., 2008). These pressure are primarily due to their regional proximity to human populations. Nonetheless human activities are increasingly proliferating into geographically remote and deep-sea environments (Gross, 2014), both directly through activities such as unregulated fishing and indirectly as with climate-driven sea-ice loss in Polar Regions.

In response to these pressures and changes to the world oceans, in 2002 a strategic plan was outlined as part of the Convention on Biological Diversity (CBD), which, by 2010, aimed to achieve a “significant reduction” in the rate of biodiversity loss at regional, national and global levels (www.cbd.int/2010-target). In addition it called for the protection of at least 10% of the world’s oceans by 2012. The global response fell well short of this target, with marine biodiversity still in decline (Butchart et al., 2010), and global coverage of marine protected areas equating to just 3.66% of the oceans area (http://www.mpatlas.org/; Date of access: 08/02/2018). Governments have however reasserted their commitment to these targets, with a further 3.6% of the World oceans subject to proposed or pending protection and the target deadline now extended to 2020 (Conference of the Parties to the Convention on Biological Diversity, 2010).

Conservation and management efforts are under significant financial, political and social constraints. This is compounded by the potentially competing or conflicting interests of multiple stakeholders from the scientific community, industry, Non-Government Organisations (NGOs) and multiple layers of regional to international government. Consequently successful marine management needs to be able to prioritise how and where to focus limited resources and effort to maximise conservation payoff in what is an increasingly exploited, yet still poorly understood marine environment.

1.2 Prioritisation of marine protection

Conceptually almost all conservation strategies are framed around the degree to which areas or taxa are vulnerable or irreplaceable (Margules et al., 2000; Brooks et al., 2006). This is balanced against the cost of implementing the strategy, and the likelihood of its success (Hobbs et al., 2003; Wilson et al., 2007; Bottrill et al., 2008). What is less consistent, however, is a clear, meaningful measure of 'conservation value'.

The popular appeal of specific charismatic or flagship species has often led to their perceived value and subsequent use in the funding and design of protected areas (Zacharias and Roff, 2000; Ray et al., 2005; Caro, 2010; Chapman 2012; Di Minin and Moilanen, 2014). To what extent this approach delivers broader ecosystem benefits is still however largely unquantified (Linnell et al., 2000; Sergio et al., 2006, 2008). Species-based approaches have also gained support in the form of EDGE (Evolutionarily Distinct and Globally Endangered) strategy conservation, aimed at maximizing phylogenetic diversity (Issac et al., 2007). This addresses the importance of preserving species that represent sole bearers of genes from a long period of evolution (i.e. monotypic or species poor clades).

Global conservation efforts have however increasingly prioritised the protection of whole regions and ecosystems rather than specific species as a holistic and geopolitically achievable approach to conservation (e.g. CBD Aichi Target 11, 2010; UN Sustainability Goal 14.5, 2015). This has seen increased recognition of marine protected areas (MPAs) as an important mechanism for conserving biodiversity (Lubchenco et al., 2003; Metcalfe et al., 2012), and increased political support for their establishment (O'Leary et al., 2012). In recent years this is manifest in the establishment of large-scale (10^5-10^6 km^2) MPAs at Pitcairn Island (UK), Ascension Island (UK), Palau National Marine Sanctuary (Palau), Naza-Desventuradas (Chile), Ross Sea (International), the extension on Papahānaumokuākea Marine National Monuments Park (USA), and the UK overseas territory of South Georgia and South Sandwich Islands which forms the geographical focus of this thesis (figure 1.1). The foundations of many of these conservation and management areas are framed around the presence of particularly vulnerable, keystone or charismatic species; the presence of large numbers (or proportions) of endemic species; and the presence of high total biodiversity both at species level and across taxonomic levels (i.e. biodiversity hotspots) (e.g. Sheppard et al., 2012; Trathan et al., 2015).

In this era of spatial protection as the paradigm of marine conservation, some criticism has focused on the targeting of 'easy gain' sites for protection, such as those with limited stakeholder opposition, as a means of meeting target driven regional, national and international commitments in a politically expedient manner (Devillers et al., 2015; Jones and De Santo, 2016). Further to this, there is often limited evidence-based science underpinning these spatial designations (Sutherland et al., 2004; Leenhardt et al., 2013). This is reflected in the lack of citable literature available for the recent large-scale marine protected areas listed above.

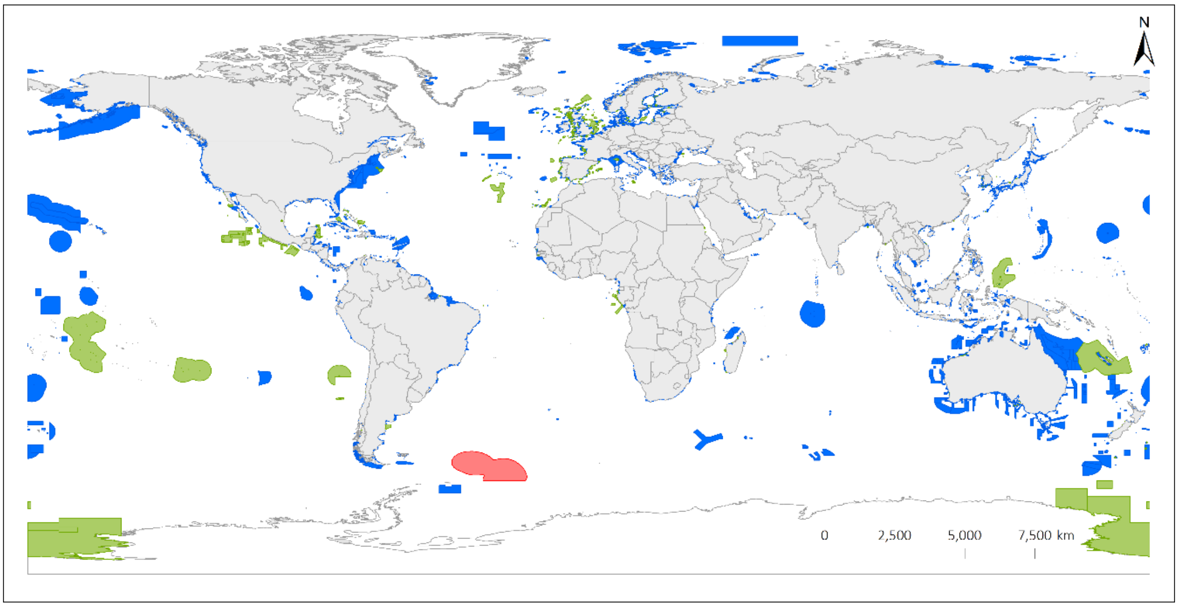

Figure 1.1. Map of the World's network of marine protected areas (as of January 2018). MPAs designated during the course of this thesis project (2014-2018) are shown in green; South Georgia and South Sandwich Islands MPA (the focus of this thesis) is shown in red; all other MPAs are shown in blue. The data presented was extracted from United Nations Environment Programme World Conservation Monitoring Centre (UNEP-WCMC) and International Union for Conservation of Nature (IUCN, 2018).

Through policy frameworks such as the CBD (2010) a key stipulation for protection is for it to be ecologically representative –

"*At least 17% of terrestrial and inland water, and 10% 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* [by 2020]"

10th Conference of the Parties (COP10) to the Convention on Biological Diversity, Aichi, Japan, 2010.

Under the CBD agreement, ecologically representative areas are defined as those encompassing typical examples of species and habitats in each of the world's 232 geographically defined marine ecoregions (see Spalding et al., 2007). A key constraint to this approach however is our current understanding of spatial trends in marine diversity, which is limited by both paucity in knowledge and complexity in ecological systems.

1.3 Patterns in global marine diversity

Biodiversity is not distributed evenly across the World's oceans. Rather, biogeographical structuring can be seen across spatial and temporal scales (Gaston, 2000; Gaston and Spicer, 2013), along spatial and environmental gradients such as latitude, longitude, depth, degree of isolation and productivity (Gaston and Williams, 1996).

Over latitudinal gradients marine diversity exhibits a general increase towards lower latitudes, often peaking at 20-30°N (Roy et al., 1998; Crame, 2000). The gradient is often considered asymmetrical with diversity increasing rapidly from northern polar latitudes towards the equator, then declining more gradually from the equator towards the Antarctic (Clarke, 2009). Conversely, some groups such as hexacorals, pycnogonids and bryozoans demonstrate equitable diversity between the Antarctic, temperate and non-reef tropical habitats (De Broyer et al., 2014).

Longitudinally, diversity peaks and radiates outwards from the Indo-Australia archipelago (Renema, 2008). This is most notable in shallow marine ecosystems (Ellison et al., 1999; Williams and Reid, 2004; Hoeksema, 2007), including diversity in corals (Rosen, 1981; Bellwood, 2001).

In the deep sea, spatial gradients are still pervasive (Rex et al., 1993). In contrast to shallower waters, deep-sea species diversity is thought to be greatest at mid-to-high latitudes (Woolley et al., 2016). Diversity-depth relationships can also been seen, with a peak in macrobenthos at intermediate depths of 2000-3000m (Pineda and Caswell, 1998; Ramirez-Llodra et al., 2010).

Centres of diversity at macroecological scales are driven by ecological processes occurring over geological timescales (Tittensor et al., 2010). Human-induced change however, such as projected changes to biodiversity due to ocean warming (Molinos et al., 2016), are occurring over much shorter time-scales (Jackson et al., 2001; Hughes et al., 2003; Pandolfi et al., 2003) adding temporal uncertainty to diversity and distribution predictions.

Trends in diversity and distributions represent a composite of inter-related local, regional and global drivers (Cornell and Lawton, 1992; Gaston, 2000). Examples of this include the relationship between species richness and geographical area (MacArthur and Wilson, 1967; Connor and McCoy, 1979) and the effect of geographical isolation on the diversity and distinctiveness of fauna (MacArthur & Wilson, 1963; Rosindell & Phillimore, 2011).

At local scales biotic interactions such as predator-prey relationships and competition for space and resources result in complexity in community ecology (Lawton, 1999). This complexity is further compounded by variation in abiotic factors such as geomorphology, hydrology and sedimentology, and the respective influence of small-scale versus large-scale ecological drivers which are often poorly constrained. In addition, though species-level is often the default level by which biological units are described, trends are not universal across taxonomic groups or taxonomic levels, with different distributions underpinned by different environmental preferences and evolutionary histories.

Given this lack of universality between regions, habitats and taxa, whilst macroecological patterns can broadly frame our understanding of patterns in diversity, many factors combine to limit our ability to talk in universal terms about diversity across scales from local to global.

1.4 Habitat mapping

Complex patterns in spatial ecology and paucity in biological data make it problematic to meet two of the key goals outlined in the CBD. Namely to: (i) spatially prioritise regions on the basis of the representative protection of species and habitats, and (ii) reduce species loss at regional, national and global levels. This raises the fundamental questions of:

1. How does one ensure representative protection when species and/or habitat types are only partially or poorly described?

2. How does one protect maximum faunal diversity when there is a fundamental lack in understanding of how diversity is spatially structured?

Biological data is typically collected through physical sampling such as trawling and dredging or through *in situ* observation by diver, camera lander, ROVs and AUVs. This type of data collection is intrinsically expensive, time consuming, and logistically difficult, especially when attempting to cover large areas, areas of deep sea or otherwise inaccessible or remote regions. As such, biological sampling typically only covers very small areas with good spatial coverage, or larger areas with poor spatial resolution. Where there is sufficient systematic sampling of biological data, for example in coastal regions or at small scale sites, it is possible for biological information to be used in isolation to inform on management decisions (e.g. Edgar et al., 1997; Gladstone, 2002). Over the larger spatial scales typified by marine spatial planning units such as MPAs the use of biological data alone is typically insufficient to form a scientifically rigorous basis to answer the questions outlined above. In the absence of sufficient biological sampling, to effectively inform on spatial and temporal management priorities, the use of habitat mapping has increasingly been adopted to aid decision making (Pressey and Bottrill, 2009; Brown et al., 2011; Harris and Baker, 2012).

Habitats are ecological units used to describe the area in which a species, or more typically a community of species, occurs (Gaston and Spicer, 2013). The description of a habitat is generally both biotic and abiotic, including mention of the associated environmental features and conditions in the area which delimit its suitability for the aforementioned biota. Depending on context, habitat categorisation can occur across a hierarchy of different spatial scales from large provinces (>1000km in extent) to micro-communities such as the association between individual commensal or symbiotic species.

Habitat mapping relates ground-truthed field observations to spatially continuous predictor variables such as remotely sensed geophysical data (e.g. topography; surficial geology) and physical environmental data (e.g. oceanographic regimes). Variations in environmental variables drive changes in faunal communities and community structure, thus in the absence of sufficient biological data, environmental variables can act as surrogates or proxies to represent and predict biological patterns on the seafloor (Roff and Taylor, 2000; Harris and Whiteway, 2009; Howell, 2010; Brown et al., 2011; Harris, 2012). This analysis of the interaction between physical and biological variables helps create a far more comprehensive spatial and temporal understanding of how biodiversity is structured across a region, and helps constrain what the bio-physical processes are that drive this structuring. Remotely sensed data is typically orders of magnitude faster and cheaper to collect per unit area than ground-truthed sampling (Harris and Baker, 2012b). As such its use enables the mapping of biotic and abiotic characteristics of a region across a much larger spatial scale than otherwise possible, particularly in regions impoverished of biological sampling.

Most marine habitat mapping focuses on the benthic (seabed) environment, in part due to the difficulties in mapping pelagic environments which exhibit a dynamic three-dimensional structure that changes quickly and contains typically mobile fauna. Exceptions to this can be seen in application such as fisheries management (Kobayashi et al., 2008; Druon, 2010), but hereon in this thesis will focus on benthic habitat mapping and refer to it more generally as habitat mapping.

Key environmental datasets commonly employed in habitat mapping include acoustic data, oceanographic data and aerial or satellite data (Harris, 2012). Acoustic data quantify depth and substrate type as well as derivative datasets such as slope and rugosity. Oceanographic data can provide information on temperature, salinity, current velocity, tides and exposure. The use of satellite and aircraft remote sensing is ubiquitous in terrestrial mapping and is increasingly being used in the mapping of shallow water environments (Leiper et al., 2014) and in the analysis of chlorophyll concentration (Behrenfeld and Falkowski, 1997) and its connectivity with seabed productivity (Smith et al., 2016; Jansen et al., 2018).

Broadly habitat mapping studies can be categorised into three strategies: abiotic surrogate mapping; assemble-first, predict-later unsupervised classification; and supervised classification (Brown et al., 2011).

Abiotic surrogate mapping is an unsupervised approach to habitat classification which relies on the integration of exclusively environmental data to look for patterns in biodiversity, without the inclusion of biological data to ground truth the analysis. Typically the reasons for this exclusion are either a complete lack of biological information, or more commonly that the studies are conducted over such large spatial scales that individual point sample data is of limited value. Through this approach, different geomorphic features such as canyons, pinnacles, rocky ridges and muddy basins can be mapped, either for their own intrinsic conservation value (e.g. Gray, 2004), or for use as proxies of particular types of benthic habitat (De Leo et al., 2010).

Assemble-first, predict later is a top-down approach to habitat classification. Environmental data layers are first segmented, delineating them into spatial units. This can either be done objectively by adopting a statistical approach to identify distinct ecologically relevant zones (Verfaillie et al., 2009; Ismail et al., 2015) or through use of automated image-analysis software (Van Overmeeren et al., 2009; Blaschke, 2010; Ierodiaconou et al., 2018). Alternatively a subjective approach can be adopted whereby distinct zones are expertly delineated by specific environmental characters or through predefined hierarchical classification systems that are deemed to be of ecological relevance, such as EUNIS (Davis et al., 2004; see also Greene et al., 1999). Correlations between abiotic clusters and biological data from each cluster can then be drawn to help inform on the environmental conditions associated with certain taxonomic groups, assemblages or communities.

Supervised classification is a bottom-up approach to habitat mapping, in which biological and environmental datasets are integrated into the model from the beginning. Supervised classification mapping can be a very effective and objective approach to generating predictive species distribution maps that preserve species-environment relationships (Roff and Taylor, 2000; Harris and Whiteway, 2009; Howell, 2010). This is particularly significant when habitat mapping at high-resolution, typically at fine spatial scales, as often the hierarchical classification systems adopted in top-down approaches don't manage to effectively represent fine-scale local conditions (Shumchenia and King, 2010). A bottom-up approach to habitat mapping is particularly effective at predicting habitats of individual species (Galparsoro et al., 2009), and due to the fine-scale nature of this approach it also useful for monitoring temporal changes within habitats (MESH, 2008). As such it has useful application in attempts to model more complex community structures (Ierodiaconou, 2011).

1.5 Habitat mapping in marine conservation

Interest in marine habitat mapping and its application in conservation and marine spatial planning has grown continuously over the last two decades (Figure 1.2), with 67% of habitat mapping studies set in the context of conservation or management (Lecours, 2017).

Countries undertaking large-scale mapping of their exclusive economic zones (EEZ) include the UK (MAREMAP-www.maremap.ac.uk), Ireland (INFOMAR-www.infomar.ie), Finland (FINMARINET) and Norway (MAREANO-www.mareano.no/en). This in turn has led to the mapping of broad-scale biotopes through collaborative projects in Europe such as EUNIS - European Nature Information System (Davis et al., 2004), MESH - Mapping European Seabed Habitats (MESH, 2008) and EMODnet – the European Marine Observation and Data Network (www.emodnet.eu). Significant work has also been undertaken in producing seascape maps of the Australian continental shelf

(Whiteway et al., 2007; Lucieer and Lucieer, 2009; Last et al., 2010), Canada's EEZ (Pickrill and Kostylev, 2007) and more recently in South Africa (Driver et al., 2012).

Such national programmes are considered to be of significant economic benefit to national economies through, amongst other things, effective fisheries management (Kostylev and Hannah, 2007; Getsiv-Clemons et al., 2012; Harris and Baker, 2012c) and the placement of offshore developments such as oil and gas drilling structures and wind farms (LaFrance et al., 2014). It is estimated for example, that the INFOMAR programme (Integrated mapping for the sustainable development of Ireland's marine resources) will have provided an estimated net benefit of €350 million to the Irish economy by 2026 (Price WaterHouse Cooper, 2008).

Conservation-based habitat mapping studies range in scale from small-scale MPAs (Henriques et al., 2015), to regional examples such as on the Norwegian (Buhl-Mortensen et al., 2015, 2015b) and Scottish (Howell, 2010) continental shelves, to areas beyond national jurisdiction (ABNJ) such as in the North-east Atlantic (Evans et al., 2015), Baltic Sea (Ekebom, 2008) and the southern Irish Sea (Robinson et al., 2011). Habitat mapping has also been adopted at a global scale (Greene et al., 1999; Agnostini et al., 2008; Harris and Whiteway, 2009), including assessment of deep sea regions (Briones et al., 2009).

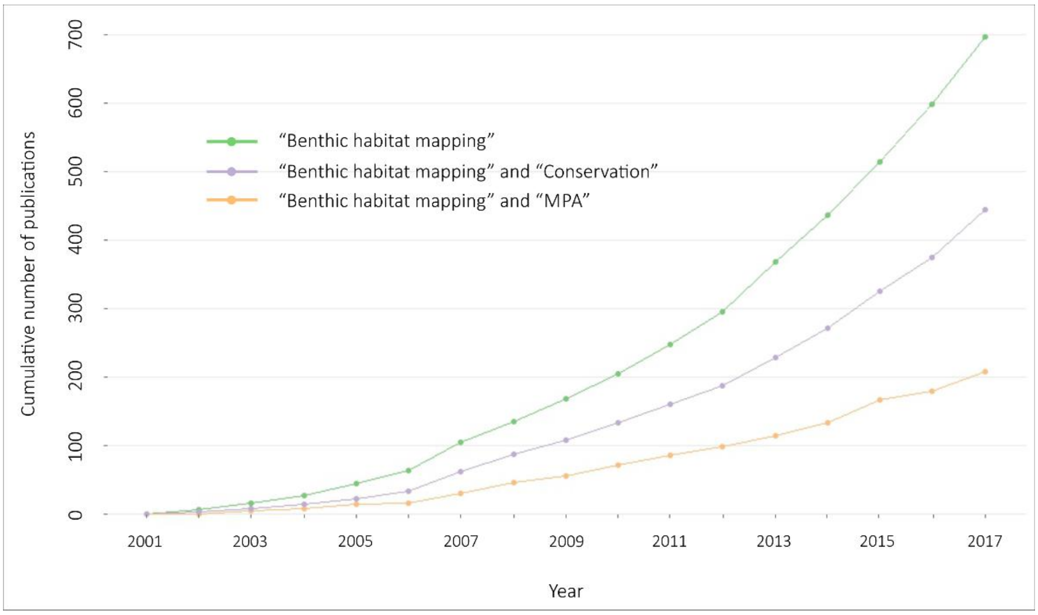

Figure 1.2. Cumulative number of original research publications related to benthic habitat mapping listed in the Scopus database mentioning specific keywords (see key), as of the end of 2017.

Habitat mapping has been applied in the conservation of vulnerable marine ecosystems (VMEs) such as coral reefs (Selgrath et al., 2016), particularly through the use of habitat suitability modelling in data poor regions (Rinne et al., 2014) such as the deep sea (Clark et al., 2011). Suitability modelling has also been applied to fish-stock assessment in Canadian waters (Kostylev and Hannah, 2007), where environmental predictors were integrated with life history traits of organisms to assess whether life cycle phases were associated with specific environments. It is used widely as a techniques for identifying regions of potential conservation importance such as specific biotopes (Davis et al., 2014), listed deep-sea habitats (Ross and Howell, 2013) and seamount communities (Clark et al., 2011).

Habitat mapping has been used as a tool for assessing habitat heterogeneity, such as in the proposed design of a global network of high seas MPAs (Harris and Whiteway, 2009) and habitat classifications for the entire Australian EEZ to ensure representative protection (Harris et al., 2008). Representative protection has also been sought through the use of pre-existing habitat classification frameworks such as EUNIS (Davis et al., 2014), as in the case of in Portuguese MPA design (Henriques et al., 2015). The concept of representative protection can also be seen in the design of the Great Barrier Reef MPA where broad-scale mapping was used to classify 70 distinct bioregions (GBRMPA Zoning Plan, 2003). The GBRMPA zoning plan enabled protection of a multi-use marine environment based on analysis of major habitat types.

Through new techniques and novel approaches, habitat mapping has also extended to previously unmapped and complex environments such as vertical canyon wall communities (Huvenne et al., 2011; Robert et al., 2017). Mapping techniques have also been utilised to map threat-levels or anthropogenic impact on environments as a means of effectively prioritising protection (Kachelriess et al., 2014; Giakoumi et al., 2015). These recent applications demonstrate the utility and adaptability of habitat mapping from the very largest (Harris and Whiteway, 2009) to the very smallest spatial scales (Robert et al., 2017) across a range of management uses.

Habitat mapping represents a tool that can be used by policy makers to aid and underpin decisions made on marine spatial panning. In itself it does not represent a panacea for marine conservation, as it still falls to scientists, policy makers, stakeholders and wider society to consider what biological or environmental attributes represent a meaningful measure of conservation value. Habitat mapping can however help explain local, regional and global patterns in biodiversity and indeed other parameters of conservation value such as functional diversity and vulnerability. It can help us better understand the complexities of benthic communities, providing objective analysis on what the biophysical processes are that drive biogeographical structuring. With pressure growing on world governments to increase the total coverage of marine protected areas, habitat mapping can facilitate the conservation, remediation and monitoring of benthic communities through an informed approach to ecosystem-based management.

This study uses the sub-Antarctic South Georgia and South Sandwich Islands MPA as a model system to assess the application of benthic habitat mapping as an evidence-based framework for the spatial prioritisation of marine conservation in very large MPAs. Using two complementary approaches to habitat mapping we will investigate its utility as a management tool for very large marine protected areas.

Chapter 2: Study area

2.1 Geophysical setting

The Southern Ocean is delineated by the Polar Front, which represents a distinctive physical discontinuity between polar and temperate waters. This discontinuity is manifest in fast, eastward-flowing jets of water which extend to a significant depth (>1000m) and form the largest temperature cline (3-4°C) in the Southern Ocean (Barker and Thomas, 2004; Thornhill et al., 2008). Consequently the Polar Front also represents a biogeographical discontinuity, greatly limiting the exchange of epipelagic and benthic fauna (Clarke et al., 2005). This is reflected in the estimated 45-97% of marine species from many taxa, including sponges, molluscs, pycnogonids and tube worms which are endemic to the waters south of the Polar Front (PF) (Arntz et al., 1997; Griffith et al., 2009; De Broyer et al., 2014).

The established paradigm of the Southern Ocean, therefore, is one of an isolated system (Dell, 1972; Angel, 1997; Longhurst, 1998). Conversely, however, in recent years phylogenetic research has supported the idea of dispersal across the Polar Front (Page and Linse, 2002; Thornhill et al., 2008; Leese et al., 2010; O'Hara et al., 2013; Poulin et al., 2014). Some of these links between the Antarctic and temperate climes are attributed to historical distributions established prior to the formation of the Antarctic Circumpolar Current (ACC) and PF ~25 ma (Clarke and Crame, 1989; Lawver and Gahagan, 2003; Hogg et al., 2011). Other mechanisms however such as slow species radiations through deep-sea environments (Griffith et al., 2008) and surface transport via vectors such as kelp (Smith, 2002; Fraser et al., 2016; Waters et al., 2018) have been suggested as potential dispersal mechanisms.

The same currents which limit latitudinal exchange between Antarctic and temperate waters, facilitate eastward dispersal within the Southern Ocean. Consequently, there is a general homogenising influence on Antarctic marine fauna (Barnes & Griffith, 2008; Chown et al., 2015), with very few barriers to dispersal across a single Antarctic province (Griffiths et al., 2009). No single region is shown to be universally dominant in diversity across taxa, with different faunal groups presenting different biogeographical patterns (Griffiths et al., 2009; De Broyer et al., 2014). Regional exceptions to this can be seen in suggested hotpots of diversity and endemism such as at sub-Antarctic South Georgia (Griffiths et al., 2009; Hogg et al., 2011), the focus of this thesis.

The sub-Antarctic archipelago of South Georgia and the South Sandwich Islands forms part of the Scotia Arc, a predominantly submarine ridge that extends in an anticlockwise arc from the Antarctic Peninsula in the south to the Terra del Fuego region of South America in the north (Figure 2.1). Though geographically they are neighbours, the two island groups are distinctly different in character.

South Georgia's snow-capped peaks and deeply furrowed glacial valleys dominate a single narrow island, which at its widest point spans just 35 km across. Underwater however, the island is surrounded by a wide continental shelf extending up to 100 km offshore and covering an area of 39,750 km^2 (48,950 km^2 including the shelf around Shag Rocks) at an average and relatively constant depth of 200 m (Fretwell et al., 2009; Hogg et al., 2011). The shelf is punctuated by a series of deep cross-shelf troughs that extend out from inshore glacial fjords to moraine fields at the shelf break. These moraines are a 20,000-year-old remnant from the Last Glacial Maximum (LGM) when an extensive ice cap surrounded the island (Graham et al., 2008; 2017) littering the shelf edge with displaced debris. From the shelf edge the seabed rapidly drops away to deep open-ocean reaching depths in excess of 6000m.

South Georgia was once joined to South America in a land bridge between what is now Antarctica and the Americas (Mukasa and Dalziel, 1996). It is thought to have moved to its current position through a process of crust subsidence and seafloor spreading between 45 and 20 million years ago (Livermore et al., 2007; Curtis et al., 2010). During the process of this spreading, a continuous network of deep-water channels stretching around the entire Southern Ocean became connected, driving changes in ocean currents, most notably with the development of the ACC. Circling the Southern Ocean clockwise, the powerful ACC transports nutrients and organisms such as krill north from the Antarctic Peninsula to the shelf of South Georgia. On reaching the island the ACC forks, with the Polar Front (PF) flowing an average 300 km to the north (Moore et al., 1999), and the Southern ACC Front (SACCF) looping anti-clockwise around the island to the south before traveling eastwards (Figure 2.1).

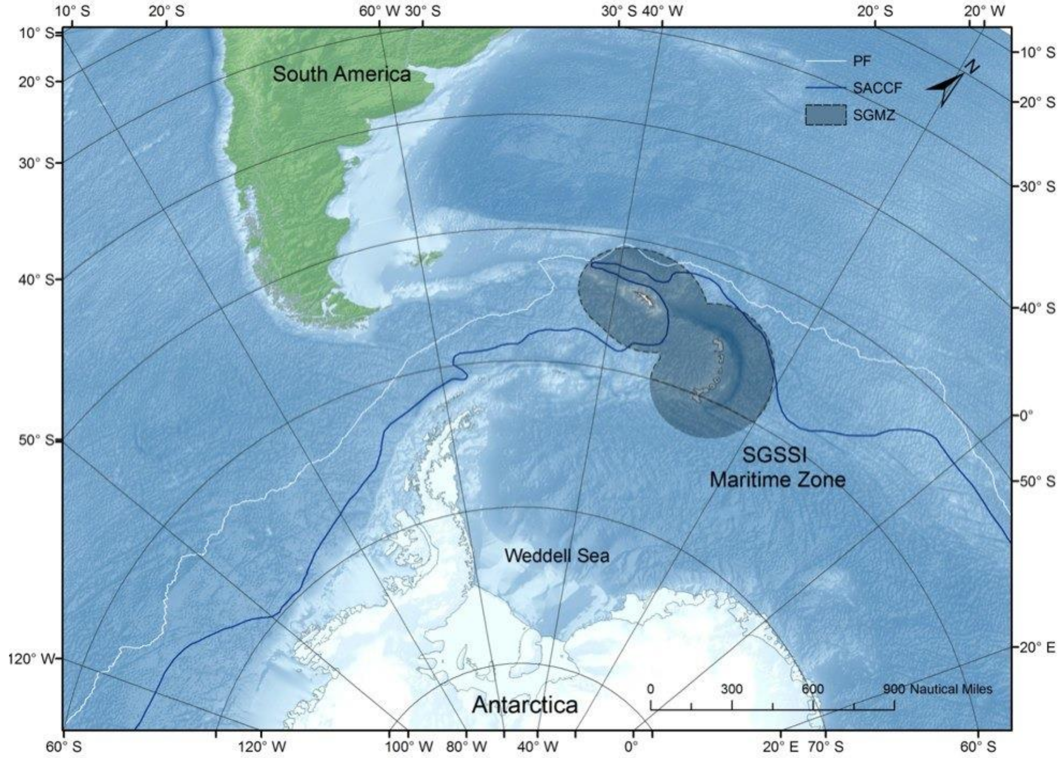

Figure 2.1. Position of South Georgia and South Sandwich Islands maritime zone relative to the Polar Front (white line) and the South Antarctic Circumpolar Current Front (SACC) (blue line).

The South Sandwich Islands consist of 11 volcanic islands stretching in a 390 km long arc on a north - south axis. In contrast to South Georgia the presence of a continental shelf around the islands is practically non-existent with the steep-sided volcanic slopes dropping away to depths in excess of 3000m within 10 km of the coastline (Figure 2.2). As such the area of seabed under 1000m depth is restricted to just 13,270 km^2, an area around a quarter of the size of neighbouring South Georgia.

At less than 5 million years old (Hawkesworth et al., 1977), the islands themselves are, in geological terms, relatively young. Unlike South Georgia, the volcanoes that form the South Sandwich Islands effectively developed in situ through the subduction of the South American tectonic plate under the South Sandwich plate (Leat et al., 2016). Through this process, not only was the island arc formed, but also the South Sandwich Trench running 100 km east and parallel to the islands reaching depths of over 8000m. Currents are deflected by the island chain with Circumpolar Deep Water (CDW) flowing northwards through the Georgia Passage between South Georgia and South Sandwich Islands (Naveira Garabato et al., 2002). Positioned south of the ACC, and thus with lower temperatures and seasonal sea-ice, the South Sandwich Islands is distinctly Antarctic in character.

2.2 Marine biodiversity

Though South Georgia and the South Sandwich Islands are geographically close, there is a considerable difference in knowledge of the marine environment between the two regions, the former having benefited from significantly more scientific sampling.

South Georgia is a globally important site due to its abundant and diverse marine fauna, and as an internationally important site for higher predators (Atkinson et al., 2001; Murphy et al., 2007; Barnes et al., 2011; Hogg et al., 2011; Clarke et al., 2012; Rogers et al., 2012; Trathan et al., 2014).

It is abundance, rather than the diversity in higher predators that is most notable at South Georgia. The waters support an estimated 3 million Antarctic fur seals (90% of the global population), 400,000 elephant seals, and 65 million nesting seabirds including immense colonies of king, gentoo and macaroni penguins (Trathan et al., 2014; Rogers et al., 2015). The waters also act as important feeding grounds for many whale species including killer, minke, southern right, humpback and blue whale (Branch et al., 2007; Jefferson et al., 2011). These high abundances result, in part, from large diatom blooms near to South Georgia, which in turn drive mega blooms in zooplankton and krill (Whitehouse et al., 2008). This productivity is enhanced by nutrient rich water to the north-west of South Georgia spilling on to the continental shelf (Whitehouse et al., 2008; Murphy et al., 2013).

The vast majority of species recorded from South Georgia are representatives of the benthic community (Barnes et al., 2011; Hogg et al., 2011). Through analysis of over 24,000 records, Hogg et al. (2011) catalogued in excess of 1500 species from the South Georgia shelf alone, with representation across 22 of a possible 28 global marine phyla. Most species recorded were rare, 35% being recorded only once. In contrast to South Georgia's diverse benthic fauna, the pelagic zone supports relatively low faunal diversity. The animals that do live there however such as Antarctic krill (Euphausia superba) constitute an enormous biomass (Atkinson et al., 2001). In addition the waters around South Georgia were also found to support a large proportion of species occurring nowhere else on earth (endemics) as well as species for which the island represented their northern or southern geographical limit (range-edge species). Species that are endemic or range-edge are arguably intrinsically more vulnerable to changing environmental conditions, especially in response to predicted rising sea temperatures (Whitehouse et al., 2008). This is because they are potentially either already at their thermal tolerance limit (range-edge species) or have nowhere else on earth that they live (endemics). This dominance of species that are either endemic or range-edge therefore raises questions about how the benthic community in the region will respond to changing environmental conditions (Hogg et al., 2011).

By analysing the rate at which new species are being recorded against the effort it takes through continued sampling to discover them, it is possible to extrapolate estimates of South Georgia's true biodiversity. With the exception of chordates which tend to be ubiquitously well documented, discovery of new species at South Georgia remains high especially amongst bryozoans, annelid worms and echinoderms (Hogg et al., 2011). The highest species diversity in macrofauna is seen in crustaceans, annelid worms and molluscs. South Georgia is also rich with vulnerable marine ecosystems such as octocoral and sponge gardens which are known to grow in abundance in the gully between South Georgia and Shag Rocks (Martin et al., 2012; Taylor et al., 2013).

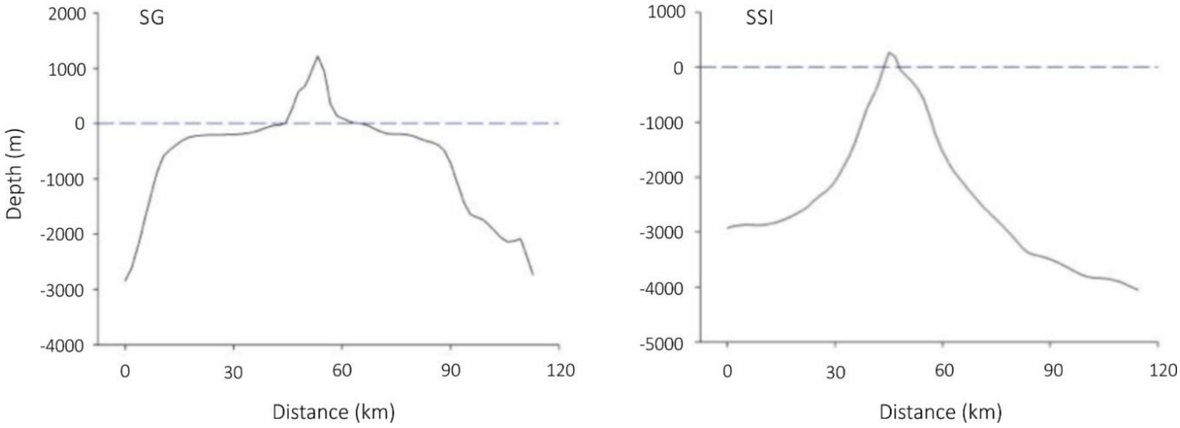

Figure 2.2. Depth profile of South Georgia and South Sandwich Islands. The profile at South Georgia (SG) is taken on a north-south transect across the South Georgia shelf and slope. The profile at the South Sandwich Islands (SSI) is taken on an east-west transect across the shelf and slope of Saunders Island.

The biodiversity of the South Sandwich Islands, in contrast, remains largely unknown. One of the reasons for this is the islands' difficult sea-bed topography (Figure 2.2). With little or no flat shelf areas optimal for benthic trawling or dredging, sample collection is inherently more difficult. What we do know from the islands typically comes from Antarctic toothfish (Dissostichus mawsoni) fisheries bycatch data, and very limited scientific sampling (Ramos, 1999; Lockhart and Jones, 2008). These limited data suggest that the South Sandwich Islands represent a biogeographical outlier in the Scotia Arc (Ramos, 1999) with regions of high biomass. At the archipelagos northerly limits (e.g. Zavodoski Island) benthic fauna demonstrates similar composition to that of South Georgia (Lockhart and Jones, 2008). Amongst mobile fauna, biodiversity is at least partially shared (Roberts and Agnew, 2008). The extent to which less mobile or sessile benthic fauna is shared is however less clear with the two island groups separated by both deep water and the strong SACC.

2.3 Marine protected area

Over the past 40 years South Georgia has been heavily exploited, notably through industrial-scale bottom fishing of marbled rockcod (*Notothenia rossii*) in the 1970s, and mackerel icefish (*Champsocephalus gunnari*) in the 1980s. This fishing was predominantly undertaken by former Soviet Union flagged vessels, with stocks reduced to critically low levels (Kock, 1992). Over recent years significant changes have been made to management practices in the region with the introduction of licencing and quotas (Trathan et al., 2014).

The South Georgia and South Sandwich Islands Marine Protected Area (SGSSI MPA) was designated in 2012 (Collins et al., 2012), with additional benthic closed areas added in 2013. The MPA covers an area of 1.07 million km^2 (see Figures 1.1 and 2.1 for geographical context and Figure 2.3 for a detailed overview). The role of the MPA is to:

1. Protect diverse benthic communities and vulnerable marine ecosystems (VMEs).
2. Avoid interaction between krill fishing and key periods of marine bird and mammal feeding and breeding.
3. Protect the recruitment grounds of juvenile toothfish (*Dissostichus spp.*).
4. Protect spawning and juvenile recruitment grounds of mackerel icefish (*C. gunnari*).

The SGSSI MPA is classified by the South Georgia Government as a sustainable-use MPA. There are currently MSC-certified, government licenced fisheries for Patagonian toothfish (*D. eleginoides*), mackerel icefish (*C. gunnari*) and Antarctic krill (*E. superba*) at South Georgia and a small Antarctic toothfish (*D. mawsoni*) fishery at South Sandwich Islands (Trathan et al., 2014). The GSGSSI currently operates on a budget of ~£5 million per annum, of which fisheries licencing represents up to 75% of income (Rogers et al., 2015). As such marine protection afforded to the region is not uniform but varies both spatially and temporally. Spatially, there is a total ban on bottom trawling with longlining restricted to just 8% of the MPA (~83,500 km^2) occupying a zone between 700m and 2250m depth (pale blue region on Figure 2.3). The exceptions to this are:

1. Waters south of 60°S (no licences are issued for this region creating a de facto extension to the MPA).
2. Additional benthic closed zones (red hatched boxes - Figure 2.3) in which both pelagic and demersal activities are restricted.
3. No-take zones (NTZs) extending 12nm from the coast of South Georgia, Clerke Rocks and Shag Rocks covering an area of 16,237km^2.

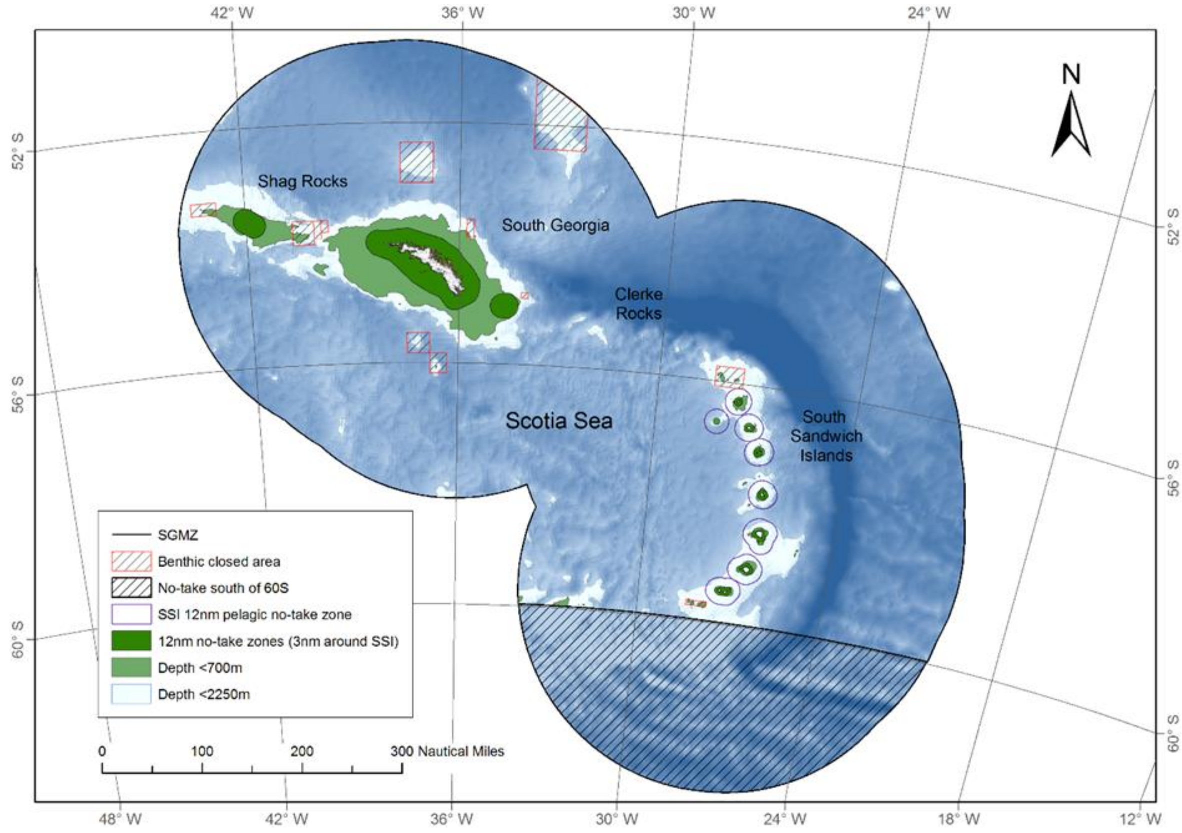

Figure 2.3. The South Georgia and South Sandwich Island Marine Protected Area. Dark green areas demark the no-take zones around South Georgia, South Sandwich Islands, Shag Rocks and Clerke Rocks. Light green indicates depths less than 700m in which bottom fishing is prohibited. Hashed boxes with red border are additional benthic closed areas established in 2013 in which bottom fishing is prohibited. The purple borders around SSI are a 12nm pelagic no-take zone. The large black hashed area south of 60° S falls within the SGSSI Maritime Zone in a region for which no fishing licenses are issued. In all other regions of the SGMZ bottom fishing is prohibited with the sole exception of the narrow pale blue region which includes the depths between 700m and 2250m. With-in this region bottom fishing by long-lining but not bottom trawling is permitted by license.

Pelagic protection is provided by a 12 nautical miles no-take zone around South Georgia and the South Sandwich Islands. In addition to these spatial restrictions is a five month seasonal closure of the Antarctic krill (*E. superba*) fisheries from November 1st - March 31st each year. The aim of this temporal closure is to reduce the potential conflict between the fishery and natural predators of krill, including seals, penguins, and other seabirds, especially during their breeding seasons.

2.4 Marine management objectives

Expanding on the four general management goals outlined in the SGSSI Management Plan (Collins et al., 2012) and summarised above, in 2011 a workshop of cross-disciplinary scientific experts working in partnership with the Government of SGSSI identified eight specific conservation priorities for the region. These are outlined in detail and assessed in relation to the current design structure of the SGSSI MPA by Trathan et al. (2014) and are summarised below:

1. Protection of representative pelagic environments

Bioregionalisation analysis of the pelagic environment was undertaken by Grant et al. (2006) and Raymond (2011) defining pelagic ecoregions based on four variables: sea surface temperature, mean sea surface height, chlorophyll a and depth. The analysis identified ten broad ecological regions for the SGSSI region (Appendix A: Supplementary materials Figure 2.1 and Table 2.1) which aligned strongly with the environmental structuring of the ACC (Longhurst, 1998). Representative protection of pelagic environments is currently provided by the 12nm no-take zone around South Georgia, Shag Rocks, Clerke Rocks and each of the South Sandwich Islands. Additional temporal protection is provided by the seasonal 151 day annual closure of the krill fisheries. Trathan et al. (2012) concluded this spatial/temporal protected afforded the region under the existing MPA exceeded the 20-30% representative protection goals of the United Nations World Summit on Sustainable Development (UN WSSD, 2002) and Decision X/2 by the CBD (Secretariat of the Convention on Biological Diversity, 2010).

2. Protection of large-scale ecological processes

Key large-scale ecological processes at South Georgia have been identified as (i) the transport and advection of krill from open ocean to neritic on-shelf environments (Trathan et al., 1995; Murphy et al., 1998; Pinõnes et al., 2011, 2013) and (ii) the flow of organic and detrital matter from pelagic to benthic environments (Ward et al., 2004; Atkinson et al., 2012). The current temporal closure of the krill fisheries was considered to provide considerable protection (Trathan et al., 2014) through protection of the summer transport and advection of krill by the ACC (Thorpe et al., 2007; Ward et al., 2007). Temporal protection from krill fisheries during the period of peak annual flux also protects the peak supply of organic and detrital matter from the pelagic to benthic realms.

3. Protection of trophically important pelagic prey species

Krill biomass at South Georgia varies both spatially and temporally (Trathan et al., 2003; Reed et al., 2010; Fielding et al., 2014). Whilst prediction of krill distributions is problematic, particularly off-shore (Trathan et al., 2003), seasonal closure during their summer spawning season mean that krill remain available to higher trophic level predators (Tarling et al., 2007; Trathan et al., 2014).

4. Protection of spatially constrained foraging areas of krill-eating predators

During the summer months South Georgia is an important breeding ground for large populations of higher predators which feed on and just beyond the South Georgia shelf (e.g. Boyd, 2012). Outside the breeding season many of these populations including Antarctic fur seals, albatrosses, petrels, macaroni penguins and southern right whales either leave the island or forage in deeper waters (Croxall et al., 2005; Phillips et al., 2005; Leaper et al., 2006; Phillips et al., 2006; Staniland et al., 2012; Ratcliffe et al., 2014). As such, these species are protected from competition with fisheries by the seasonal krill fishing closure. Others such as king penguins are considered year-round, central-place foragers at South Georgia or have breeding cycles outside the summer closure. In general however the majority of the foraging grounds are offshore (Hill et al., 2012) or their diet doesn't compete with the krill fisheries (Trathan et al., 2008).

5. Protection of localised areas of ecological importance

One such example is the localised protection of neritic and near-shore fish assemblages (Loeb et al., 1993) as a means to aid the recovery of previously depleted finfish stocks. (Trathan et al., 2014). Under the current MPA these assemblages are protected by a 12nm no-take zone around South Georgia, Shag Rocks, Clerke Rocks and each of the South Sandwich Islands. Knowledge of areas of ecological importance that overlap with the open fisheries zone is however limited, and so to therefore is our ability to mitigate damage to these areas.

6. Protection of representative benthic environments

The benthic diversity of South Georgia is extremely rich (Hogg et al., 2011) with a high proportion of species either endemic to the region or existing on the northern or southern limit of their geographical ranges (Barnes et al., 2009; Hogg et al., 2011). As such the region is recognised as of high priority with respect to conservation and management (Barnes et al., 2011). Analysis of vulnerable by-catch species (Martin et al., 2012) has led to the establishment of benthic closed areas around South Georgia and Shag Rocks and notably the West Shag Rocks and Gully are closed areas due to high abundances of gorgonians. The only depths open to bottom long-line fishing under current protection are between 700 and 2250m (8.01% of the SGSSIMZ). Paucity in biological data however, particularly at the South Sandwich Islands (but also South Georgia), provides us a very poor understanding of the region's biogeography. As such, there are significant limitations in our ability to inform on how representative benthic protection currently is.

7. Protection of areas important to Patagonian toothfish (D. eleginoides) life-cycle processes

Fifty-two percent of GSGSSI gross income come from toothfish licences (Trathan et al., 2014). Closure of inshore regions at South Georgia, closed areas on the slope and seamounts coupled with precautionary quota limits are aimed at protecting a proportion of the spawning stock biomass. Furthermore given toothfish are known to undertake down-slope migration with age (Collins et al., 2010), the cut-off in fishing at 2250m is designed to protect the largest, most fecund individuals (Trathan et al., 2014).

8. Protection of rare or vulnerable benthic habitats

As with benthic fauna (point 6), little is known of the spatial distribution of rare and vulnerable benthic habitats around South Georgia. The shelf environment is the most speciose region of the Southern Ocean recorded to date, with a large proportion of species recorded as rare or endemic (Hogg et al., 2011). Analysis of octocoral habitat suitability (Taylor et al., 2013) identified large areas of the South Georgia and Shag Rocks slope and continental shelf troughs as suitable for the presence of VME species. There is also good documentation of specific isolated examples of vulnerable habitats around South Georgia and South Sandwich Islands. These include hydrothermal black and white smokers with associated chemosynthetic communities along the East Scotia Ridge (Rogers et al., 2012); shallow water spirulid reef structures near Clerke Rocks on the South Georgia shelf, reported to be one of the largest such structures recorded anywhere in the World (Ramos and San Martin, 1999); a number of isolated seamounts which are potentially vulnerable to bottom fishing (Rowden et al., 2010). These named habitats are known to be or are potentially vulnerable and are protected through closure of the South Georgia shelf, deep sea (>2250m) or are afforded specific closed status (e.g. seamount and chemosynthetic communities). Universally however, there remains significant paucity in our knowledge of benthic habitat vulnerability around SGSSI, including the region that is currently open to long-line fishing.

Through the CBD, which was extended to South Georgia in 2014 (Barnes, 2011; GSGSSI Press Release, 2014), South Georgia and South Sandwich Islands represent two of the World's classified marine ecoregions (220 and 219 respectively), categorised under the Scotia Sea province 60 (Linse et al., 2006; Spalding et al., 2007). On top of the management objectives outlined above therefore, the CBD also stipulates the need for spatial protection to be representative of taxa and habitats, as outlined in section 1.2.

Chapter 3: Rationale and objectives

The Government of South Georgia & the South Sandwich Islands is undertaking the first 5-year review of its MPA since its establishment in 2012. Of the management priorities outlined preceding the review (see Trathan et al., 2014), the two pertaining to the benthic environment (namely section 2.4, points 6 and 8) are currently unresolvable due to a lack of quantitative assessment and thus understanding of the benthic environment. Consequently there is a significant gap in our knowledge which hinders the effective review of existing management measures and the evaluation of the extent to which the objectives of this purportedly sustainable-use MPA are met.

This thesis proposes to investigate the spatial distribution of benthic habitats and associated faunal communities at the sub-Antarctic island of South Georgia over a variety of spatial scales. The analysis will be framed within the context of marine spatial planning and as such will assess the utility of habitat mapping to inform and underpin marine management both at South Georgia and more universally. In doing so the following seven research objectives will be addressed:

1. Develop a methodology suitable for objectively partitioning the benthic environment based on its abiotic attributes.

2. Map the spatial distribution of these physical habitat classifications in a hierarchical framework that is able to reflect changes in environmental conditions across spatial scales.

3. Evaluate whether abiotic-derived habitat maps correlate to changes in the faunal structure of benthic communities both in terms of taxonomic and functional metrics.

4. Produce habitat suitability models relevant to the management of the region's marine resources, including modelling of taxonomic and functional groups, and occurrence of vulnerable marine ecosystems (VMEs).

5. Quantify the respective influences of environmental predictor variables on the region's benthic fauna.

6. Compile the aforementioned analyses to address whether current marine protection at South Georgia ensures protection of benthic diversity, vulnerability and representative protection of habitats.

7. Examine how the habitat mapping approaches adopted in this study are transferable to large marine protected areas in general.

The thesis is structured into three data chapters and a concluding synthesis chapter.

In the first data chapter I outline the development of an automated, objective and unsupervised marine landscape mapping protocol. The approach adopts a hierarchically nested clustering methodology to classifying physical habitat types across different spatial scales, from broad-scale (10–100s km) abiotic gradients (e.g. depth and temperature) to finer-scale features (100m–1 kms) such as local topography.

The robustness of this approach is tested through the use of spatial confusion indices. Given that such analysis is lacking from most marine spatial panning frameworks, the requirements of this protocol were that it should be robust, repeatable and have universal application for other proposed or established marine protected areas. It should provide a holistic overview of the marine environment, enabling the assessment of the ecological relevance of physical habitat classifications, their application as proxies for benthic biological structuring, and the application of the landscape mapping protocol for informing marine spatial planning. In addition this chapter also summarises the abiotic datasets used throughout this thesis and describes the development of a new high resolution interpolated digital elevation model of the region.

Building on the marine hierarchical landscape map developed in the first chapter, the second data chapter aims to assess the ecological relevance of marine landscape maps constructed using abiotic variables. Broad-scale mapping approaches are often applied at the regional level for the purposes of bio-regionalisation, conservation and management. Rarely, however, are environmental mapping clusters integrated with biological data to test the correlation between the physical environment, mapping clusters and the biological communities inhabiting those clusters. This chapter integrates biological data compiled for the benthic environment around South Georgia (see Hogg et al., 2011) with the hierarchy of landscape maps developed in the first data chapter for the South Georgia region. Using ordination techniques we assess whether broad-scale landscape mapping at South Georgia produces ecologically relevant results, i.e. do landscape mapping clusters at South Georgia exhibit a distinct benthic faunal signature. Within the global context of an increasing number of designated very large scale marine protected areas, we discuss whether hierarchical landscape maps represent an effective tool in addressing the mismatch between large-scale marine spatial planning and paucity in biological data.

Based on having described the spatial distribution of physical habitat types around South Georgia and their relationship to the faunal composition of the benthic environment, the third data chapter adopts a bottom-up approach to habitat mapping using an ensemble of predictive habitat mapping models. Benthic fauna is categorised by taxonomic group as well as assigned in to functional groups based on traits including feeding and reproductive strategies, mobility and affinity to specific substrata. This chapter aims to, (i) model the spatial distribution of key taxonomic groups, functional traits and management-specific metrics such as VMEs around South Georgia, and in doing so (ii) assess how modelled spatial data can help inform on marine spatial planning for the region. Using a split-sample assessment approach different modelling algorithms are compared and assessed. Modelled distributions are assessed in the context of the current zoned MPA in place at South Georgia, and specifically in relation to the regions open and closed to long-line fisheries. We therefore make an assessment as to whether the current spatial configuration of the MPA is best placed to protect benthic functional and taxonomic diversity.

In the concluding chapter the results and analyses outlined in the preceding three chapters are synthesised. In doing so, the respective merits and limitations of a top-down and a bottom-up approach to habitat mapping are assessed within the context of current and future marine management at South Georgia (as outlined in Chapter 2). Specifically, focus is placed on the applied nature of this PhD to undertake an evidence-based assessment of the effectiveness of current marine management measures, specifically whether the current spatial configuration of the MPA (i) protects a representative selection of benthic habitat (management objective 6, section 2.4), and (ii) whether spatial protection is optimised to maximise its protection of taxonomic and functional diversity and vulnerability (management objective 8, section 2.4). The degree to which evidence might support any future revisions to marine management is evaluated. Finally the application of different approaches to habitat mapping in large-scale MPAs and management areas more generally is discussed in a global context.

Chapter 4: Landscape mapping at sub-Antarctic South Georgia provides a protocol for underpinning large-scale marine protected areas

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Abstract

Global biodiversity is in decline, with the marine environment experiencing significant and increasing anthropogenic pressures. In response marine protected areas (MPAs) have increasingly been adopted as the flagship approach to marine conservation, many covering enormous areas. At present, however, the lack of biological sampling makes prioritising which regions of the ocean to protect, especially over large spatial scales, particularly problematic. Here we present an interdisciplinary approach to marine landscape mapping at the sub-Antarctic island of South Georgia as an effective protocol for underpinning large-scale (10^5–10^6 km^2) MPA designations. We have developed a new high-resolution (100 m) digital elevation model (DEM) of the region and integrated this DEM with bathymetry-derived parameters, modelled oceanographic data, and satellite primary productivity data. These interdisciplinary datasets were used to apply an objective statistical approach to hierarchically partition and map the benthic environment into physical habitats types. We assess the potential application of physical habitat classifications as proxies for biological structuring and the application of the landscape mapping for informing on marine spatial planning.

4.1 Introduction

Rates of species extinction currently exceed those of speciation, leading to a decline in global biodiversity (Butchart et al., 2010; Hooper et al., 2012; Ceballos et al., 2015) , Anthropogenic activities are significant drivers of this decline (Halpern et al., 2008), with the marine environment experiencing significant and increasing pressure from extractive industries such as fishing, marine deposit mining, and oil and gas extraction, activities, which are increasingly proliferating into deep-sea environments (Gross, 2014). Furthermore, the world's oceans are becoming warmer and more acidic (Stocker et al., 2013), driving changes in the distributions of marine species (Burrows et al., 2014), and impinging on ecosystem services (Worm et al., 2006; Cardinale et al., 2012).

Under financial, political and social constraints, two key questions that precede any conservation strategy are how and where to prioritise limited resources and effort to maximise the scientific robustness of conservation strategies in an increasingly exploited, yet still poorly understood marine environment. In response to international frameworks such as the Convention on Biological Diversity (Secretariat of the Convention on Biological Diversity, 2010), conservation efforts have increasingly prioritised the protection of regions and ecosystems as a holistic and geopolitically achievable approach to conservation. In recent years this has led to the establishment of several large-scale (10^5–10^6 km^2) marine protected areas (MPAs) at sites including Ascension Island (2016), Pitcairn Island (2015), South Georgia and South Sandwich Islands (2012) and the Chagos Archipelago (2010). The basis of many of these MPAs centre on the presence of particularly vulnerable, keystone, or charismatic species; the presence of large numbers (or proportions) of endemic species; and the presence of high biodiversity across taxonomic levels (i.e. biodiversity hotspots) (Sheppard et al., 2012; Trathan et al., 2015). The scientific underpinning for the creation of such vast reserves is based predominantly on *in situ* data such as biological sampling (e.g. by trawling, dredging and diving) and direct observation (e.g. by divers or camera systems). *In situ* sampling and observation, however, is intrinsically expensive, time-consuming, and logistically difficult, especially when attempting to cover large areas, inaccessible or remote regions. As such, biogeographical knowledge of the marine environment through *in situ* sampling is typically spatially very patchy and in some instances, notably the deep sea, virtually non-existent.

This paucity in knowledge is particularly problematic for the scientific underpinning of large-scale MPA designations. Frequently, ambitious political and social demand for high-impact, low-cost and large-scale management solutions conflict with scientific data that only support designation on localised scale, or in a generalised way (i.e. a region is known to have high faunal diversity but little is known about its distribution). As a consequence, MPA designation tends to be scientifically underpinned by the data that are available, but not scientifically driven in their design. By default the spatial configuration of many MPAs therefore tends to be delineated by geopolitical boundaries (e.g.

extent of Exclusive Economic Zones) and located in often remote overseas territories that elicit minimal stakeholder opposition.

In response to the challenge of limited biological data, habitat mapping can be used to greatly increase the value of limited *in situ* data for marine conservation, by inferring associations between ground-truthed sample data, remotely sensed geophysical data (e.g. topography; surficial geology), and physical environmental data (e.g. oceanography). In this way, in the absence of sufficient biological data, geophysical and biophysical attributes such as depth, substrate type, and geomorphology can act as useful surrogates for biological communities or assemblages (Zacharias & Roff, 2000). Analysis of the interaction between physical and biological variables helps create a more comprehensive spatial and temporal understanding of how biodiversity is structured across a region, and can help constrain the bio-physical processes driving this structuring. Furthermore remotely sensed data are typically orders of magnitude faster and cheaper to collect per unit area than ground-truthed sample data (Harris & Baker, 2011).

Marine landscape mapping is a form of top-down habitat mapping that delineates and describes the marine environment on the basis of physical characteristics. Biological data are then used to ground-truth the map to test how effective proxy habitat classification is for modelling biological distributions. Marine landscape mapping is often adopted as a broad-scale approach to habitat classification (Connor et al., 2006; Al-Hamdani & Reker, 2007) but is a technique with application across spatial scales (Cook et al., 2008; Verfaillie et al., 2009; Ismail et al., 2015). Through this approach, different geomorphic features such as canyons, pinnacles, rocky ridges and muddy basins can be mapped, either for their own intrinsic conservation value (Gray, 2004), or for use as proxies of particular types of benthic habitats (De Leo et al., 2010). This makes it a technique with potential application for assessing risk to benthic communities and in the proposing of MPAs designations.

The waters surrounding the sub-Antarctic island of South Georgia are one of the largest recently designated MPAs, and include one of the largest and most isolated continental shelf areas in the Southern Ocean. A combination of early separation from a continental land mass, a large shelf area, a high degree of geographic isolation, and the proximity of nutrient-rich currents have led to the evolution of a biologically rich and distinct island (Hogg et al., 2011). In 2012 the region (including the South Sandwich Islands archipelago to the south-east) was designated an IUCN category IV marine protected area, covering a total area of over one million km^2 (Trathan et al., 2014).

The regional waters around South Georgia represent a particularly good model system in which to develop, test, and implement a landscape mapping protocol. The region is one of a number of recent additions to the list of extremely large-scale MPAs. There has been no concerted effort (expeditions to the region) with the specific purpose of mapping physical habitats or biotopes. As such, all data from the region are (from a habitat mapping perspective) based on opportunistic historical data collection. This is important in developing a protocol that has transferability to other marine systems, as the suite of data available at South Georgia is comparable with most other potential large-scale MPA sites. The existence of a number of comprehensive datasets including seabed geophysical data; modelled oceanographic data, sediment data, and an extensive biological dataset provides an ideal opportunity for interdisciplinary habitat mapping. In addition to being a good location to test landscape mapping models, it is also an internationally important site to understand and conserve because of its speciose and unique benthic fauna, commercially important fisheries and the presence of a globally important population of higher predators (Hogg et al., 2011; Trathan et al., 2015).

The aim of this study is to develop a fully automated and objective marine landscape mapping protocol that adopts a hierarchically nested clustering approach to classify physical habitat types across spatial scales. This protocol should be robust, repeatable and have universal application for other proposed or established marine protected areas. It should also enable assessment of the ecological relevance of physical habitat classifications, their application as proxies for benthic biological structuring, and as such the application of the landscape mapping protocol for informing marine spatial planning.

4.2 Methodology

4.2.1 Study area

The greater South Georgia region, which forms the focus of this paper, is defined here by a bounding box of ~900 km (45°E to 19°E) by ~580 km (63°S to 50°S), covering an area of 530,000 km^2 (Figure 4.1). The region includes the South Georgia shelf, the Shag Rock shelf (to the west of South Georgia), the surrounding continental slopes and adjacent deep sea. It does not, however, extend to include the South Sandwich Islands region of the SGSSI MPA. The rationale for this geographical delimitation at the expense of covering the entire > 1 million km^2 of the SGSSI MPA was based on the limited spatial extent of input datasets (notably the modelled oceanographic dataset).

4.2.2 Data compilation

Bathymetry gridding process

We constructed a new high resolution (100 m) bathymetric grid of the South Georgia continental shelf, slope and surrounding open-ocean. The grid was derived from multibeam and single-beam echo-sounding data compiled from numerous research institutes, universities and commercial fisheries (see Appendix B: Supplementary materials Table 4.1). Given the diverse range of data sources, the echo-sounding data varied greatly in terms of collection method, data quality, and file format. As such the process of incorporating different data streams into the compilation varied depending on their provenance.

Data curated at the BAS Polar Data Centre and collected during 36 research cruises between 1994 and 2013 were gridded at a 100m resolution using MB-System (Caress & Chayes, 1996). Unprocessed data from recent BAS cruises to the region were cleaned using CARIS HIBS & SIPS (version 8.1) to remove erroneous points. Data collected by the Alfred Wegener Institute, Bremerhaven (AWI) over the course of 22 cruises to the region between 1985 and 2013 as well as data collected on a recent R/V Nathaniel B. Palmer cruise were processed and gridded to 100m resolution using Fledermaus (version 7.0).

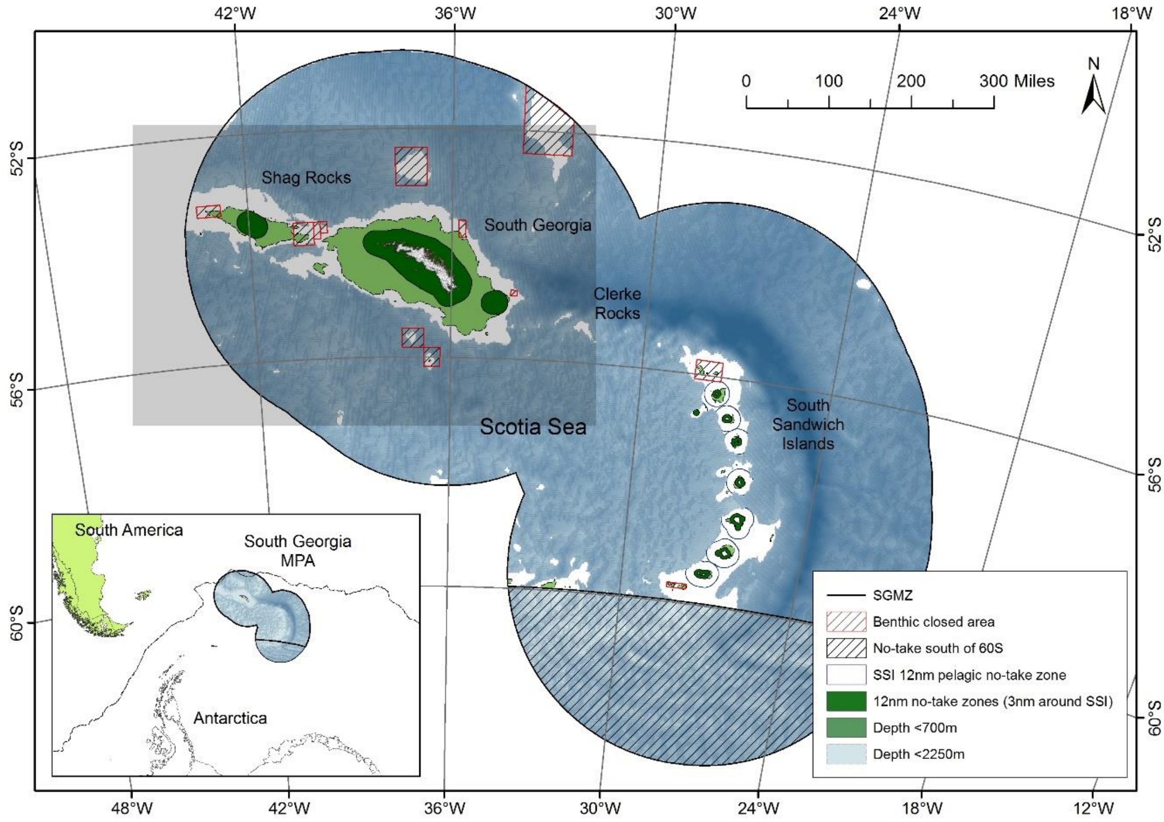


Figure 4.1. The South Georgia and South Sandwich Islands marine protected area. Dark green areas demark the no-take zones around South Georgia, South Sandwich Islands, Shag Rocks and Clerke Rocks. Light green indicates depths less than 700 m in which bottom fishing is prohibited. Hashed boxes with red border are additional benthic closed areas established in 2013 in which bottom fishing is prohibited. The purple borders around SSI are a 12nm pelagic no-take zone. The large black hashed area south of 60° S falls within the SGSSI Maritime Zone in a region for which no fishing licenses are issued. In all other regions of the SGMZ bottom fishing is prohibited with the sole exception of the narrow pale blue region which includes the depths between 700m and 2250m. Within this region bottom fishing is permitted by license. The region of interest for this study is delineated by the grey shaded box. The inset shows the position of the South Georgia and South Sandwich Islands MPA relative to South America, the Antarctic continent and the Polar Front (dashed line). Figure was created using ArcGIS (version 10.1 [www.esri.com/software/Arcgis]). Background bathymetry is The GEBCO_2014 Grid, version 20141103 (http://www.gebco.net).

Single-beam bathymetry data were obtained from the UK Hydrographic Office (UKHO), BAS and commercial fisheries vessels. The spatial coverage of respective datasets is summarised in Figure 4.2.

As with a number of previous bathymetric compilations (Fretwell et al., 2008; Fretwell et al., 2013; Dickens et al., 2014) we used TOPOGRID to grid the digital elevation model. TOPOGRID is an interpolation function in ArcGIS (version 10.1) built around the ANUDEM algorithm (Hutchinson, 1989; Hutchinson et al., 2011), which has been shown as an effective approach to integrating spatially discontinuous data with different sampling densities whilst minimising standard error in the model (Dickens et al., 2014). The ANUDEM algorithm runs over multiple iterative cycles. It starts by gridding data at a coarse spatial resolution before interpolating at successively finer resolutions, until the pre-defined resolution (in this case 100m) is reached. TOPOGRID is particularly well-suited to constraining fine-scale topographic features whilst imposing constraints to prevent erroneous sinks being formed in the output digital elevation model (DEM) (Young et al., 2011).

The quality of the data varied between surveys as a result of a number of factors including the echo-sounder equipment used, the calibration of this equipment (i.e. the use of different sound-velocity profiles), the sea state conditions at the time of data collection, and the degree and quality of data post-processing and cleaning. This variability was manifest in two key regards: the effective spatial resolution of the data (i.e. at what spatial scale the bathymetry could be rendered at), and the presence of acquisition artefacts (artificial 'sinks' or 'peaks') in the data.

TOPOGRID reads data as point 'xyz' (longitude, latitude, depth) records for each data source. Creating a bathymetric compilation from a point cloud is inherently problematic given the variability in the quality of the data from different sources. Specifically, this is a problem when regions of data points from different sources (which may vary in spatial resolution by 10 s or 100 s of meters) overlap. The algorithm will treat each point as equally valid, and draw a spline between them, potentially creating steps in the data as it moves between points from different sources. To remove this artefact, we ranked our datasets hierarchically based on data quality. Using spatial coverage masks of each dataset, regions of overlapping data were cut from all masks except for the mask representing the best-quality data available from that particular region. In this way we created a continuous mosaic of masks for the entire South Georgia region with no overlapping parts and only the best available data representing each region. To avoid artificial 'steps' in the data, a 500m buffer was used to create a region of no-data on the boundaries between different data layers. This had the effect of 'smoothing out' any abrupt changes at the boundaries of adjoining data layers during interpolation. These masks were then used to extract the respective point data to input into TOPOGRID.

Ideally, only cleaned data would be input into the interpolation. Given the number of data points involved in an analysis of this scale ($> 1.0 \times 10^8$), however, this was impractical. After gridding the data with TOPOGRID, the new interpolated 100m resolution raster data was therefore overlaid with the point cloud of original input data.

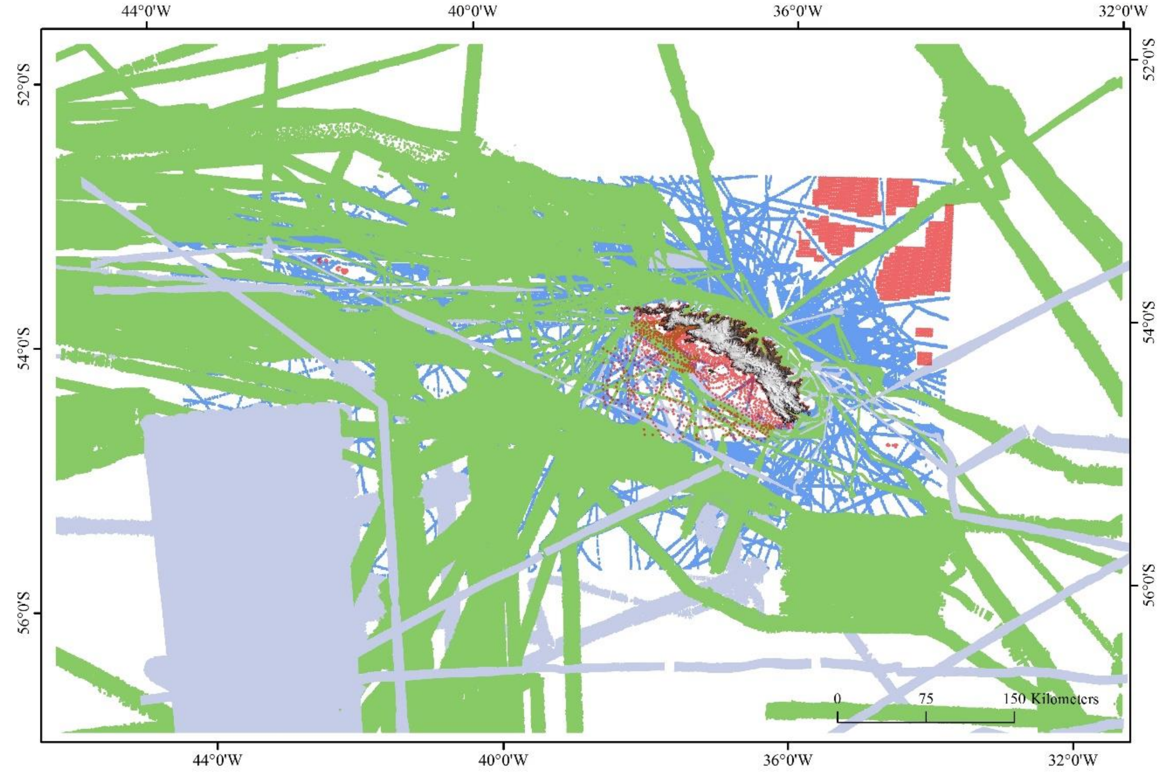


Figure 4.2. The spatial coverage of data sources used in the bathymetry compilation. Multi-beam data derived from BAS cruises are shown in green; AWI and other multi-beam (see Appendix B: Supplementary materials Table 2.1 for sources) are shown in grey; single-beam data is shown in blue and UK Hydrographic Office and coastline data is shown in red. For the remaining white areas The GEBCO_2014 Grid, version 20141103 (http://www.gebco.netdata) was used. Figure was created using ArcGIS (version 10.1 [www.esri.com/software/Arcgis]).

Points that were deemed to be creating false peaks and sinks were manually removed using the ArcGIS Editor toolbox. After this iterative process, the final DEM was considered to be as accurate as possible, with a minimum amount of sampling artefact but without excessive data smoothing.

Bathymetry derivatives

The new 100 m resolution DEM was used to calculate five bathymetry derivative datasets, which alongside oceanographic and net primary productivity data (summarised in Table 2.1) formed the basis for the landscape mapping analysis. These bathymetry derivatives included measures of slope angle, seabed rugosity, topography, aspect and curvature.

Slope was calculated using LandSerf (version 2.3) multi-scale analysis. To 'smooth out' sampling artefacts and noise in the data, the effective resolution of the slope was reduced by introducing a window scale of 10 grid cells (i.e. 1000 m) with an inverse linear distance decay, whereby the analysis takes into account the slope value of surrounding cells (in this case with a diameter of 10) to give greater importance to cells closer to the target cell. The effect of this is to remove finer-scale variation in slope morphology but retain larger topographic features.

Topographic position index (TPI) was calculated using Land Facet Corridor Tools extension for ArcGIS. TPI provides a measure of whether a cell is positioned on a peak, in a depression, or in a region of constant gradient (flat or constant slope) relative to the surrounding cells. It can account for local scale topography versus broader-scale features by changing the size of the window of reference. For this analysis a window size of 10 was used.

Terrain ruggedness index (TRI) was calculated using SAGA GIS Terrain Analysis Morphometry tools as a measure of rugosity. TRI is calculated as the square root of the sum of squared difference between the bathymetric value of a cell and its 8 surrounding cells.

Aspect was calculated using the spatial analyst toolbox in ArcGIS. It provides a measure of the geographical orientation of a region as a circular data variable, from which we created two variables: northness = cos (aspect*π/180), as a measure of orientation on the north-south axis, and eastness = sin (aspect*π/180), as a measure of orientation on the east-west axis.

Profile curvature was calculated using the spatial analyst toolbox in ArcGIS. It is a second derivative index of bathymetry that measures the surface shape of the seabed in the steepest downhill direction quantifying the rate at which slope gradient changes. Regions with constant gradient return a value at or approaching zero, concave and convex slopes return large negative and positive values respectively.

Other abiotic variables

Oceanographic data were derived from a high-resolution 3D hydrodynamic model of the South Georgia shelf and adjacent open-ocean (Young et al., 2011). The model is based on the Proudman Oceanographic Laboratory Coastal Ocean Modelling System (POLCOMS) providing salinity, temperature, current magnitude and current direction data at a spatial resolution of 2.8km. Surface and seabed data, taken as a summer (Dec–Feb) and winter (Jun–Aug) mean were averaged over three years (1999–2001). The model is validated against an extensive CTD dataset at South Georgia, shore-based tide gauges, and satellite temperature data. It has been shown to be particularly good at resolving tidal processes, topographically steered currents, and freshwater fluxes from island runoff (Young et al., 2011).

Satellite derived net primary productivity data (NPP) were accessed through Oregon State University (http://www.science.oregonstate.edu/ocean.productivity/). Here NPP is defined as a function of chlorophyll, available light, and photosynthetic efficiency. The data are derived from the Vertically Generalized Production Model (VGPM) (Behrenfeld & Falkowsk, 1997), MODIS surface chlorophyll concentrations (Chl_{sat}), MODIS 4-micron sea surface temperature data (SST4), and MODIS cloud-corrected incident daily photosynthetically active radiation (PAR).

Table 4.1. Abiotic variables included in the landscape mapping analysis.

Abiotic Variables	Description	Unit	Scale
Topography			
Digital elevation model (DEM) of bathymetry	Bathymetric compilation of multibeam, singlebeam and soundings data (see Table 1 for sources) interpolated using TOPOGRID algorithm.	m	100m
Slope	A first derivative of DEM representing the rate of change in depth from one cell to its neighbours.	°	100m
Terrain Ruggedness Index	A measure of rugosity calculated as the ratio of the three-dimensional DEM surface area to the two-dimensional planar area of a cell.	-	100m
Eastness = sin(aspect/57.296)	A first derivative of DEM providing a measure of the easterly orientation of the slope on a continuous scale (-1 to +1).	-	100m
Northness = cos(aspect/57.296)	A first derivative of DEM providing a measure of the northerly orientation of the slope on a continuous scale (-1 to +1).	-	100m
Profile curvature	A second derivative of DEM measuring the rate of change in the slope gradient.	-	100m
Topographic Position Index (TPI)	A measure of whether a cell is positioned on a topographic peak, in a depression on in a region of constant gradient.	-	100m
Satellite derived variables			
Net primary productivity	5-year mean net primary productivity calculated using VGPM, *a global "chlorophyll-based" model that estimate net primary production from chlorophyll using a temperature-dependent description of chlorophyll-specific photosynthetic efficiency* [31].	Mg C/m^2 /day	1/12°
Oceanography	Three year means derived from the Proudman Oceanographic Laboratory Coastal Ocean Modelling System (POLCOMS) South Georgia high-resolution dataset [29].		
Summer Seabed Temperature	Three-year austral summer (Dec-Feb) bottom temperature mean.	°C	2800m
Summer Seabed Salinity	Three-year austral summer (Dec-Feb) bottom salinity mean.	PSU	2800m
Summer Seabed Current U	Three-year austral summer (Dec-Feb) mean measure of the easterly orientation of the current on a continuous scale (-1 to +1).	-	2800m
Summer Seabed Current V	Three-year austral summer (Dec-Feb) mean measure of the northerly orientation of the current on a continuous scale (-1 to +1).	-	2800m
Summer Seabed Current Magnitude	Three-year austral summer (Dec-Feb) mean measure of current magnitude	m/s	2800m
Winter Seabed Temperature	Three-year austral winter (Jun-Aug) bottom temperature mean.	°C	2800m
Winter Seabed Salinity	Three-year austral winter (Jun-Aug) bottom salinity mean.	PSU	2800m
Winter Seabed Current U	Three-year austral winter (Jun-Aug) mean measure of the easterly orientation of the current on a continuous scale (-1 to +1).	-	2800m
Winter Seabed Current V	Three-year austral winter (Jun-Aug) mean measure of the northerly orientation of the current on a continuous scale (-1 to +1).	-	2800m
Winter Seabed Current Magnitude	Three-year austral winter (Jun-Aug) mean measure of current magnitude	m/s	2800m
Seabed Temperature Range	Temperature differential between three-year summer and winter means.	°C	2800m

Euphotic depths are calculated from Chl_{sat}. The data were extracted as monthly means over a five year period (2010–2014) with a grid cell resolution of 1/12 degree of latitude (~9275 m) by longitude (~5465 m). R (version 3.1.2) was used to define the geographic region of interest, create a data matrix of each month's mean NPP, and transpose this into a raster dataset with the correct geographic projection and each grid cell pixel representing a mean NPP for five-year of monthly data.

To standardise the spatial extent and resolution of each input variable, each dataset was converted to the same file format (.img), spatial units (meters) and projection (South Georgia Lambert Conic Conformal, WGS1984), with each raster resampled using nearest neighbour analysis to the same spatial resolution. For the oceanographic and satellite primary productivity data which had coarser spatial resolutions (see Table 4.2), data were resampled to 100m using ArcGIS spatial analyst spline (with barrier) interpolation. Spline with barrier interpolation was selected on the basis of its suitability for environmental variables that change over gradients. The spline barrier used was a polygon of the coastline of South Georgia to prevent values being interpolated across the physical boundary of the island.

Landscape mapping

The statistical approach to mapping marine landscapes presented in this study is based on an unsupervised mapping protocol developed for shallow water shelf environments (Verfaillie et al., 2009) and subsequently adapted for use in the high–resolution analysis of submarine canyon systems (Ismail et al., 2015).

The protocol for landscape mapping can be summarised in five steps. (1) principal component analysis (PCA) of the gridded environmental variables; (2) determination of the optimal cluster solution; (3) *K*-means clustering of the principal components; (4) plotting the optimal cluster solution as a landscape map and assigning environmental meaning to each cluster based on the relationship between the original environmental variables and each cluster; (5) assessment of the stability of the clustering solution based on calculation of membership values and corresponding confusion indices (Burrough et al., 1997).

The software used for PCA, *K*-means clustering, cluster validation, and raster map creation was R version 3.0.0. Given the large size of the South Georgia datasets, this was run remotely on the University of Southampton Iridis4 high performance cluster computing system high memory nodes.

Principal components analysis

Principal component analysis was conducted on 19 abiotic environmental variables (Table 4.1). The input variables were all standardised to have zero-means and unit variance, thus giving them equal weight in the PCA. PCA reduces the input variables down to a new set of linearly independent variables called principal components (PCs) that account for most of the variance observed in the original data (Legendre & Legendre, 1998). It acts as an objective means of data reduction when dealing with multiple input variables without the need for an *a priori* assessment of which variables should form the basis of the analysis (Kabacoff, 2013), whilst removing collinearity in the data. We followed the Kaiser-Guttman criterion (Legendre & Legendre, 1998), retaining only PCs with Eigen values greater than one. In order to maximise the independence of the PCs and simplify the interpretation of the factor loading pattern, a varimax rotation of the PCs was computed. These rotated PCs were the input for the *K*-means analysis.

K-means clustering and defining optimal number of clusters

The *K*-means clustering algorithm is a widely used method for partitioning marine environmental data (Legendre et al., 2002; Verfaillie et al., 2009; Ahmed & Demsar, 2013; Ismail et al., 2015). *K*-means works by partitioning *n* observations into a pre-defined *k* number of clusters whereby each observation is assigned to the cluster that minimises the distance of that point to the cluster centroid. The most subjective element in *K*-means clustering is the requirement for the input of a predefined number of clusters into the algorithm. There are several indices that can be used to define the optimal number of clusters (Milligan & Cooper, 1985), with many available in *R* through the NbClust package (Charrad et al., 2014). We used two separate indices that have been shown to be offer effective solutions. The C-H criterion (Lucieer & Lucieer, 2009) evaluates the validity of different cluster solutions based on the proportion of the total variance explained by variance between clusters (between group sum of squares - SSB) (Milligan & Cooper, 1985). The second approach was an 'elbow' method which plots variance within clusters (within group sum of squares – SSW) against an increasing number of *K*-means clusters (here ranging from 2 to 15). As the number of clusters increases the SSW decreases. The optimal cluster solution is defined by a change in gradient or elbow in the graph representing the point at which increasing the number of clusters further will not greatly reduce SSW.

Marine landscape and confidence map

Once the optimal cluster solution was decided, the results of the subsequent *K*-means analysis (predefined for number of clusters) were converted to a raster grid in R and exported to ArcGIS to create a marine landscape map of the region at the same spatial resolution and projection as the original abiotic input variables. Boxplots of the abiotic input variables against the *K*-means cluster solutions were used to characterise and offer interpretation of the environmental conditions driving the classification of each cluster. Interpretation of these boxplots was used to assess the performance of the automated landscape classification in terms of the perceived ecological meaningfulness of the classifications. Given that all input variables were standardised at the start to provide them equal weight in the PCA analysis, qualitative assessment was made as to whether any of the variables were disproportionately influencing cluster classification and if so whether these needed to be removed and the analysis re-run.

Once the final clustering solution was achieved, the stability of the clusters was assessed by creating a separate set of cluster membership maps. Cluster membership is a methodology adapted from fuzzy *K*-means classification (Burrough et al., 1997; Lucieer & Lucieer, 2009; Ismail et al., 2015), and is defined by calculating the relative inverse distance squared in attribute space between each individual data point and the centroids of all the *K*-means clusters. The sum membership value to all centroids of any given point equals 1. As such, a data point with a high membership value (approaching 1) would indicate that point is dominated by membership to one cluster. A data point with lower membership values, spread over a number of clusters, is less well characterised by membership to its *K*-means designated cluster. Membership value is expressed by formula 1:

$$\mu_{ik} = \frac{1}{(d_{ik}^2)} \times \frac{1}{\sum_{k=1}^{n} \frac{1}{(d_{ik}^2)}} \qquad (1)$$

where μ_{ik} is the membership value of the ith data point to cluster k, n is the number of clusters, and d_{ik} is the distance between data point i and cluster centroid k. Using the highest and second highest membership value for each data point, the confusion index can be calculated for all points to offer a quantitative measure of the uncertainty associated with the classification of each point into clusters by *K*-means. The confusion index is calculated by formula 2:

$$CI = \frac{\mu_{(max-1)i}}{\mu_{\max i}} \qquad (2)$$

where CI is the confusion index, $\mu_{\max i}$ is the membership value of the cluster with maximum μ_{ik} at location i, and $\mu_{(\max-1)i}$ is the second largest membership value at the same i location. The CI of any given point can range between 0 and 1, with uncertainty in the *K*-means clustering solution between two or more clusters at that location increasing as CI approaches 1.

Nested-hierarchical clustering

Once a stable landscape map is produced which minimises within-cluster variance, and is qualitatively assessed to offer a good representation of the physical marine landscapes of the region, the landscape mapping protocol can begin again. This time the analysis is delineated by, and done in isolation for each of the cluster solutions derived from this first iteration. In this way a nested hierarchical clustering structure for the region is created, whereby each successive level of the hierarchy provides progressively more detail on the physical environment characterising each region. This method of hierarchically nested clustering provides a physical habitat classification system that is specific to a given region of interest. This is in marked contrast to more generalised models of habitat classification (Davis et al., 2004), which offer a one-size-fits-all solution that is not always ecological meaningful across all marine environments (e.g. deep-sea environments (Ross & Howell, 2013)). This hierarchical approach also offers the opportunity to assess environmental conditions across spatial scales and in turn the interaction between faunal communities and environment over these different scales.

4.3 Results

4.3.1 Bathymetric compilation

The new 100 m resolution South Georgia Bathymetric Dataset (SGBD) (Figure 4.3) covers an area of 530,000 km^2, of which 54.4% (288,470 km^2) is derived from multibeam data, 10.2% (54,022 km^2) from singlebeam data and the remaining 35.4% (187,508 km^2) is derived from The GEBCO_2014 Grid, version 20141103 (http://www.gebco.netdata). The SGBD offers significant improvements on the pre-existing bathymetric knowledge of the region (Fretwell et al., 2008), specifically in terms of the inclusion of new high resolution datasets in the interpolation, the resulting increased spatial resolution of the grid (100m), and its wider geographical extent. The grid is projected in Lambert Conformal Conic (LCC) projection optimised for South Georgia to give a more realistic representation of the shape of topographical features.

The high resolution of the SGBD enables us to better constrain fine-scale topographic features. The shelf is dominated by deeply incised glacial cross-shelf troughs (Figure 4.3), extending from coastal fjords, in most cases to terminal moraine fields at or near the shelf break. The troughs form deep (100–160 m) and narrow depressions (~2 km) that converge further offshore to form large (up to 20 km) canyons cut into the shelf. The higher resolution grid enables us to delineate the extent of the shelf itself far more accurately, and pick out in much sharper detail the shelf break, including the presence of complex gully systems on the steep continental slope. The SGBD covers a bathymetric range of 0–5500 m. The inclusion of the deep sea in the compilation reveals that these regions are not homogenous but exhibit complex and sudden changes in topography (Appendix B: Supplementary materials Figure 4.1). This includes geological features with some of the steepest slopes in the region (drop-offs from 2500 m to > 4500 m with slope angle > 45°).

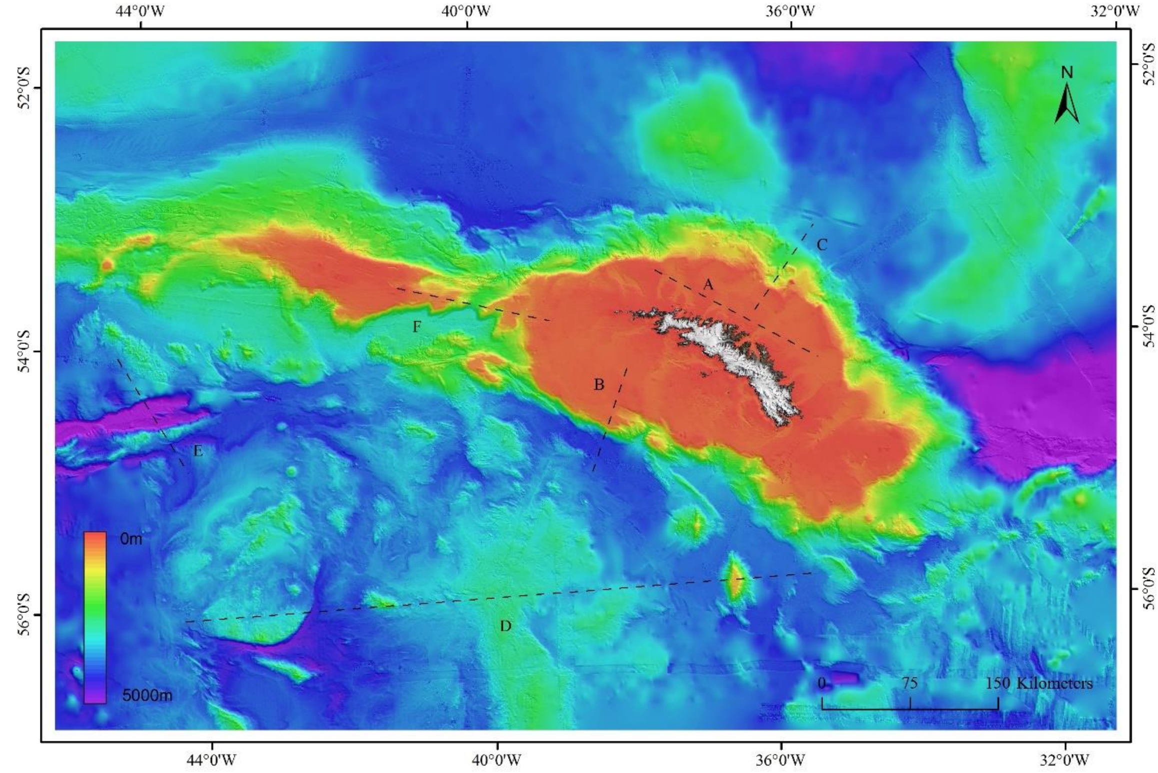


Figure 4.3. New bathymetric compilation for South Georgia gridded to a spatial resolution of 100 m. Transects (A–F) denote depth-profile plots shown in Appendix B: Supplementary materials Figure 4.1. Figure was created using ArcGIS (version 10.1 [www.esri.com /software/Arcgis]) TOPOGRID (Spatial Analyst Tools) to grid datasets listed in Appendix A: Supplementary materials Table 4.1.

4.3.2 Landscape mapping

Principal components analysis

Principal component analysis was conducted using 19 abiotic input variables (Table 4.1). After running the entire landscape mapping protocol and conducting a qualitative assessment of the output map however, aspect was excluded from the analysis as it was creating ecologically meaningless clusters in the deep sea (i.e. regions > 3000m depth with very low slope gradients but different orientation). As such the principal component analysis was re-run with the remaining 17 abiotic variables from Table 4.1. Retaining only PCs with Eigen values greater than 1, PCA resulted in six PCs, explaining 81% of the total variance. The rotated components matrix (Table 4.2) shows the factor loads which explain the correlation between Varimax rotated PCs (with Eigen values > 1) and the original abiotic input variables and excludes any factor loads < 0.3. Assessment of the rotated components matrix showed only one variable (depth) had a high factor load for multiple PCs, all other variables had an exclusive relationship with specific PCs. PC 1 had high loads ($r < -0.6$ or $r > 0.6$) for the variables depth, seabed

Table 4.2. Component matrix showing correlation between the Varimax rotated PCs and the original input variables. High factor loads (r < -0.6 or r > 0.6) are highlighted in bold; Low factor loads (r < -0.3 or r > 0.3) are omitted.

Abiotic Variables	PC1	PC2	PC3	PC4	PC5	PC6
Depth	**-0.652**	-	-	-	**0.673**	-
Slope	-	-	-	**0.958**	-	-
Terrain Ruggedness Index	-	-	-	**0.959**	-	-
Curvature	-	-	-	-	-	**0.807**
Topographic Position Index	-	-	-	-	-	**0.812**
Primary Productivity	-	-	-	-	-	-
Summer Seabed Temperature	-	-	-	-	**0.926**	-
Summer Seabed Salinity	**0.951**	-	-	-	-	-
Summer Seabed Current U	-	**0.875**	-	-	-	-
Summer Seabed Current V	-	-	**0.968**	-	-	-
Summer Seabed Current Magnitude	-	**0.861**	-	-	-	-
Winter Seabed Temperature	-	-	-	-	**0.970**	-
Winter Seabed Salinity	**0.933**	-	-	-	-	-
Winter Seabed Current U	-	**0.882**	-	-	-	-
Winter Seabed Current V	-	-	**0.974**	-	-	-
Winter Seabed Current Magnitude	-	**0.861**	-	-	-	-
Seabed Temperature Range	**-0.763**	-	-	-	-	-
Variance Explained (%)	16.60%	18.40%	11.70%	11.80%	14.80%	7.70%
Cumulative Variance (%)	16.60%	35.00%	46.70%	58.50%	73.30%	81.00%
Eigenvalues	**3.7053**	**3.3623**	**2.0678**	**1.8257**	**1.5012**	**1.3138**

temperature range and seabed salinity; PC 2 for current magnitude (specifically on an easterly axis); PC 3 for current on a northerly axis; PC 4 for slope gradient and terrain ruggedness; PC 5 for depth and seabed temperature; and PC 6 for curvature and topographic positioning. Primary productivity was not related to a specific PC, but did play a role in the distinction between classes (see below).

K-means

A total of 52,996,140 grid cells with six rotated PC variables were clustered using *K*-means, in a cascade from two to fifteen cluster solutions. The resulting within group sum of squares were plotted against number of clusters (Figure 4.4a). Using the 'elbow' method, where a change in the gradient of the graph identifies the optimal cluster solution, seven clusters were assessed to be a good fit for the data. To validate this result, the C-H criterion was applied to the data with the same cascade in cluster solutions (Figure 4.4b). A clear optimum of seven clusters was found, hence a final K-means clustering using seven clusters was carried out.

Marine landscape

The results of the seven cluster K-means is presented in Figure 4.5a. A description of the physical characteristics of each cluster was obtained based on interpretation of boxplots showing the correlation between the original 17 abiotic input variables and each of the seven clusters (Figure 4.6). Four of the seven clusters (1, 4, 5, and 6) demonstrated a clear, distinct suite of physical conditions.

Clusters 1 and 6 were characterised by the prevalence of relatively strong bottom currents in a northerly ($\bar{x}$=0.05 m/s) and south-easterly ($\bar{x}$=0.1 m/s) direction respectively. These currents appeared to be associated with large-scale, deep-sea topographic features (especially cluster 6). Cluster 4 was regionally widespread but locally spatially constrained. It demonstrated no dependence on depth or oceanography but was dominated by locally complex seabed topography. Cluster 4 exhibited steep slopes (> 10°), high terrain ruggedness (rugosity) and a large range in curvature and topographic position values suggesting a region of topographic peaks and depressions. Cluster 5 was the most spatially discrete cluster and was characterised by shallow water; flat terrain; large annual temperature range; low salinity; and high primary productivity. We interpret this cluster as the continental shelf of South Georgia and Shag Rock.

The three remaining clusters (clusters 2, 3 and 7) are more difficult to constrain. All three clusters have a deep sea element (depths > 2500 m). Cluster 3 had a large but northerly-restricted distribution. It exclusively represented deep-sea environments with low sea-bed temperature ($\bar{x}$=0.5 °C), but was primarily defined by its significantly higher sea-surface primary productivity ($\bar{x}$=420 Mg C/m2/day). Cluster 2 also represented exclusively deep sea (2500–4500 m) environments with low sea-bed temperature ($\bar{x}$=0.75 °C). It had a largely, but not exclusively southern spatial distribution. However it was the drivers of other clusters (primary productivity for cluster 3 and temperature for cluster 7) that distinguished them from it rather than its own characterisation that sets it apart. As such depending on the interpretation of the importance of surface primary productivity on deep-sea benthic environments (cluster 3) it is entirely plausible to group clusters 2 and 3 together as a generic deep sea, flat abyssal plain with stable low temperature.

Cluster 7 was characterised by annually-stable, warmer sea-bed temperatures ($\bar{x}$= 1.4 °C). Though mostly occurring in depths of 2000–3000 m the overall bathymetric range of the cluster was wide with the deeper extremities of the South Georgia shelf and the lower gradient regions of the slope represented by cluster 7. The only bathymetric exclusion from cluster 7 were shelf environments with depths < 250 m.

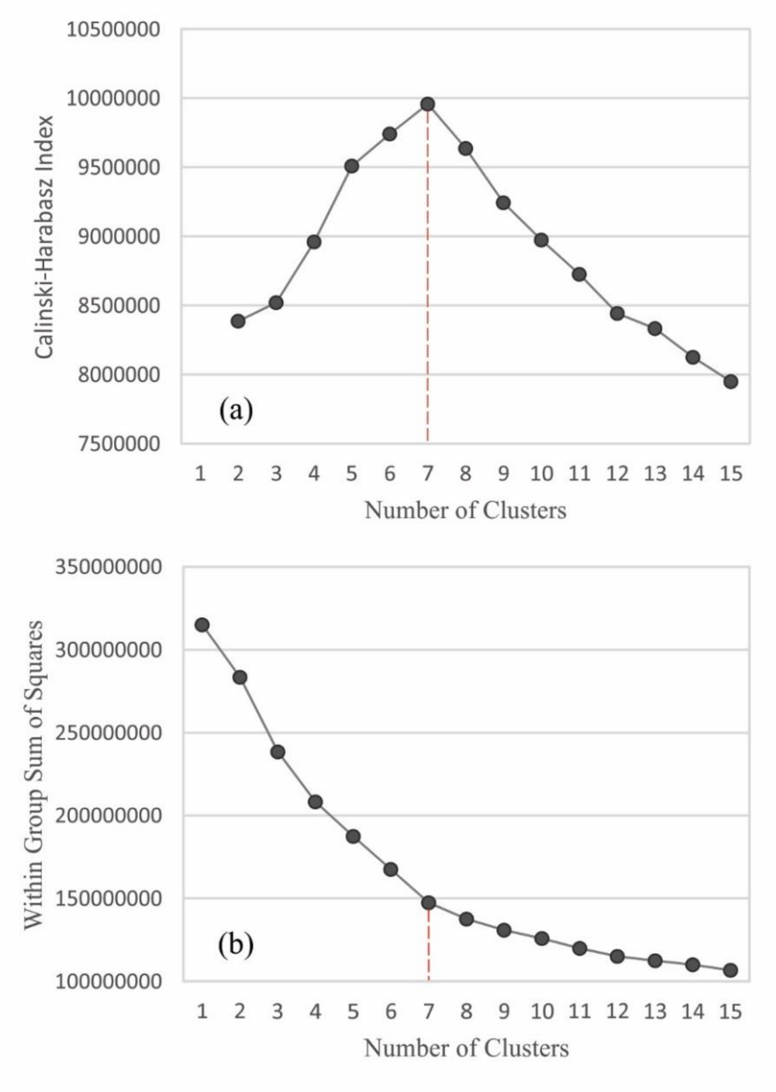


Figure 4.4. Optimal K-means cluster solution. Calculated as, (**a**) the number of clusters versus the Calinski-Harabasz (C–H) criterion, whereby the optimal cluster solution corresponds to the first local maximum of the C-H value; and (**b**) the number of clusters versus the within group sum of squares based on Varimax rotated PCs, whereby the optimal cluster solution is identified by an 'elbow' or change in the gradient of the slope. For both indices the best solution is identified as 7 clusters (marked in red). Figures created using R (version 3.0 [www.r-project.org]).

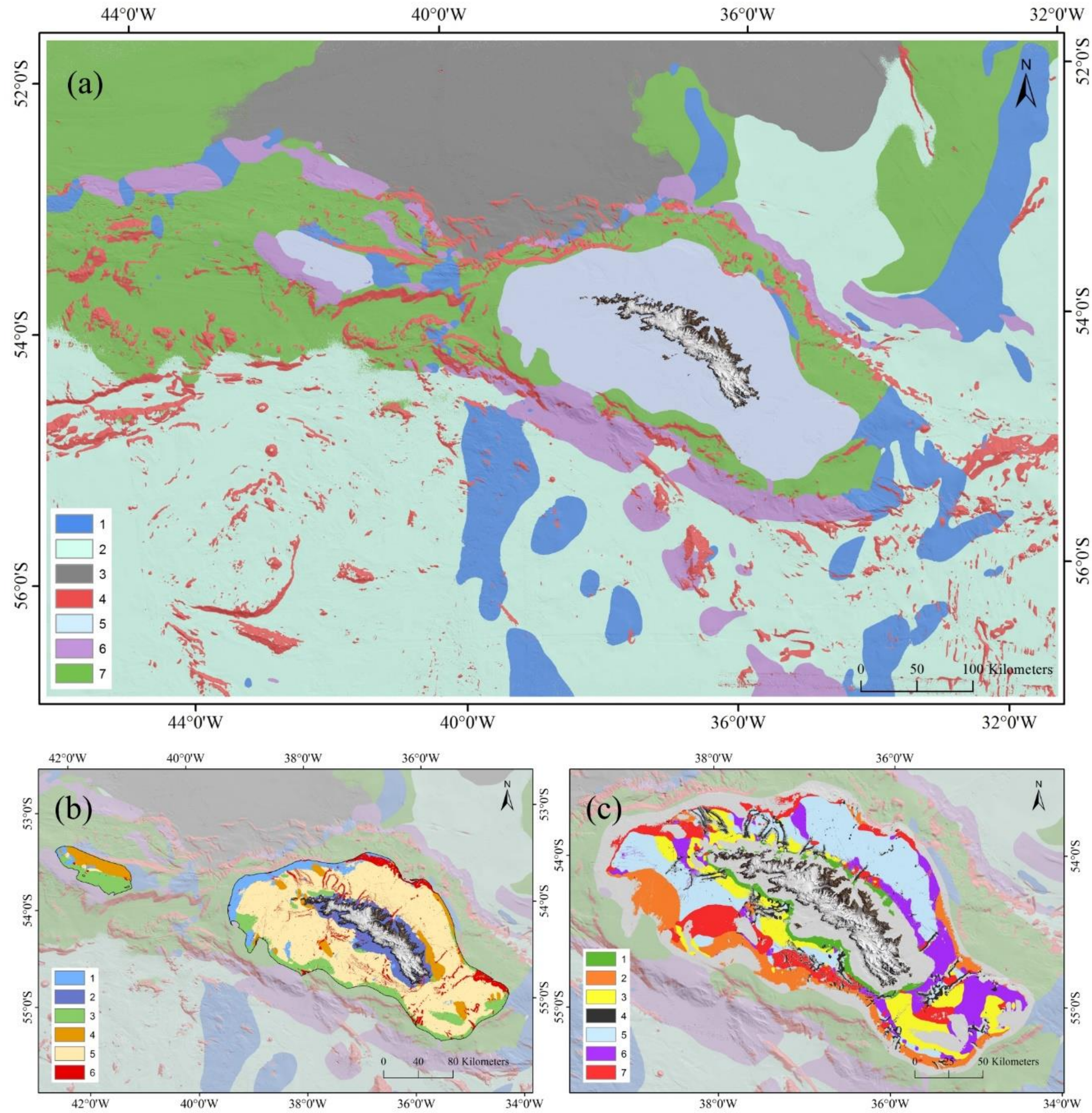
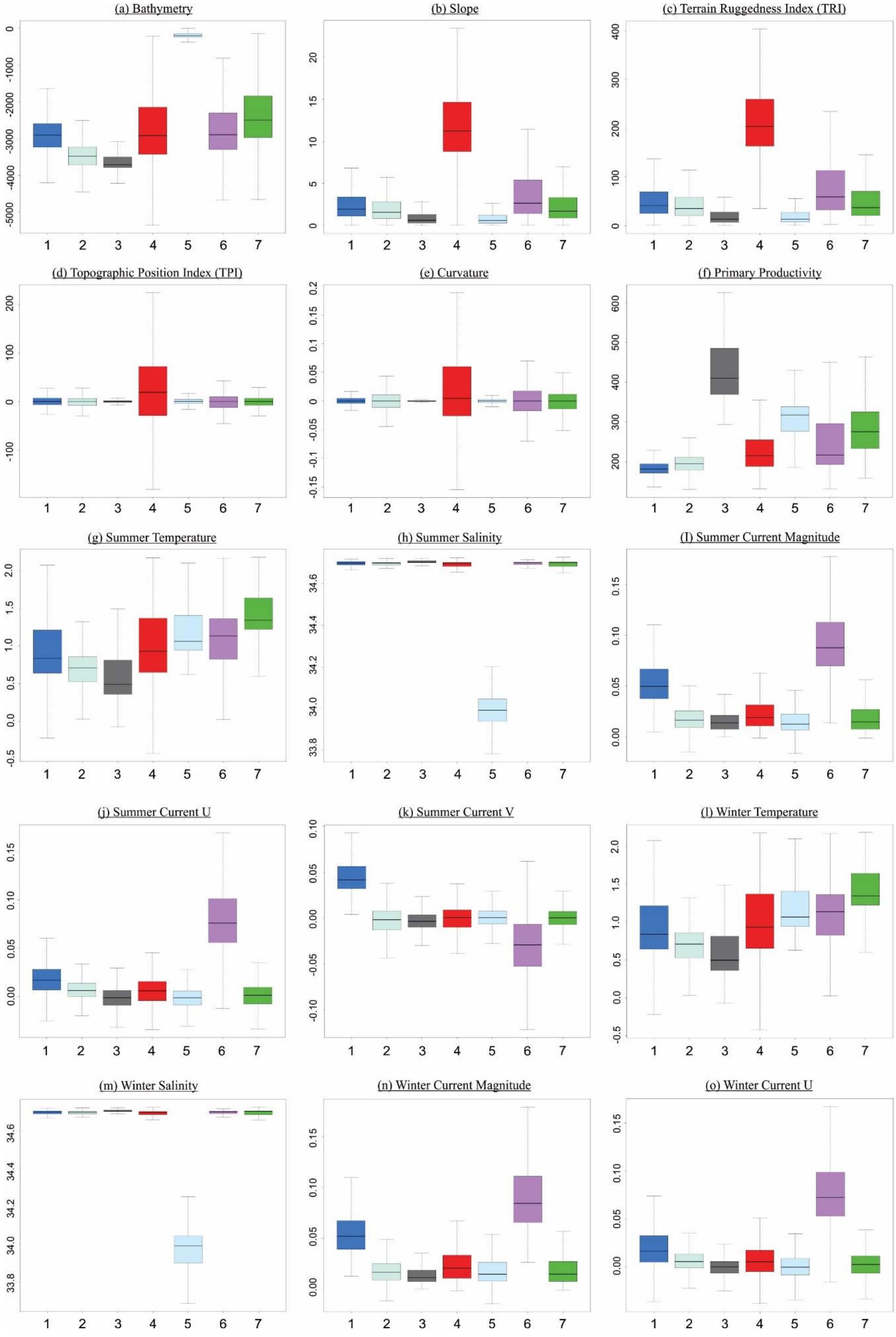


Figure 4.5. Hierarchically nested marine landscape maps. Showing (a) distribution of 7 cluster classes across the whole study region as defined by k-means cluster analysis; (b) re-clustering of cluster 5 taken from first k-mean partition (Figure 4.5a) whereby the shelf (previously a single cluster) is now split into 6 sub-clusters; and (c) re-clustering of cluster 5 - sub-cluster 5 (Figure 4.5b) whereby sub-cluster 5 is partitioned into 7 further third-tier clusters. Data for Figures gridded in R (version 3.0) and visualised using ArcGIS (version 10.1 [www.esri.com/software/Arcgis]).


(a) Bathymetry
0
-1000
-2000
-3000
-4000
-5000
(b) Slope
20
15
10
5
0
(c) Terrain Ruggedness Index (TRI)
400
300
200
100
0
(d) Topographic Position Index (TPI)
200
100
0
-100
(e) Curvature
0.2
0.15
0.1
0.05
0
-0.05
-0.1
-0.15
(f) Primary Productivity
600
500
400
300
200
(g) Summer Temperature
2.0
1.5
1.0
0.5
0.0
-0.5
(h) Summer Salinity
34.6
34.4
34.2
34.0
33.8
(I) Summer Current Magnitude
0.15
0.10
0.05
0.00
(j) Summer Current U
0.15
0.10
0.05
0.00
(k) Summer Current V
0.10
0.05
0.00
-0.05
-0.10
(l) Winter Temperature
2.0
1.5
1.0
0.5
0.0
-0.5
(m) Winter Salinity
34.6
34.4
34.2
34.0
33.8
(n) Winter Current Magnitude
0.15
0.10
0.05
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(o) Winter Current U
0.15
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1
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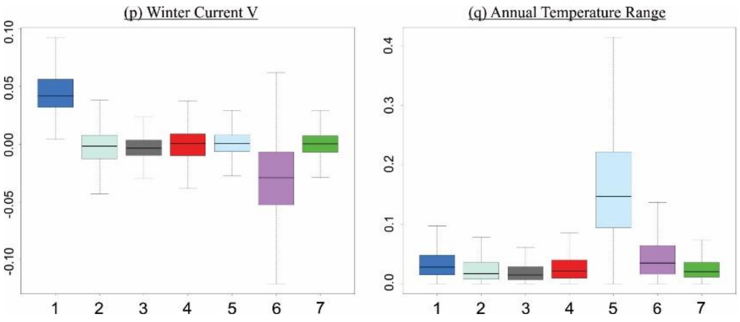

Figure 4.6. Box plots of K-means derived clusters versus 17 original abiotic variables. The x-axis denote the seven k-means clusters, and the y-axis the respective units of each original abiotic variable. Descriptions of each variable including their units are summarised in Table 4.1. In each box plot the middle line represents the median, the upper and lower extent of the box represent the first and third quartiles. The whiskers are the maximum and minimum observed values (excluding statistical outliers - values > 1.5 x the interquartile range). Box plot colours denote the corresponding landscape map cluster colours from Figure 4.5a. Figures created in R (version 3.0 [www.r-project.org]).

Confidence map

The confusion index map (Figure 4.7) provided an assessment of the confidence values associated with the membership of each grid square to its given cluster defined through K-means partitioning. In general under a good cluster solution, high confusion values (denoted by white in Figure 4.7) would be expected to only occur in the ‘transition zone’ on the boundaries between clusters. Confusion within clusters however would imply the clustering solution is not particularly stable and that those particular grid-cells do not have a strong affinity with a single K-means cluster.

Mapping the confusion indices revealed high confidence in the clustering of the South Georgia shelf (and to a lesser extent Shag Rocks). There was very little within-cluster confusion, which was restricted to the edges of cross-shelf troughs (presumably as a result of seabed topography), inshore shelf (presumably resulting from a distinct salinity and temperature gradients) and at a single anomaly on the south-western edge of the shelf break. With these exceptions the cluster is delineated by a well-defined uncertainty ‘halo’. Generally there was an increased level of background confusion (most notably in deep water) as a result of sampling artefact caused by high-resolution multibeam swath lines transecting regions of lower data quality. This was notable across clusters but was particularly apparent in the bottom-left quadrant of the plot that had been subject to a large-scale AWI multibeam survey (Figure 4.2).

Both clusters defined by prevailing currents (clusters 1 and 6) were characterised by regions of well-defined zones of lower uncertainty. Cluster 3 was subdivided by a well-defined line of uncertainty forming an arc in the top-centre of the map. Inspection of the bathymetry dataset revealed the arc demarked the contour of a large topographic dome 100 km in diameter and 1000 m in height, with the uncertainty reflecting this change in topography (potentially conflicting with cluster 4). In contrast the boundary of clusters 2 and 3 in the top-right quadrant were not delineated by any uncertainty. The major driver of the separation of these two clusters was higher net primary productivity occurring in cluster 3. Inspection of the primary productivity data revealed an abrupt change in primary productivity at this boundary. This lack of a gradual change would explain the subsequent confidence in the cluster designation. The certainty of cluster 4 was hard to quantify given it consisted of predominantly spatially small topographic features. In general however the well constrained clusters of lower uncertainty delineated by narrow transition zones between clusters supports the *K*-means partition as robust physical landscape classification of the region.

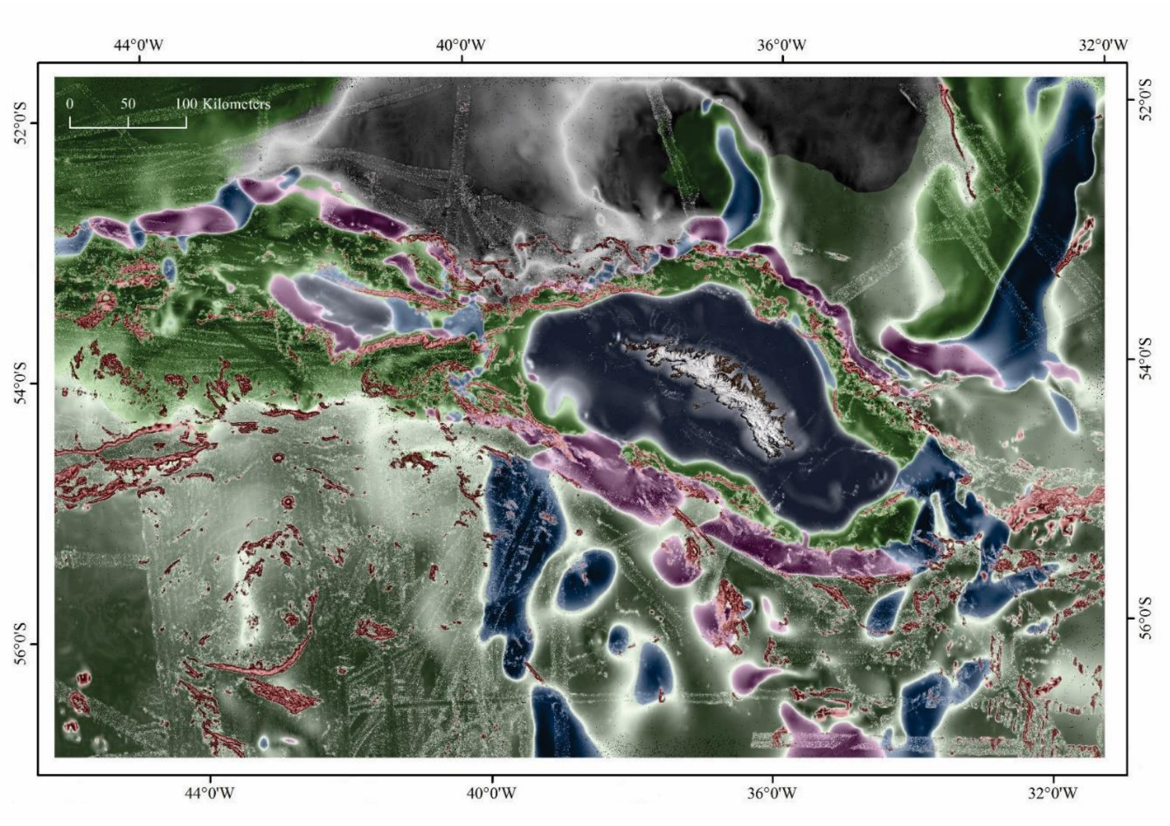

Figure 4.7. Confusion index map quantifying clustering uncertainty across the study region. The confusion index is overlaid on the seven-cluster landscape map showing where zones of higher uncertainty (white) correspond with the boundaries between clusters and where there are instances of intra-cluster uncertainty. Data for Figures gridded in R (version 3.0[www.r-project.org]) and visualised using ArcGIS (version 10.1 [www.esri.com/software/Arcgis]).

Nested-hierarchical clustering

Given the stability and spatially discrete nature of the shelf cluster, cluster 5 was selected to test the functionality of a nested hierarchical clustering solution. The original abiotic input datasets were clipped to the spatial extent of cluster 5. The landscape mapping protocol was then re-run to create a new set of shelf sub-clusters (Figure 4.5b; 4.5c). Assessment of the shelf sub-clusters (Appendix B: Supplementary materials Figure 4.2) revealed that annual temperature range, salinity, and slope dominated near-shore locations (cluster 2). A combination of depth (cluster 1), stronger current regimes (cluster 3 and 4), and complex topography (cluster 6) dominated on the outer shelf locations. A body of annually-stable cold bottom water drove designation of the large spatial coverage of sub-cluster 5. A third nested clustering of this sub-cluster 5 partitioned the shelf environment further still, delineating seven distinct clusters (Figure 4.5c; Appendix B: Supplementary materials Figure 4.3).

4.4 Discussion

The TOPOGRID algorithm, as in previous studies (Fretwell et al., 2008; Fretwell et al., 2013; Dickens et al., 2014) proved a robust methodology for gridding a digital elevation model from a compilation of disparate datasets, integrating spatially discontinuous data with different sampling densities. The input bathymetry data varied considerably in terms of the state of its post-processing. Approximately ten iterative cycles were required to obtain a final DEM, cleaning most erroneous soundings. TOPOGRID was notably sensitive when interpolating joins between bathymetry datasets. Hence a large buffer of 500m was created to smooth the boundary zone.

When compiling and interpolating multiple disparate bathymetry datasets into a DEM, the effective resolution of each grid is limited to, but not necessarily equal to, the pre-defined resolution (in this case 100m). As such when the interpolated bathymetric grid is used to create derivative datasets for landscape mapping, areas where the interpolation is underpinned by many data points will contain far more detail (albeit limited to 100m resolution) than regions of sparse data which appear comparatively smooth. The effect of this is that these high-density data regions appear to have higher topographic complexity (e.g. high rugosity) when in fact the model is simply recording an artefact of sampling provenance. Rather than gridding the DEM at the resolution of the coarsest resolution data (in this case ~900 m), and in doing so removing fine-scale topographic details, we advocate the high-resolution analysis undertaken here with the caveats discussed taken into account when qualitatively assessing partitioning of environmental parameters.

The statistical approach to marine landscape mapping adopted in this study was proposed by Verfaillie et al. (2009). The utilisation of a statistical approach is intended to remove highly subjective decisions associated with classical landscape mapping protocol (Roff & Taylor, 2000; Roff et al., 2003), namely the selection of ecologically relevant abiotic input variables and the classifying of those variables into relevant classes. An objective means of defining partitions in the physical environment should be considered particularly useful for regions such as South Georgia where proposed and reviewed hierarchical definitions (Davis et al., 2004) have not yet been established. This study represents the first application of this methodology over such a large regional scale (10^5 km^2). The results demonstrate that a statistical protocol is highly effective at reducing large numbers of sometimes collinear environmental input variables to a smaller number of relevant principal components. It is also effective at defining the optimal number of clusters and the spatial delineation of those clusters.

Adopting a 'blind' statistical approach to the data partitioning is problematic, however, as it does not remove all need for subjective supervision of the abiotic input variables and a careful evaluation of the process and its results is necessary. Firstly, PCA will remove collinearity in the data but if the model input includes for example many oceanographic variables and few topographic derived variables, then the output will be oceanographic-centric placing greater emphasis on the importance of these variables than anything else. Hence a balanced choice of input variables is needed. Secondly, K-means finds similar sized clusters based on spherical partitions in the multi-dimensional PC space. This is not always a correct representation of the reality, as meaningful clusters can vary in spatial extent and shape: for example, large numbers of data points might be clustered as deep-sea environments with fairly wide-ranging characteristics, whilst smaller rocky outcrops that punctuate that homogenous region would have much tighter environmental constraints. An alternative approach could be density-based spatial clustering (e.g. DBSCAN (Ester et al., 1996), in which clusters are not restricted to a spherical designation. Such an approach may also be advantageous to large-scale datasets due to the 'noise' of data outliers that exists in datasets of this scale. The disadvantage of such an approach, however, is the requirement for a definition of high point-density. Finally, the protocol ensures that input variables are standardised and given equal weighing in the PCA. Not all input variables will drive biological distribution patterns to the same degree, but for areas that have not been studied much before, it is impossible to estimate these varying degrees of importance *a priori*.

To resolve these problems, our protocol is based on iterative refinement of each cluster solution. So whilst the process starts as an unsupervised classification based on statistical clustering, the resultant landscape map is qualitatively assessed on the basis of perceived biological, oceanographic and geomorphological meaningfulness. Any input variable deemed to be confounding the results is removed from the analysis and the protocol is re-run. For example, after the first iteration of this analysis, slope aspect was excluded from the analysis as deep-sea environments with relatively low slope gradients (<3°) were being partitioned based on minor variations in orientation of the slope. The aim of this approach is to strip down the analysis to retain only partitions with potential ecological relevance at a broad spatial scale. The process can then be re-run over iteratively smaller spatial subsets forming a nested hierarchical landscape classification (Figure 4.5). As the importance of input variables as ecological drivers is scale-dependent, all input variables were included at the start of each new clustering level. This approach retains broad-scale gradients driving clusters across the entire region whilst identifying finer-scale geomorphic features nested within these broad-scale clusters.

A significant omission from this analysis is substrate type, which has been shown as a major driver of species composition (Solan et al., 2012). It was not included in this analysis given the limited spatial extent of the sedimentology dataset in the region, and as such the difficulty in interpolating across such a wide area. Backscatter data were available for the regions with multibeam coverage (see Figure 4.2), but interpretation was particularly sensitive to ship-specific calibrations which made a backscatter compilation problematic. It was our assessment, therefore, that the inclusion of geomorphology data layers in the PCA (slope angle, topography, rugosity) should effectively represent different sediment regimes in the analysis. For example homogenous flat regions are likely to be mud at South Georgia and steep escapements hard substrate. The downside of this approach is the spatial scale of the analysis will tend to pick out large-scale features (e.g. large escarpments, canyons, and gullies) but not sedimentary features with lower topographic profiles such as moraine fields, which have been suggested as important driver of marine biodiversity (Barnes et al., 2015).

Our results demonstrate that the iterative unsupervised landscape mapping protocol is effective at creating meaningful (Figure 4.5) statistically stable (Figure 4.7) partitions. Depth, current, and seabed topography are all shown to drive broad-scale clustering. At a finer scale on the South Georgia shelf, current regimes were shown to be less important with clustering driven by depth, sea-bed temperatures, coastal salinity, and topography (Figure 4.5b; 4.5c; Appendix B: Supplementary materials 4.1 and 4.2). Taken in isolation this analysis provides valuable information pertaining to the nature of different physical habitats, their spatial distribution, and degree of heterogeneity (Gray, 2004). In itself, this provides useful information for policy makers in terms of physical proxies for faunal richness with application in predictive modelling of taxa, functional traits, assemblages, and diversity (Zacharias & Roff, 2000; De Leo et al., 2010; Taylor et al, 2011).

The next step will now be to quantify the biological meaningfulness of our physical landscape partitions. In the first instance, this will involve the inclusion of a regional biological dataset into the analysis (Hogg et al., 2011), to test for correlations between our proposed hierarchical clusters and biogeographical trends. The advantage of a landscape mapping approach for underpinning large-scale MPAs such as at South Georgia and South Sandwich Islands (SGSSI), as opposed to more holistic bottom-up approaches that integrate biological data in the analysis from the outset (Galparsoro et al., 2009; Shumchenia & King, 2010; Ierodiaconou et al., 2011), is largely on account of the spatial scale of the analysis. For example, although at South Georgia more than 25,000 biological point samples have been recorded (Hogg et al., 2011), spread over an area in excess of 1 million km^2, the data exist at a spatial scale that is of limited application to draw statistically meaningful conclusions. Furthermore knowledge of benthic communities rapidly declines as a function of distance from the South Georgia continental shelf, with significant paucity in sampling of the region's deep-sea environments. The biological data will be invaluable, however, in testing the output of the model to see how well it acts as a proxy for biological distributions. In doing this it will be important to better constrain other confounding influences on regional biogeography such as, paleo-environment and the presence of glacial refugia during the last glacial maximum (Barnes et al., 2016); the impact of iceberg scouring on biological communities (Gutt, 2001; Barnes & Souster, 2011) and the effect of bathymetric divides (such as between South Georgia and Shag Rocks) as barriers to genetic transfer (Allcock et al., 1997; Griffiths, 2008).

Given sampling effort for many groups is uneven and most species in the region are rare, inferring distribution patterns at high taxonomic resolution (i.e. genus or species) over a large spatial extent will be problematic. More achievable (and perhaps with greater application in spatial planning) would be the mapping of a standardised (for sampling effort) measure of species level biodiversity to identify the presence of 'biodiversity hotspots' and correlate these with our physical landscape clusters. This approach would be helpful in understanding the role of habitat heterogeneity as a potential proxy for biodiversity (i.e. beta diversity). In addition to this, it would also be feasible to categorise certain taxa into functional groups (based on traits such as feeding, locomotive and reproductive strategies) and assess the relationship between these faunal aggregations and the clusters solutions. This could be used to assess the distributions of vulnerable marine ecosystems or habitat forming taxonomic groups.

It is also important to consider what the priorities are in terms of marine management. For example, is it the presence of rare or endemic species? If so then the methodology will have to reflect the fact that most species are rare (Hogg et al., 2011), so distribution is not well constrained. Is it the presence of species richness zones? Or the presence of habitat forming fauna including vulnerable marine ecosystems (VMEs) such as coral gardens and sponge assemblage? Alternatively benthic communities that offer an ecosystem service such as fisheries or carbon sequestration (Barnes et al., 2015) may be considered of importance to identify. The marine landscape map produced here provides a first-level, baseline picture of the spatial pattern in the marine regions around South Georgia, and can be used as a tool to start developing a method to answer each of the questions above.

4.5 Conclusions

The methodology presented here provides an objective assessment of the physical attributes of the benthic environment over nested spatial scales, providing analysis from broad-scale drivers of biogeography such as large-scale (10–100km) abiotic gradients (e.g. depth and temperature) to smaller-scale features (100m–1km) such as local topography. Currently this level of analysis on the factors driving biogeography is lacking from most marine spatial planning frameworks. We argue that it provides the potential for a holistic overview of the marine environment, and meaningful information to aid policy-makers to manage the region's marine environment. Furthermore the approach is adaptable to different input variables and as such transferable globally to different proposed or established MPAs.

4.6 Acknowledgements

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Chapter 5: On the ecological relevance of landscape mapping and its application in the spatial planning of very large marine protected areas

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Abstract

In recent years very large marine protected areas (VLMPAs) have become the dominant form of spatial protection in the marine environment. Whilst seen as a holistic and geopolitically achievable approach to conservation, there is currently a mismatch between the size of VLMPAs, and the data available to underpin their establishment and inform on their management. Habitat mapping has increasingly been adopted as a means of addressing paucity in biological data, through use of environmental proxies to estimate species and community distribution. Small-scale studies have demonstrated environmental-biological links in marine systems. Such links, however, are rarely demonstrated across larger spatial scales in the benthic environment. As such, the utility of habitat mapping as an effective approach to the ecosystem-based management of VLMPAs remains, thus far, largely undetermined.

The aim of this study was to assess the ecological relevance of broad-scale landscape mapping. Specifically we test the relationship between broad-scale marine landscapes and the structure of their benthic faunal communities. We focussed our work at the sub-Antarctic island of South Georgia, site of one of the largest MPAs in the world. We demonstrate a statistically significant relationship between environmentally derived landscape mapping clusters, and the composition of presence-only species data from the region. To demonstrate this relationship required specific re-sampling of historical species occurrence data to balance biological rarity, biological cosmopolitism, range-restricted sampling and fine-scale heterogeneity between sampling stations. The relationship reveals a distinct biological signature in the faunal composition of individual landscapes, attributing ecological relevance to South Georgia's environmentally derived marine landscape map. We argue therefore, that landscape mapping represents an effective framework for ensuring representative protection of habitats in management plans. Such scientific underpinning of marine spatial planning is critical in balancing the needs of multiple stakeholders whilst maximising conservation payoff.

5.1 Introduction

Currently, there is a disconnect between a global trend towards the establishment of very large-scale marine protected areas (VLMPAs), and the data available to underpin their establishment and inform on their zonation. Biological sampling, especially in isolated locations, is logistically difficult, time consuming and prohibitively expensive to conduct over large spatial scales. As such, large-scale spatial protection inevitably equates to paucity in biological sampling at a scale relevant to management (Lecours et al., 2015; McHenry et al., 2017). Nonetheless, within international frameworks such as the Convention of Biological Diversity (CBD) (Secretariat of the CBD, 2010), over the past decade VLMPAs (here defined as reserves > 100,000 km^2 in area) have increasingly been adopted as a holistic and geopolitically achievable approach to conservation of the marine environment. Through initiatives such as the Big Ocean Network (Wilhelm et al., 2011), the proportion of the World's oceans afforded protection has increased to 3.27% (Boonzaier and Pauly, 2016). This increase has overwhelmingly been met by VLMPAs (Figure 5.1). Taking the UK as an example, 22% of its territorial waters are afforded some form of marine protection. Excluding VLMPAs from this analysis, however, reduces that figure to < 1% (Shugart-Schmidt et al., 2015). Recent estimates suggest that the wide-scale adoption of VLMPAs globally has expedited international compliance with the CBD's Aichi target of 10% protection, by thirty years, bringing it forward from 2055 to 2025 (Toonen et al., 2013).

Advocates of VLMPAs highlight the holistic, entire-ecosystem level protection they offer (Sheppard et al., 2012), maintaining connectivity to adjacent ecosystems (Toonen et al., 2011), ensuring protection of ecosystem services (Toonen et al., 2013) and greater resilience to environmental change in the marine environment (Micheli et al., 2012; Toonen et al., 2013; Roberts et al., 2017). They are seen as better able to protect mobile habitats such as upwelling zones (Toonen et al., 2013), and as particularly beneficial to highly mobile species, mega fauna and species which are migratory or transitory through regions (Lester et al., 2009; Fox et al., 2012; Maxwell and Morgan, 2013). Furthermore, VLMPAs are demonstrably more cost-effective than multiple smaller reserves (McCrea-Strub et al., 2011), offering policy makers and advocates such as NGOs, the high-profile benefits of safeguarding large areas of pristine environment in a politically expedient manner. The protection of 10% of the world's oceans, and notably the majority use of VLMPAs, as an effective target by which to measure the success of global marine conservation is however open for debate (see Leenhardt et al., 2013; Wilhelm et al., 2014; Agardy et al., 2016; Jones and De Santo, 2016). A key criticism is that the target-driven nature of VLMPA protection prioritises quantity over the representativeness of the habitats it protects or the effectiveness of that protection (Leenhardt et al., 2013; Jones and De Santo, 2016).

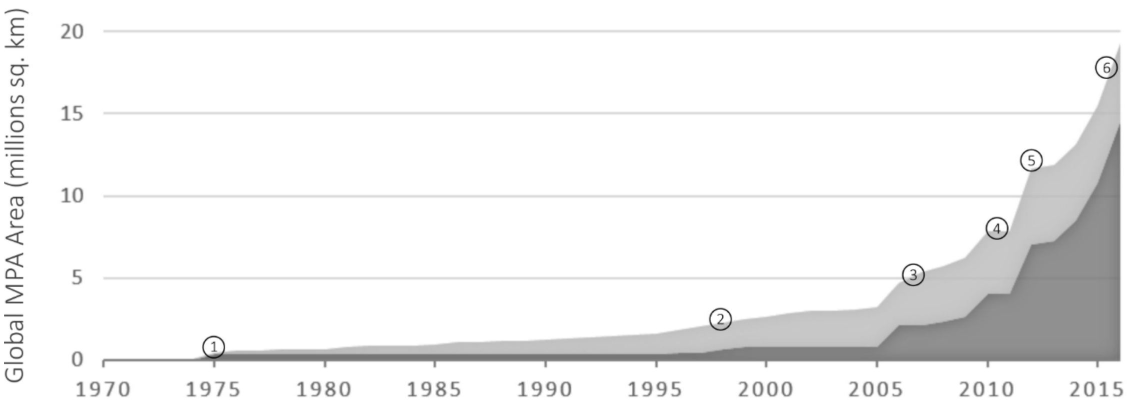

Figure 5.1. Change in global MPA coverage between 1970 and 2016. Total MPA coverage is symbolised in light grey, with the proportion of that coverage attributed to large-scale MPAs (> 100,000 km2) symbolised in dark grey. Data adapted from MPAtlas online portal (http://www.mpatlas.org/; date of access: 25/05/2017) and includes all IUCN levels of protection (Categories Ia to VI), but excludes taxa-specific exclusion zones (e.g. shark sanctuaries). Analysis includes formal commitments for recent MPAs. Circled numbers indicate the establishment of key large-scale MPAs: 1. Great Barrier Reef marine park (Australia); 2. Galapagos Marine Reserve (Ecuador); 3. Papahānaumokuākea Marine National Monuments Park (USA); 4. Chagos (UK) and Charlie Gibbs North High Seas MPA (International); 5. South Georgia & South Sandwich Islands (UK) and Coral Sea (Australia); 6. Pitcairn Islands (UK), Ascension Island (UK), Palau National Marine Sanctuary (Palau), Naza-Desventuradas (Chile), Ross Sea (International) and the extension on Papahānaumokuākea Marine National Monuments Park (USA).

Representative protection of marine realms is a key requirement of CBD Aichi goals (Secretariat of the CBD, 2010). Consequently, protection of a representative range of habitats is often central to MPA design, notably when an MPA is designed in a multi-use or zoned way, such as with the inclusion of demersal fisheries in certain areas at South Georgia and South Sandwich Islands MPA (Rogers et al., 2015). Many MPAs, however don't assess the physical habitat types within their protective sphere. Those that do, often don't take the next step of establishing a link between these environmental classifications and the biological communities which inhabit them (often the key attribute of the environment the MPA serves to protect). A key reason for this is often paucity in regional biological datasets at a scale relevant to management (Lecours et al., 2015; McHenry et al., 2017).

Increasingly VLMPA placement has demonstrated strong bias towards very remote overseas territories (Devillers et al., 2015), most notably waters within national jurisdictions of the USA, UK and France. Such regions typically exhibit minimal stakeholder activity and/or local populations with limited powers of recourse, resulting in fast implementation of marine protection. As these more easily implemented MPAs are fulfilled however, future designations will have to target less remote - more populated regions of the world. Such regions are more likely to be in more contentious national waters, and thus subject to ongoing commercial exploitation. As such, future designations will become progressively more challenging, and so too our ability to fulfil the Aichi targets. Already this has led to the development of more politically complex VLMPAs that transcend national jurisdictions

(BALANCE, 2008; Notarbartolo di Sciara et al., 2008 ; Protection of the Arctic Marine Environment (PAME), 2015), transnational cooperative frameworks (Jeftic et al., 2011), and high-seas MPAs in areas beyond national jurisdictions (ABNJs), such as South Orkney Islands (2009), Charlie-Gibbs (2010) and Ross Sea (2016). It may also lead to proposals for future MPAs undergoing increased negotiation and compromise in order to finalise such potentially politically-complex protection. In such cases there would be an increased likelihood of spatial and temporal complexity within the MPA design (e.g. multi-use or zoned MPAs). Such zoning aims to protect the marine environment, whilst offering ecosystem services and sustainable use of living marine resources. Under such scenarios there is a growing need for spatial and temporal prioritisation to balance the need of multiple stakeholders whilst maximising conservation payoff.

In the absence of sufficient biological sampling, to effectively inform on spatial and temporal management priorities, the use of habitat mapping and modelling approaches have increasingly been adopted to aid decision making (Pressey and Bottrill, 2009; Brown et al., 2011; Harris and Baker, 2012). These approaches map and analyses physical attributes of the marine environments (often derived from remote sensing) and employ these alongside known biological information as proxies or surrogates for marine habitats. This analysis can be used to help predict biological and community distributions. Habitat mapping depends on an understanding in the links between environmental variables as surrogates, and the marine fauna for which their surrogacy is intended. Variation in environmental factors drive changes in faunal communities and community structure. This ranges from broad-scale spatial measures such as latitude, longitude and depth (Hawkins, 2001; Cox and Moore, 2005; Passlow et al., 2006; Sanders et al., 2007), which in turn drive changes in temperature, day length and light penetration (Rex et al., 1993; Hawkins and Diniz-Filho, 2004; Tittensor et al., 2010; Chaudhary et al., 2016), to finer scale features such as rugosity (Allee et al., 2011), slope (Beaman et al., 2005; Beaman and Harris, 2007), wave and current exposure (Pearce et al., 2011), substrate (Solan et al., 2012), geomorphology (Kostylev et al., 2003; Beaman and Harris, 2007), and disturbance processes such as slope instability and turbidity currents (Paull et al., 2010) and, at higher latitudes, iceberg scouring (Jutt and Starmans, 2001; Potthoff et al., 2006). Combinations of these factors result in habitat heterogeneity and complexity, which is often associated with higher species richness (Gladstone, 2007), providing habitats for both juvenile and adult organisms (Beck et al., 2001; Kostylev et al., 2003) and decreasing dominance by individual taxa by interrupting predator-prey relationships (McClain and Barry, 2010).

Marine habitat mapping has been used as a means of synthesising marine spatial distribution data for ecosystem-based management globally (Wright and Heyman, 2008; Cogan et al., 2009; Ehler and Douvere, 2009). Its use as a framework for the representative protection of habitats can been seen through international management objectives such as the CBD, and regional policy frameworks such as CCAMLR (Convention for the Conservation of Antarctic Marine Living Resources) in the Southern Ocean and OSPAR in the North-East Atlantic. Examples of landscape-scale habitat mapping as a tool for informing on marine spatial planning can be seen across spatial scales. At a global level, there have been suggestions for representative networks of high seas MPAs (Gjerde, 2003; Harris and Whiteway, 2009) and seamount classification aiding in the design of MPA networks (Clark et al., 2011). In the Southern Ocean, large-scale studies using geomorphology have been used to map vulnerable marine ecosystems (O'Brien et al., 2009), as well as large-scale bioregionalisation studies to feed into CCAMLR (Grant et al., 2006 ; Ainley et al., 2010), hierarchical classification systems (Douglass et al., 2014) and taxa-specific eco-regionalisation (Koubbi et al., 2011). Hierarchical habitat classification systems have been used for managing Australia's marine biological resources (Last et al., 2010) and MPA network (GBRMPA Zoning Plan, 2003; Harris et al., 2008), whilst universal classification systems such as EUNIS (Davies et al., 2004) have been used to underpin regional MPAs (e.g. Galparsoro et al., 2015; Henriques et al., 2015) and large-scale OSPAR MPAs (O'Leary et al., 2012).

Small-scale studies have demonstrated clear environmental-biological links in both benthic and pelagic systems (Howell et al., 2010; Ierodiaconou et al., 2011; Copeland et al., 2013; Rees et al., 2014). Such links, though essential for effective ecosystem-based management (Cogan et al., 2009), are however often not sought, tested or demonstrated across larger spatial scales relevant to the marine spatial planning of VLMPAs (Day and Roff, 2000; Roff and Taylor, 2000; Harris and Whiteway, 2009). As such, whilst habitat mapping is demonstrably an effective tool at smaller spatial scales (often at finer spatial resolution), with conservation initiatives prioritising VLMPAs, its utility at very large spatial scales is less clear. In this paper, we assess the application of marine landscape mapping over a large spatial scale, and specifically whether classification of the benthic environment into broad-scale marine landscapes demonstrates associated broad-scale changes in benthic faunal communities.

South Georgia and the South Sandwich Islands (SGSSI) form an archipelago in the Atlantic sector of the sub-Antarctic (Fig. 2). The islands host one of the largest MPAs in the world (1.07 million km^2). An extensive marine biological (Hogg et al., 2011), geomorphological (Hogg et al., 2016) and oceanographic dataset (Young et al., 2011), coupled with the pre-existing landscape map of the region (Hogg et al., 2016), make it a particularly good model system in which to test the interactions between broad-scale physical environmental conditions and the biological community structure. Using the data available for the SGSSI MPA, this paper will assess, 1. Whether broad-scale landscape mapping produce ecologically relevant results, and as such, 2. Whether they represent an effective tool in addressing the mismatch between large-scale marine spatial planning and paucity in biological data?

5.2 Methodology

5.2.1 Study area

Positioned 1800 km east of the South American continental shelf, the island of South Georgia represents one of the most isolated continental shelf areas in the World (Figure 5.2). The region supports high levels of biological richness across taxonomic levels (most notably at species level); a high proportion of endemic species and species at the edge of their geographical ranges (Barnes et al., 2011; Hogg et al., 2011). This highly diverse and distinct fauna, coupled with the region hosting some of the largest aggregations of higher predators anywhere in the world (Trathan et al., 2015) make South Georgia a site of global importance. In 2012 the region (including the South Sandwich Islands archipelago to the south-east) was designated a IUCN category IV marine protected area, adding to the growing number of VLMPAs covering areas of over 1 million km^2 (Trathan et al., 2014; Rogers et al., 2015). This protection is currently in a period of review in which the spatial and temporal nature of the protection in the region will be assessed.

The SGSSI MPA is, by Southern Ocean standards, well studied in terms of environmental and biological characterisation due to a long history of exploitation (whaling and fisheries), and scientific study dating back to the 19th Century.

5.2.2 Physical landscape data

Environmental data for the region includes an extensive bathymetry dataset (Hogg et al., 2016) and oceanographic data modelled at mesoscale (Young et al., 2011). Nineteen environmental data layers were included in the analysis, to characterise physical geomorphology (depth, slope, rugosity, topographic position, aspect and curvature), surface productivity (net surface chlorophyll) and physical oceanography (temperature, salinity and current velocity). All input variables are summarised in Table 5.1 and discussed in detail in Hogg et al. (2016). The statistical approach to mapping marine landscapes was based on an unsupervised mapping protocol which can be summarised in five steps. (1) principal component analysis (PCA) of the gridded environmental variables; (2) determination of the optimal cluster solution; (3) K-means clustering of the principal components; (4) plotting the optimal cluster solution as a landscape map, and assigning environmental meaning to each cluster based on the relationship between the original environmental variables and each cluster; (5) assessment of the stability of the clustering solution based on calculation of membership values and corresponding confusion indices. The resulting landscape map covers an area of 530,000 km^2, encompassing the South Georgia shelf and surrounding deep sea of the MPA. It provides a three-tiered nested clustering of the MPA, with regions delineated on the basis of similar environmental conditions. Conceptually this approach is similar to other top-down habitat classification systems (e.g. EUNIS) (Davies et al., 2004).

In this study, we used the landscape clustering results of Hogg et al. (2016) to assess the link between the physical environment, and the faunal composition of the benthic communities. The landscape mapping clusters form a nested hierarchy with a top-level classification (Figure 5.3a), hereafter referred to as level-1 cluster (or clusters 1–7), covering an area of 530,000 km^2 from coastal to abyssal environments; level-2 cluster (clusters 5.1–5.6) which provides a sub-clustering of shelf environments (cluster 5) from level-1 (Figure 5.3b); and finally level-3 cluster (Clusters 5.5.1–5.5.7) which provides a 3rd tier re-clustering of cluster 5 from level-2 (i.e. a detailed clustering of the shelf region of South Georgia). Descriptions of physical environmental characteristics underpinning each cluster can be found in Hogg et al. (2016), and are summarised here in Table 5.2.

5.2.3 Biological data

The biological dataset comprises 30,299 presence-only data records compiled from 6593 sampling stations across the MPA as part of a 2011 baseline assessment of the region's benthic environments (Hogg et al., 2011). These data were collated from a comprehensive review of reports and papers representing over 130 years of polar exploration and assimilated with data from recent BAS research cruises to the region (JR262 Cruise Report, 2011; JR287 Cruise Report, 2013). Knowledge of benthic communities rapidly declines with increased distance from the South Georgia continental shelf, with significant paucity in sampling and subsequently knowledge of the region's deep-sea environments.

The scientific cruises, from which the data were drawn, differed in collection techniques and sampling effort. Most commonly Agassiz trawl and to a lesser extent epi-benthic sledges were used, but benthos was also collected using inshore SCUBA surveys, analysis of camera footage, longline fisheries collection and dredges. As a result of the data collection methods, there are no abundance nor true presence/absence data. Here we report these findings in a standardised format, recording all scientific classification to species level and the location at which the specimens were found with the geo-reference linked to a Geographical Information System (ArcGIS 10.4). Discrepancies in species classification were reconciled using the World Register of Marine Species (http://www.marinespecies.org) thus avoiding synonymies, which were especially prevalent in some of the older collections. Data management was undertaken using Microsoft Access 2013 and R (Version 3.4.1).

To assign functional trait information to South Georgia's benthic species, species lists were created for each higher level taxonomic group (typically phyla or class) and sent out to ten taxonomic experts at universities and research institutes around the world (see acknowledgments). As many of South Georgia's species are rare and poorly studied, functional information was not always available or known. Where it was, data were collected on 10 functional traits. A breakdown of these traits and their definitions are summarised in Table 5.1.

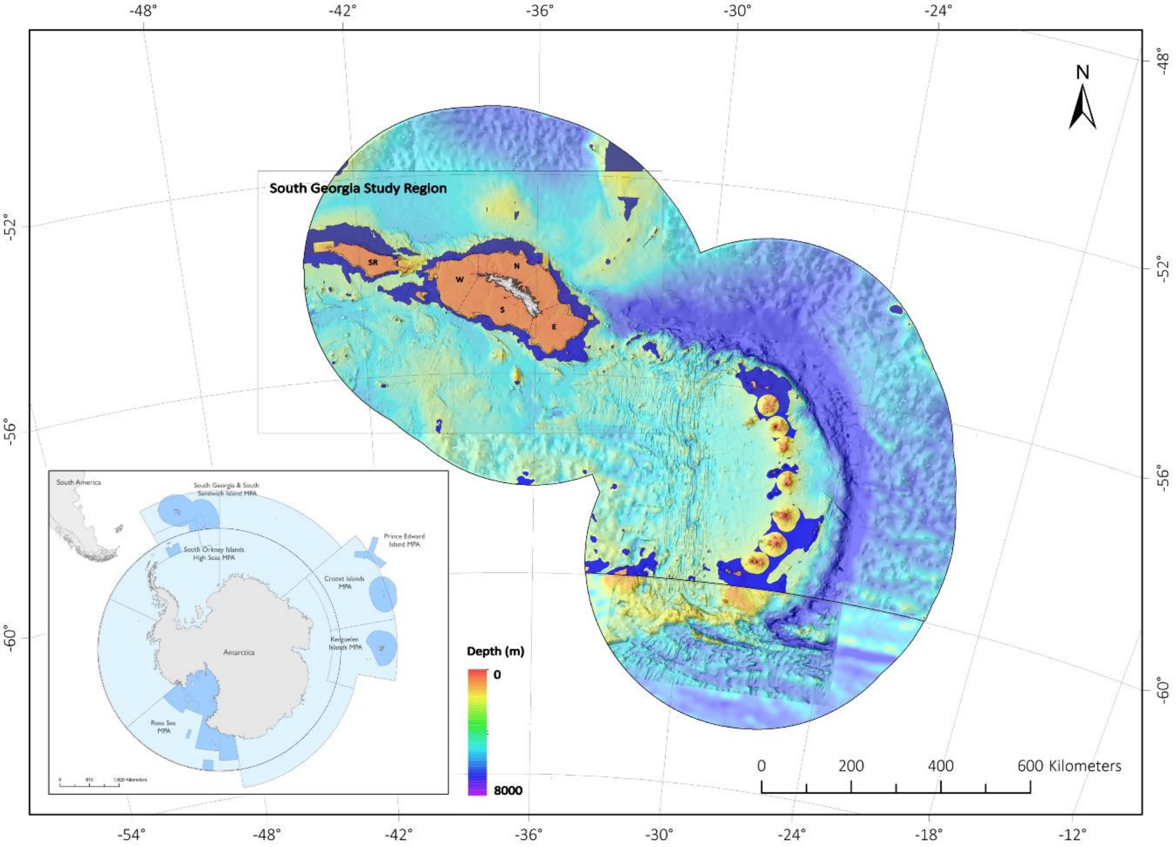

Figure 5.2. Geographical setting of South Georgia & the South Sandwich Islands MPA. Background bathymetry data demarks the extent of the MPA. The geographic extent of the analysis presented in this paper is represented by the study region box. Symbols N, S, E, W & SR (and associated hashed) lines denote the geographical analysis described in Section 2.4. Blue polygons represent the regions of the MPA between depths of 700 m and 2250 m still open to a licenced long-line fishery. Bathymetry data represents a compilation of South Georgia (Hogg et al., 2016) and South Sandwich Islands (Leat et al., 2016) bathymetric datasets. Inset: South Georgia in the geographical context of other Southern Ocean Marine Protected Areas. The pale blue background polygons denote the nine CCAMLR marine spatial planning domains. CCAMLR data were obtained from the CCAMLR online GIS resource. Other data were accessed through the MPAtlas online portal.

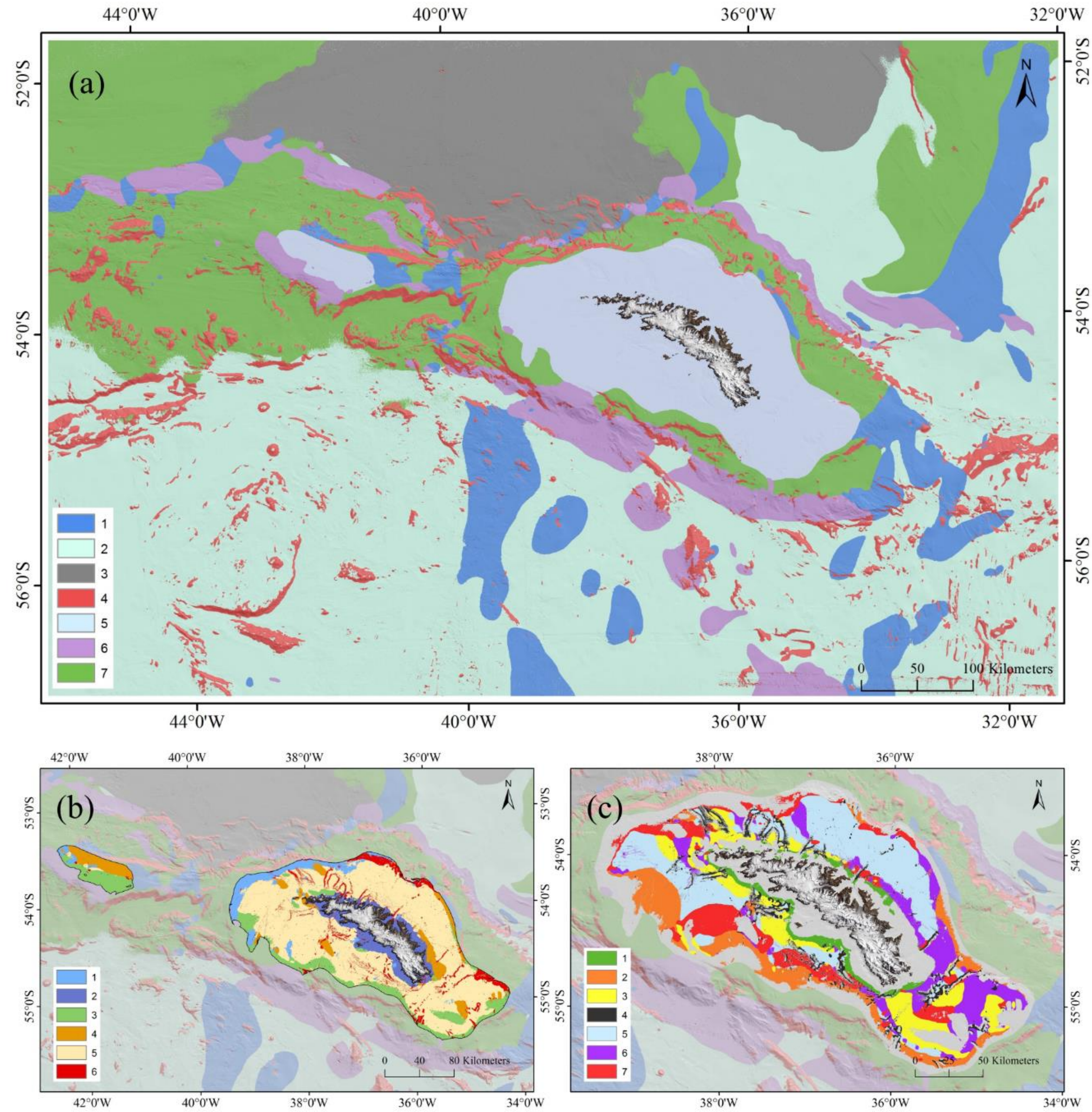

Figure 5.3. Hierarchically nested marine landscape maps (Hogg et al., 2016) Showing (a) distribution of level-1 cluster classes across the whole study region as defined by k-means cluster analysis; (b) level-2 clusters whereby the shelf (Fig. 2a, cluster 5) is now split into 6 sub-clusters; and (c) level-3 clusters in which the shelf cluster 5.5 (Fig. 2b) is partitioned into 7 further third tier clusters. Data for figures gridded in R (version 3.0) and visualised using ArcGIS (version 10.4 [www.esri.com/software/Arcgis]).

Table 5.1. Functional traits and their associated definitions used to characterise South Georgian species in this study.

DEVELOPMENT TYPE	Brooder	The incubation of eggs either inside or outside the body. Eggs may be brooded to a variety of developmental stages. Males or females may be responsible for brooding
	Direct Developer	Development without a larval stage
	Planktotrophic	Feeding at least in part on materials captured from the plankton
	Lecithotrophic	Development at the expense of internal resources (i.e. yolk) provided by the female
REPRODUCTIVE MODE	Asexual	Offspring arise from a single organism. This can include reproduction by budding, parthenogenesis or fission
	Sexual	The process of sexual reproduction involves two parents. Both parents normally contribute one gamete or sex cell to the process
	Hermaphrodite	Organism capable of producing both ova and spermatozoa either at the same time or sequentially, where one mature and is shed before the other
FEEDING STRATEGY	Suspension (Passive)	Any animal which feeds on particulate organic matter, catching food on a filter held into flowing water or collecting detritus on sticky apparatus other than a filter
	Suspension (Active)	Any animal which feeds on particulate organic matter, catching food on a filter from water by actively sweeping or pumping
	Detritivore	Any animal which feeds on fragmented particulate organic matter from the substratum
	Herbivore	Any animal that feeds on plants (including phytoplankton)
	Generalist Predator	Any animal that feeds by preying on a wide variety of other organisms, killing them for food;
	Specialist Predator	Any animal that feeds by preying on a specific organism, killing them for food
	Scavenger	Any animal that actively feeds on dead organic material
	Commensal/Symbiotic	A partner in a symbiosis in where one species derives benefit from a common food supply, whilst the other species is not adversely affected or mutually benefits
	Parasite	An animal that lives in or on another living organism (the host), from which it obtains food and other requirements. The host does not benefit from the association and is usually harmed by it
MOBILITY	Sessile (encrusting)	Non-motile; permanently attached at the base; forming or resembling a crust or thin coating
	Sessile (erect)	Non-motile; permanently attached at the base
	Burrower	An organism that lives or moves in a burrow
	Crawler	An organism that moves along on the substratum via movements of its legs, appendages or muscles
	Swimmer	An organism that moves through the water column via movements of its fins, legs or appendages, via undulatory movements of the body or via jet propulsion
	Drifter	An organism whose movement is dependent on wind or water currents
LIFE STYLE	Infauna	Benthic animals which live within the seabed
	Epifauna	An animal living on the surface of the substratum
	Epibiotic	An animal living on the surface of another animal or plant
	Demersal	Living at or near the bottom of a sea but having the capacity for active swimming
	Pelagic	Inhabiting the open waters of the sea or ocean, excluding the bottom layers

SUBSTRATUM AFFINITY	Mud	Predominantly mud
	Muddy-Sand	Mixture of Sand and mud with either component representing no more than 80% of the described sediment
	Sand	Predominantly sand
	Small Boulders/Cobbles	Small, unstable hard substrate
	Hard Substratum	Any stable hard substratum, not separated into small boulders or smaller sediment units.
REEF BUILDING	Yes	An organism that creates a massive biogenic physical structure raised above the surrounding seabed creating a consolidated habitat for epibenthic species
	No	Does not do the above
HABITAT FORMING	Yes	An organism that creates or modifies a habitat facilitating the existence of other species; ecosystem engineers ; play a major role in organizing community structure, and have an important function in determining community productivity
	No	Does not do the above
ECOLOGICAL SUCCESSION	Early	Rapidly colonising & rapid growing; early successional pioneers ; Tend to be R-strategists
	Mid	Members of a community at an Intermediate stage of succession
	Late	Late successional members of climax community; members of a very stable ecological community; K-strategists
FRAGILITY	Fragile	Likely to break, or crack as a result of physical impact; brittle or friable
	Intermediate	Liable to suffer minor damage, chips or cracks as result of physical impacts
	Robust	Unlikely to be damaged as a result of physical impacts, e.g. hard or tough enough to withstand impact, or leathery or wiry enough to resist impact

Table 5.2. Descriptions and interpretation of physical environmental variables underpinning each landscape mapping cluster (adapted from Hogg et al., 2016).

Cluster	Description
1	Strong oceanographic currents at seabed ($\bar{x}$=0.05 m/s) on a northerly trajectory
2	Exclusively deep sea (2500-4500m), low sea-bed temperature ($\bar{x}$=0.75°C), predominantly southerly distribution
3	Exclusively deep sea (>2500m), low seabed temperature ($\bar{x}$=0.5°C), northerly distribution, high sea-surface primary productivity, ($\bar{x}$= 420 Mg C/m2/day)
4	Locally complex topography, steep slopes (>10°), high rugosity, large range in topographic position values and curvature
5	Shallow, spatially discrete, flat, large annual temperature range, low salinity, high primary productivity
6	Strong oceanographic currents at seabed ($\bar{x}$=0.10 m/s) on a south-easterly trajectory, associated with large-scale, deep sea topographic features
7	Wide bathymetric range (all <250m and predominantly 2000-3000m), Annually-stable warmer sea-bed temperatures ($\bar{x}$=1.4°C)
5.1	Deeper outer shelf, flat homogenous topography, higher sea-surface primary productivity
5.2	Shallow coastal environment, higher seabed temperature and larger annual temperature range, low salinity, large range in slope gradient (up to a maximum of 8°), high rugosity, lower or negative TPI
5.3	Stronger oceanographic currents at seabed on an easterly trajectory
5.4	Stronger oceanographic currents at seabed on a northerly trajectory
5.5	Colder annually stable water, topographically homogenous with flat terrain and weak currents
5.6	Complex topography, steep slopes (max = 8°), high terrain ruggedness (rugosity), large range in TPI and curvature
5.5.1	Shallow coastal water, large annual temperature range (cold in winter warm in summer), low salinity, Slight negative slope gradient
5.5.2	Deeper water, flat topography, higher salinity, high winter temperatures (though not summer)
5.5.3	Shallow-medium depth water, flat topography, low salinity
5.5.4	Complex topography with slopes up to 5°, negative TPI
5.5.5	Mid-depth, stable cold water, higher primary productivity
5.5.6	Stronger oceanographic currents at seabed on a northerly trajectory
5.5.7	Stronger oceanographic currents at seabed on a easterly trajectory

5.2.4 Data analysis

To assess changes in faunal composition between landscape mapping clusters, we used non-metric multidimensional scaling (NMDS) ordination, using Primer (version 6). ArcGIS (Version 10.4) was used to overlay physical landscape mapping clusters with the biological data points. Spatial joins were then used to assign cluster and sub-cluster classifications to each biological sampling station. To enable ordination analysis of the data, a species-sample station matrix was populated with pseudo-absences whereby if a species was not recorded at a station, it was recorded as absent from that station. A similarity matrix for the faunal composition of the 6593 sampling stations was then constructed in Primer (version 6) using the Jaccard similarity coefficient. NMDS was run on the results of the similarity matrix with the cluster designation for each sampling station added as a factor in the analysis.

The statistical significance of each ordination run was assessed using Analysis of similarities (ANOSIM). Where statistically significant trends in faunal structure were observed between factors, the taxonomic drivers of these trends (i.e. which species made each cluster distinct or cosmopolitan) were assessed using similarity percentage (SIMPER) analysis. Simper species lists were constructed to represent the first 50% of cumulative species-level dissimilarity for a given cluster. This list was limited to include only species with a weighting > 1%.

NMDS was undertaken in iterative cycles, each time refining the biological input in an attempt to extract the strongest possible signal from the biological data. In the first instance this included all biological data, at all three hierarchical cluster levels (Figure 5.3), and at six taxonomic levels (Phyla, Class, Order, Family, Genus and Species). Ordination was then re-run, with the exclusion of data for minor, uncommon phyla (typically with restricted geographical distributions), as these records were thought to be creating a geo-spatial skew in the results. To remove the confounding influence of rare species and stations with very few data records, the biological data were filtered to exclude singleton and doubleton species and stations with two or fewer records. Over iterative cycles, this was extended to exclude any stations with 20 of fewer records. Data records were also filtered on the basis of collection methodology to assess the effect of sampling gear bias in the dataset. Whilst collection method was not an explicitly searchable factor in the biodiversity database, restricting records to species level, removing selected taxonomic groups and removing species in the top 5% of record counts (mainly encompassing species of demersal fish, crab, and copepods) represented a de facto means of identifying and excluding fisheries derived data.

NMDS analysis assessing the biogeographical structure to the data was undertaken by dividing the region into six zones (Figure 5.2): 'South Georgia North', 'East', 'South', 'West', 'Shag Rocks' and 'other' (typically defined as offshore regions). These categories were used as factors in the ordination analysis. Analysis was also undertaken in isolation for shelf environment and then separately for non-shelf environment. Geo-regions were delineated on the basis of depth contours in the case of shelf (< 400 m) vs. non-shelf, and South Georgia's shelf area was arbitrarily divided into four zones: North, East, South, and West (Figure 5.2).

In order to smooth out fine-scale variability in species composition between sample stations, biological data records were assimilated for each of the seven level-1 clusters. 50 records were then randomly resampled (with replacement) from each of the clusters 50 times, creating 50 series of 350 cluster-specific samples. This same protocol was undertaken for each of the three cluster levels. In an alternative approach, but with the same aim, the region was also sub-divided into hexagon cells of 5, 10, 20 and 50 km cell size with the aim of reducing fine-scale differences between spatially neighbouring stations, whilst retaining any broader biogeographical trends. This analysis included all stations irrespective of sample size, but excluded singleton and doubleton records. Subdivision of the South Georgia region into equal hexagonal grids was undertaken using the hexagon tessellation geoprocessing tool in ArcGIS (version 10.4).

5.3 Results

5.3.1 Biogeographic analysis

Biological sampling at South Georgia has been spatially patchy, with a strong bias towards shallow water sampling on the South Georgia continental shelf (cluster 5). 58.5% of all recorded sampling has occurred in cluster 5, in comparison to < 8% from the exclusively deep-water clusters 1–3 (Table 5.3a). Disparity in reported species richness between clusters is even greater with 83.1% of all reported species present in cluster 5, compared to a mean of 14.45% ($\sigma = 7.2\%$) across the remaining clusters. Of the 1670 distinct species recorded in this study, 69% (1152) were distinct to a specific cluster. The majority of these species (1118) were rare, recorded as singleton or doubleton records (Table 5.3b, Figure 5.4). The number of species recorded ≤ 2 times were far higher in cluster 5 (59%) and cluster 2 (44.5%) than any of the other clusters ($\bar{x} = 16.5\%$, $\sigma = 3.0\%$). Nonetheless species rarefaction curves (Figure 5.5) demonstrated that the rate of novel species accumulation through increased sampling remained high in all clusters, with the exception of cluster 7, which appeared to be nearing asymptote. Some caution should be taken in this interpretation of cluster 7 however, as unaccounted-for sampling bias from fisheries derived data may have a disproportionate effect on cluster 7 (i.e. multiple captures and recordings of the same commercially valuable species diluting other scientific sampling). Higher richness and distinctiveness (i.e. cluster specific taxa) was observed in cluster 5 than in all other clusters, across taxonomic levels (Table 5.3a).

Table 5d summarises the breakdown of biological records by cluster. Cluster 5 was dominated by targeted sampling of fish and crustaceans. In addition however, cluster 5 notably accounted for 87.6% (432) of mollusc records and 66.1% (738) of annelid worm records. Conversely despite significantly more sampling occurring on the cluster 5 shelf environment, abundances of cnidarians were relatively low, with only 5% of stations recording the presence of corals. By comparison clusters 4 and 7 both reported occurrence of corals at 67% and 53% of stations respectively.

Table 5.3a. Summary of biological records by level-1 cluster

Cluster	Stations	Records	Phylum	Class	Order	Family	Genus	Species
Cluster 1	293	1328	12	24	42	131	183	258
Cluster 2	62	655	9	17	31	85	124	173
Cluster 3	35	311	8	12	18	47	61	88
Cluster 4	778	2761	12	27	44	145	212	312
Cluster 5	3316	17713	18	49	78	424	798	1388
Cluster 6	377	1515	11	22	46	118	172	223
Cluster 7	1753	6016	13	31	61	187	284	394

Table 5.3b. Summary of distinct (cluster specific) taxa by level-1 cluster

Cluster	Phylum	Class	Order	Family	Genus	Species	Singletons	& Doubletons
Cluster 1	0	0	0	4	12	23	21	48
Cluster 2	0	0	1	9	31	54	42	77
Cluster 3	0	1	1	2	2	7	7	11
Cluster 4	0	1	1	5	16	30	30	60
Cluster 5	5	16	17	204	478	978	422	820
Cluster 6	0	0	2	3	12	19	17	31
Cluster 7	0	0	2	5	22	41	35	71

Table 5.3c. Summary of the functional traits of biological records by level-1 cluster

Cluster	Reef-building		Substrate			Mobility		Dispersal	
	Yes	No	Hard	Soft	Cosmo	Sessile	Mobile	Pelagic	Non-pelagic
Cluster 1	7	138	96	3	59	91	140	174	196
Cluster 2	0	118	21	25	1	20	115	72	67
Cluster 3	0	53	0	7	0	0	67	33	47
Cluster 4	26	118	128	11	27	124	91	146	136
Cluster 5	241	4010	1440	366	41	1305	3268	1922	3030
Cluster 6	18	149	48	17	56	47	131	103	111
Cluster 7	21	469	98	37	13	92	431	255	353

Table 5.3d. Summary of biological records by level-1 cluster

Taxa	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	Cluster 6	Cluster 7
Porifera	29	1	1	133	234	35	196
Crustacea	322	416	229	774	5374	382	2019
Annelida	49	50	38	69	738	41	131
Cnidaria	283	48	23	1006	345	364	1628
Mollusca	2	0	1	13	432	1	44
Fish	349	1	0	96	7580	418	812
Ascidian	11	11	0	35	528	13	57
Echinodermata	173	78	8	530	1250	219	982
Cephalopoda	8	0	0	13	107	15	52

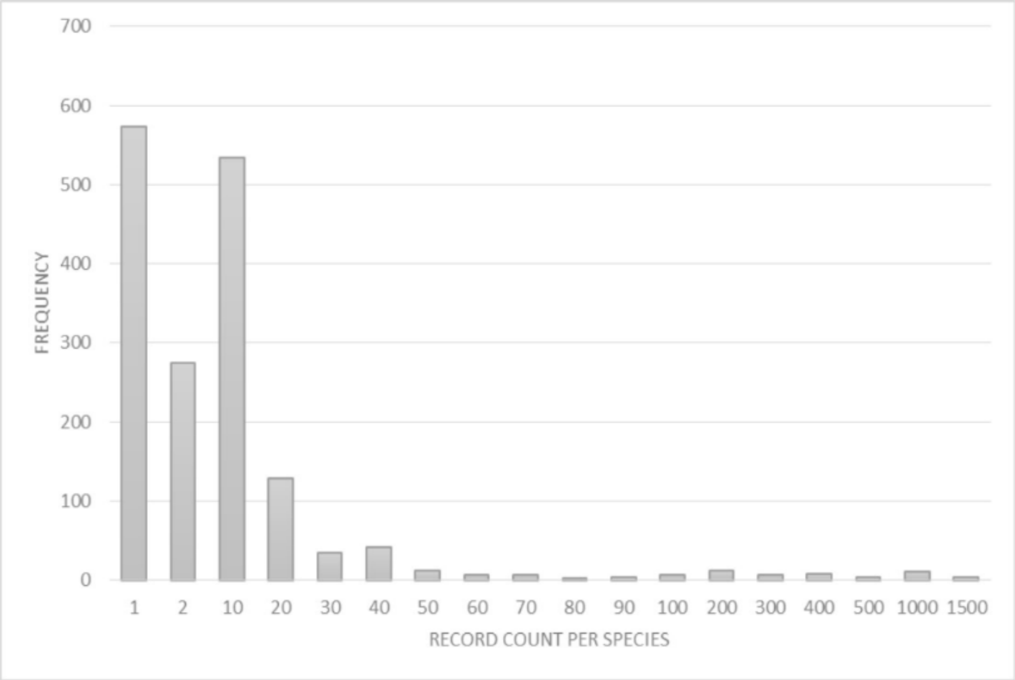

Figure 5.4. Species frequency at South Georgia. Species are ranked according to the number of distinct locations at which samples were recorded. Species records at South Georgia were dominated by a large number of species recording very low record counts or by a small number of species recording very high record counts.

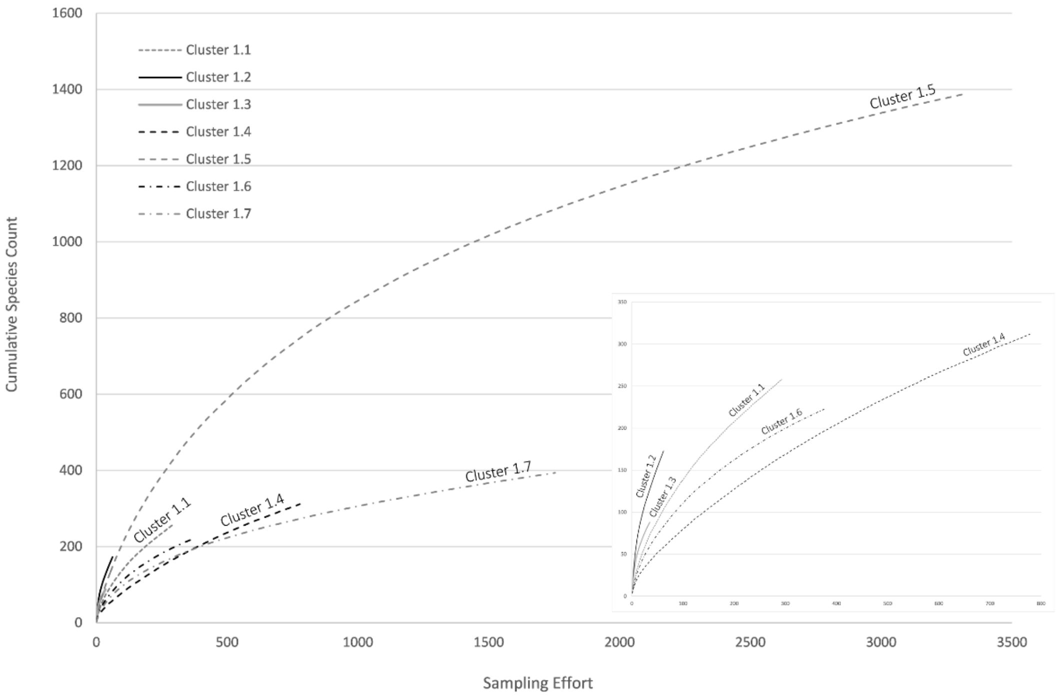

Figure 5.5. Rarefaction curves showing the rate of species accumulation with increasing sample effort across level-1 landscape mapping clusters. Sample effort is defined by number of distinct sampling sites. Inset: Highly sampled clusters 5 and 7 are excluded.

Analysis of level-2 clustering of the South Georgia shelf showed that over half the distinct records for the shelf (53.7%) had been sampled in the large cluster 5.5 (Appendix C: Supplementary materials Table 5.2). This resulted in high taxonomic richness across taxonomic levels reported for this sub-cluster. Other clusters (notably the coastally adjacent cluster 5.2) which, despite having received almost 6 times less sampling in terms of unique sample sites, also demonstrated high species richness and much higher species richness per sampling event. To a degree this may be explained by the presence of a number of dive surveys along the northern coast of the island producing very high-resolution analysis and species identification for this inshore region. This region (Cluster 5.2) also reported a greater number of distinct species than all other sub-clusters combined (Table 5b). With the exception of cluster 5.5, sampling was far more uniform in terms of numbers of records across the shelf than between the shelf and the broader South Georgia region.

5.3.2 Functional traits

Classifying species based on their functional traits demonstrated further distinction between clusters (Table 5c). Cluster 4 was characterised by steep slopes (> 10°), high terrain rugosity and a large range in curvature and topographic position values, suggesting a region of complex topographic peaks and depressions. 77.1% of species (128) attributed functional traits for this cluster were considered to have exclusive affinity with hard substrate (bedrock, large rocks, boulders or cobbles). By comparison only 6.6% (11) of species were shown to inhabit exclusively soft sediment environments. 18% of species (26) in cluster 4 were considered reef-building species (i.e. they create biogenic physical structures raised above the surrounding seabed creating a consolidated habitat for epi-benthic species). By comparison, 10.8% (18) of cluster 6 species were reef-building species, and amongst the remaining five clusters reef-building species averaged only 2.9% (σ = 2.9%) of total species. Cluster 4 also had a higher proportion of sessile species (57.7% (124)) compared to other clusters ($\bar{x}$ = 21.1%, σ = 13.5%) and represented the only cluster for which sessile species outnumbered mobile species.

With the exception of cluster 3, which was the most poorly sampled cluster, and for which functional trait information was lacking, and cluster 2 which had a mix of hard and soft substrate species, species inhabiting hard substratum were dominant in all other clusters. This however could be an artefact of sampling technique with hard, larger epibenthic specimens more likely to be collected in trawl samples than soft, smaller and infaunal specimens. The proportion of species exhibiting pelagic larval dispersal versus brooding or direct development was shown to be roughly equal for clusters 1, 2, 4 and 6. In clusters 3 and 7 this balance shifted towards a greater proportion of brooders and direct developers ($\bar{x}$ = 58.4%, σ = 0.5%), with the highest proportion of brooders (61.2%) occurring on the South Georgia shelf (cluster 1.5).

Analysis of functional traits demonstrated no clear broader biogeographical trends. For example no distinct correlation in functional traits was found between deep-sea and shelf environments, or regions with strong current regimes, and those without. The strongest differentiation in functional traits was seen between cluster 4 and the other level-1 clusters.

5.3.3 Ordination analysis

NMDS was conducted on 30,299 presence-only biodiversity records, representing 1670 species from 18 phyla collected at 6593 sample stations from the study area. Initial NMDS runs including all records run at species, genus and family level, demonstrated no statistically significant delineation in the composition of biological records on the basis of the landscape mapping clusters to which the records belonged (Figure 5.6.1). Significant sampling bias corresponding to far higher sampling levels in cluster 5 on the South Georgia shelf (which was dominated by rare, infrequently sampled species), was deemed to be creating significant noise in the data, as to obscure any possible underlying, more subtle signals, in the data differentiating clusters. As such the NMDS was run again, at different taxonomic levels, but this time done in isolation for shelf based records (only cluster 5) and non-shelf based records (all clusters except cluster 5). NMDS results again demonstrated such a high degree of heterogeneity between sample stations that no significant relationship could be shown between the species composition of sample stations and the cluster in which they were assigned. Intra-cluster variability was therefore shown to be as high, or higher, than inter-cluster variability. In order to remove the confounding influence of rare species, notably the high proportion of singleton and doubleton species (Figure 5.4), and taxa with highly localised or spatially skewed distributions (for example very high resolution biological data collected in the sublittoral zone through dive surveys), NMDS was re-run with the removal of all spatially restricted taxa, and all minor phyla (which tended to have very few and spatially constrained records). It was then re-run again with the additional removal of all stations containing two records or less (3323 records) and the removal of all species with two records or less (1118 species; 1662 records), reducing the station count to 3291 and the record count to 25,314. The resulting ordination demonstrated no division between clusters. To remove the possibility that stations with greater than two records, but still low numbers of records, could be having a disproportionate effect on increasing intra-cluster variability based on a relatively small number of samples, two more NMDS iterations were run, again excluding singleton and doubleton species, but in addition excluding all stations with fewer than 10 records and 20 records respectively.

This reduced the total record count of the analysis considerably to 8625 and 5857 respectively. The NMDS was run at species, genus and family level; at no taxonomic level was landscape cluster shown to be a good determinant of species composition. In an attempt to reduce the noise created by fine-scale heterogeneity in the dataset (i.e. high levels of distinctiveness between individual sampling stations) at the expense of visualising larger-scale trends in the data (i.e. at the level of our landscape clusters), retaining only stations with > 20 samples seemed effective. It did however remove the majority of records collected from the region from the analysis. To circumvent this, the study region was divided into an equal hexagonal grid. All stations occurring inside the same grid cell (and belonging to the same cluster) were then merged to form one species list per grid cell (excluding singleton and doubleton species). This was run at a grid cell resolution of 5 km, 10 km, 20 km and 50 km. Separation across clusters was low in the 5, 10 and 20 km cell sizes. For the 50 km subdivision of the region separation across all clusters was also low (Global R = 0.129, P = 0.001). Pairwise tests between individual clusters however, demonstrated separation between the shelf environment (cluster 5), and both deep-water environments (clusters 1–3) (Global R $\bar{x} = 0.549$, $\sigma = 0.135$, P = 0.001), and regions of complex topography (cluster 4; Global R = 0.446, P = 0.001). Clusters with greater geographic connectivity with the shelf (i.e. areas of continental slope - clusters 6 and 7) demonstrated lower degrees of separation (Global R = 0.323 and 0.195 respectively).

In running the same protocol for the shelf environment (level-2 cluster classification), a 50 km hexagonal grid did not provide sufficient sample points for effective ordination analysis. As such a 20 km grid was used for the level-2 analysis. No significant relationship was shown.

Removing the landscape mapping clusters as a factor in the analysis, we ran an ordination on the data with geographical region as a factor, to look for simple biogeographical trends in the data. The South Georgia shelf (> 400 m) was subdivided into four broad geo-regions, with the geographically and bathymetrically isolated Shag Rocks forming a fifth region. As before species with fewer than two records, and stations with fewer than two records were excluded from the analysis. The ordination was run at three taxonomic levels; family, genus and species. Across all taxonomic levels no statistically significant bio-regional trends were shown.

All ordination analyses thus far demonstrated high variability between the faunal compositions of individual sample stations. This could be accounted for by natural variability in the environment and the animals that live there, sampling bias or the rarity of many of the species recorded. To address the question of whether landscape mapping clusters can act as predictors for the species composition of the benthic communities which live there, and as such can be considered ecologically relevant, we attempted to assess species composition at the landscape-level (as defined in Figure 5.3) rather than between individual sampling stations. NMDS of this dataset demonstrated a strong degree of separation between clusters (Global R = 0.861, P = 0.001).

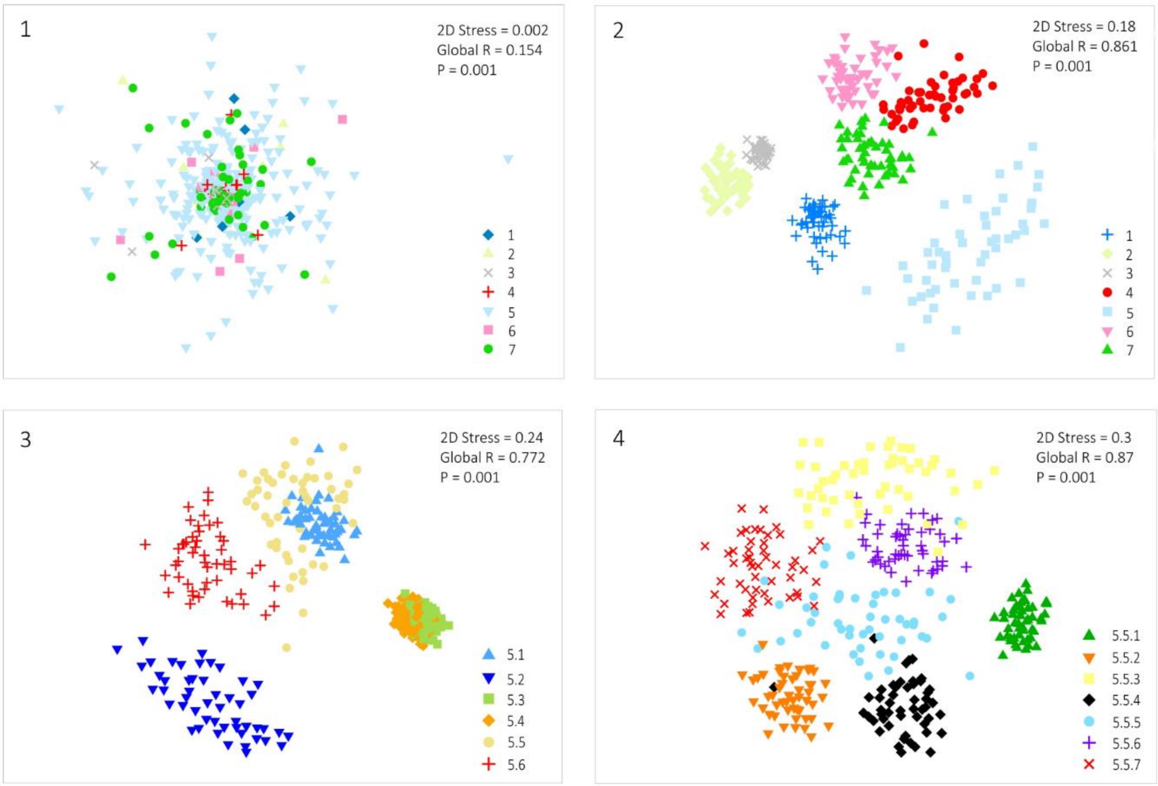

Figure 5.6. Non-metric multidimensional scaling analysis of the taxonomic composition of South Georgia's benthic environment. Sample stations are colour-coded on the basis of the landscape mapping cluster in which they occur (Figure 5.3). Analysis shows: 1. All species-level biological data available for the level-1 cluster region, for which no statistically significant relationship was shown (Global R = 0.154, P = 0.001); 2. Species-level biological data filtered to exclude all singleton and doubleton species for the level-1 cluster region. Species lists for each station occurring within the same cluster were merged and randomly re-sampled for 50 records with replacement 50 times. Two-dimensional stress was good (0.18). Separation was strong (Global R = 0.861, P = 0.001); 3. Species-level biological data filtered to exclude all singleton and doubleton species for the level-2 cluster region (South Georgia shelf). Species lists for each station occurring within the same cluster were merged and randomly re-sampled for 50 records with replacement 50 times. Separation was strong (Global R = 0.772; P = 0.001). 2D stress was high (0.24); 4. Species-level biological data filtered to exclude all singleton and doubleton species for the level-3 cluster region (South Georgia inner shelf). Separation was strong (Global R = 0.87; P = 0.001). 2D stress was very high (0.3), only reducing to 0.22 in 3-dimensional space.

The same protocol was applied to level-2 and level-3 clusters. Both showed strong separation between clusters (Global R = 0.772, P = 0.001; Global R = 0.87, P = 0.001 respectively). In the level-2 analysis (Figure 5.6.3) clusters 5.3 and 5.4 showed significant overlap. These clusters were both similarly characterised by strong current regimes. Clusters 5.1 and 5.5 also showed a degree of overlap and both included regions of deeper more stable water temperatures. The complex topography of cluster 5.6 and the near-shore environment of cluster 5.2 both appeared most distinct in terms of faunal composition. A significant weakness in visualising this analysis however is the high two-dimensional stress value (0.24) of the graph indicating that it was problematic for an accurate reflection of the data to be rendered in two-dimensional space. An acceptable three-dimensional value (0.19) however gives greater confidence in the three-dimensional representation. Figure 5.6.4 shows the NMDS results from the level-3 resampling analysis. Though separation was shown to be strong (Global R = 0.87; P = 0.001), high stress values in both 2D and 3D space suggest the visual representation on the data in Figure 5.6.4 is not a good reflection of the true nature of the data.

5.3.4 SIMPER analysis

SIMPER analysis of level-1 clusters demonstrated that cluster separation was driven, to a large degree, by the species composition of a relatively small number of classes or phyla. In all but cluster 4 (rocky escarpments) the composition of amphipods and echinoderms accounted for 55.8% (σ = 5.3%) of species-level dissimilarity between clusters. Cluster 4 was driven by a more extensive groups of taxa including echinoderms but also hydrozoans, hexacorals, octocorals and crinoids. Corals accounted for 26.7% of species-level dissimilarity in cluster 4. Simper analysis of the shelf environment (cluster levels-2 and 3) again showed the dominance of species of amphipods in defining a number of cluster designations (e.g. the predominantly shelf-edge clusters 5.3 and 5.4). The simper analysis species lists for both levels-2 and 3 clusters were comparatively taxonomically diverse. Species of ascidians, pycnogonids, gastropods, echinoderms, bryozoans and sponges were all shown to drive the faunal differentiation of different clusters.

5.4 Discussion

This study aimed to assess whether broad-scale habitat mapping approaches employed at South Georgia (Hogg et al., 2016), and adopted more generally in management plans globally (Davies et al., 2004; Ainley et al., 2010; Last et al., 2010), produce ecologically relevant results. Secondly, if they do, whether they represent an effective tool in addressing the mismatch between large-scale marine spatial planning, and paucity in biological data that is ubiquitous for large-scale marine protected areas?

5.4.1 Linking landscape and biology

Ordination was used to assess the relationship between an extensive biodiversity dataset for the region (Hogg et al., 2011), and a physical habitat classification derived from abiotic attributes of the environment (Hogg et al., 2016). The biological data demonstrated a high level of taxonomic variability between sample stations, both between and within habitat classifications. This concurred with a previous attempt (Barnes and Sands, 2017) to link biological data with habitat designations at South Georgia (Barnes et al., 2016; Hogg et al., 2016). We report that even geographically neighbouring sampling stations often shared few, or no common species. The data did not demonstrate clear biogeographical trends, or obvious broad-scale zonation over depth, latitude or longitude. Nor did it support species-level discontinuity between the shelf waters of South Georgia and neighbouring Shag Rocks, as previously recorded in a range of mobile taxa (Allcock et al., 1997; Shaw et al., 2004; Kuhn and Gaffney, 2006; Strugnell et al., 2012). Instead biological records were dominated by the presence of rare, singleton or doubleton species (Figure 5.4).

Only when records were randomly re-sampled within each cluster designation, thus removing the integrity of individual sampling stations, was a statistically significant relationship between landscape mapping clusters and species composition demonstrated (Figure 5.6). This approach highlighted that though benthic taxonomic composition at South Georgia is highly heterogeneous, a clear biological signature is nonetheless associated with physical habitat mapping classifications. At the broadest spatial scale (level-1 clustering), clear biogeographical trends were evident in the resampled data. Deep-sea clusters 2 and 3, clustered closely together, as did clusters 4, 6 and 7 (representing predominantly neighbouring terrains along the South Georgia continental slope), whilst the shelf environment of cluster 5 was shown as a clearly separate grouping. This geospatial correlation in the data was also apparent when the region was gridded and analysed on a 50 km2 hexagonal grid. Here the shelf environment (cluster 5) exhibited a distinct faunal composition from all other clusters. The degree to which other landscape clusters differed biologically from the shelf environment was shown to be dependent on their geographic connectivity. Adjacent continental slope regions were shown to be biologically most similar to the shelf and the more remote deep-sea environment, most dissimilar.

Level-2 and level-3 landscape mapping classifications, which focused on the South Georgia continental shelf, demonstrated similar trends to the level-1 clusters. Most species were recorded very infrequently and there was a high degree of heterogeneity in faunal makeup within and between clusters. Ordination of the raw biological data demonstrated no statistically significant separation of faunal composition on the basis of landscape clusters. When randomly resampled however, clear divisions were seen between certain clusters. As with level-1 clustering, greatest dissimilarity appeared to be related to the geospatial distribution of different clusters, with neighbouring clusters often forming stronger biological association. As spatial scale reduced further in level-3 clustering, though the relationship between biological assemblages and landscape cluster remained strong, the NMDS analysis demonstrated a far greater degree of cross-over between clusters than in level-1 and level-2 clustering.

There are certain features in the marine environment such as coral reefs (Andrefouet et al., 2006), canyons (Huvenne et al., 2011), gullies (Gales et al., 2016) and continental shelf breaks (Harris and Macmillan-Lawler, 2016), for which sharp discontinuities in environmental conditions, notably depth and substrate, delineate a boundary between consolidated habitats. Most marine habitats however, depending on the spatial scale at which they are observed, are not clearly delineated by abrupt boundaries. Instead conditions that define habitats change over gradients and biological communities transition, with a degree of turnover between regions. As such there is a fundamental inconsistency between this continuum of environmental variables and categorical classification systems (Wallace, 1876), which will always make this sort of analysis problematic.

Whilst some elements of the environment demonstrate gradual change, the benthic environment also represents a complex mosaic of different conditions and structures. Some are continuous, driving gradual change, others are seasonal, driving temporal change, whilst others are stochastic and isolated in nature. By randomising the biological dataset we attempt to smooth out this boundary effect at the edge of clusters where there is likely a lot of spill-over between cluster designations. Furthermore, it also acts as a means of smoothing out fine to medium scale features driving biological heterogeneity in the landscape. In doing so we demonstrate a simplified, broad-scale view of benthic life around South Georgia, but one which identifies landscape mapping clusters, across spatial scales as ecologically relevant.

5.4.2 Biological drivers of landscape clusters

SIMPER analysis identified a relatively narrow suite of animals as responsible for driving distinct faunal compositions in each landscape cluster. At level-1 clustering, these lists were dominated by amphipod crustaceans and echinoderms belonging to the classes Ophiuroidea (brittlestars and basketstars), Asteroidea (seastars) and Echinoidea (urchins). The ubiquity across clusters of these higher taxonomic groups as indicator species is noteworthy, given they weren't shown to be particularly dominant in terms of general record or species counts at South Georgia. As such this could be an indication that these particular faunas have benefited from a degree of taxonomic differentiation not afforded to all other taxonomic groups. Morpho-species of these taxa may have been subdivided to a far greater degree, due to increased attention, or ease of identification. One cluster that differentiated from others in terms of SIMPER analysis was cluster 4. This cluster was defined by a much broader group of animals including various sub-classes of coral. Cluster 4 also demonstrated the greatest differentiation from other clusters in terms of the functional composition of its biological communities. Unlike other cluster designations, cluster 4 was not defined by broad-scale classification variables (e.g. depth or temperature), which tended to form spatially discrete, continuous and large landscape groupings. In contrast, cluster 4 was geographically widespread, but spatially very constrained to regions of specific geomorphology. The region had high rugosity, high slope angles, a large range in topographic positions (peaks and troughs), and a large range in curvature (the rate at which slope gradient changes). Such attributes of the benthic environment are often used as geomorphological surrogates for hard rock environments (Harris, 2012), an inference supported here by the higher number of species recorded in cluster 4, that demonstrate an exclusive affinity to hard substrate, as well as animals known to be reef-building organisms. Substrate type was not in itself explicitly tested in this analysis, due to a lack of available data. However, using cluster 4 as a surrogate for rocky environments, the categorical, and in this case binary, hard/soft nature of substrate type as an environmental driver offers a possible explanation as to why this cluster is so distinct in terms of its functional and taxonomic composition. If many species demonstrate a preference or exclusivity for hard or soft habitat types, then with the effect of other environmental drivers limited by the narrow spatial window of cluster 4, the more categorical nature of the topography or substrate seems likely to have the most directing, and quantifiable influence on the faunal composition of the habitat. Indeed the original analysis of the cluster designations (Chapter 4: Figure 4.6; Appendix B Supplementary materials Figures 4.2 & 4.3) demonstrates how marked the environmental divide is between cluster 4 and all other clusters.

In contrast, other clusters covered very large spatial areas, and as such, though they were characterised by distinct combinations of broad scale trends in environmental conditions (Table 5.2), it seems likely that within each of these clusters, there was a large range of different habitat types driven by smaller scale drivers. For example a series of isolated rocky outcrops such as a glacial dropstones within an otherwise homogenously muddy, flat environment would create significant variability in the biological dataset (Meyer et al., 2016; Meyer, 2017). The stochastic nature of this variability would make it very difficult to characterise fauna representative of a particular landscape mapping cluster.

SIMPER analysis for level-2 and level-3 landscape mapping classifications, provided significantly different results from that of level-1 clustering. On the South Georgia shelf, landscape clusters were driven by a much broader group of taxa with the inclusion of species from 13 different phyla including species of ascidian, bryozoans and shelled molluscs. This greater diversity in species is likely on account of more comprehensively analysed samples and research campaigns on the South Georgia shelf compared to the adjacent regions.

With reference to Hogg et al. (2016), when interpreting the strength of any faunal association with landscape mapping clusters, it is important to note that not all landscape mapping clusters were equal in terms of physical environmental dissimilarity between one another. Some, notably the shelf environment (cluster 5) and rocky escarpment environments (cluster 4), were much more clearly delineated than for example, some of the deep-sea clusters. Other clusters were designated on the basis of very strong environmental signals, yet in the context of the ecology of the region might be called into question. For example is it ecologically meaningful to create a landscape division on the basis of the directional flow of a seabed current (as in the case of clusters 1 and 6) or is it only important how strong the current is? Over very large spatial scales directional flows in currents may prove informative of the nutrient or food carrying potential of the water mass, for example transportation of krill to

South Georgia from the Antarctic Peninsula to the south (Hofmann et al., 1998). This, however, may not be informative at finer spatial resolution. For all clusters therefore, it is entirely reasonable to assume that the factors that drive the cluster designations will in turn impact the strength of the biological response that we observe between clusters.

5.4.3 Application of landscape mapping in marine spatial planning

This paper assesses how landscape mapping can inform, if at all, on the underpinning and implementation of marine management at South Georgia. Representative protection is a key requirement of CBD Aichi goals (Secretariat of the CBD, 2010). Indeed one criticism of VLMPAs generally, has been that they do not provide representative protection of realms across the marine environment (Leenhardt et al., 2013; Jones and De Santo, 2016).

Biological data collections at South Georgia date back over 130 years. As such the dataset, though extensive, often lacks accurate metadata (collection method; whether sampling was targeted; geo-referencing; taxonomy), and a standardised experimental design or sampling protocol. This makes biogeographical analysis at South Georgia problematic, with underlying and often unaccountable sampling and taxonomic biases. The type of sampling gear used in different studies, will by itself have a profound influence on the ability to characterise the biology of an area in a way that can be linked to the remotely sensed data sets (Solan et al., 2003). Conversely however, these limitations also make analysis of the South Georgia dataset a real-world example of addressing VLMPA data management. Over very large spatial scales, biological data collection is not likely to be standardised, as such, South Georgia represents a good analogue for large-scale analyses of VLMPAs more broadly.

Despite clear limitations, notably in the underlying high variability in the biological data, landscape mapping is demonstrated at species-level to be ecologically meaningful. This provides the opportunity of a quantitative assessment of how representative current protection is of benthic habitats at South Georgia. Currently the MPA covers the majority of the exclusive economic zone (Trathan et al., 2014). Long-line fishery activity is restricted (under licence) to a depth band of 700–2250 m around the South Georgia slope. Landscape mapping can help us access whether certain habitat types are disproportionately exposed to such activity. Preliminary analysis would suggest that fishing activity is currently predominantly occurring over clusters 4 and 7. Our analysis suggests these clusters have high affinity with hard rock environments with higher levels of reef-building organisms, notably corals. Furthermore previous analysis has identified this to be a region of higher species richness, notably in brooding species and low-dispersal model taxa (Barnes et al., 2016). This therefore is an example of how landscape mapping, integrated with other analyses, can be used to identify regions that may be important to protect, but under the current framework may be disproportionally impacted by current human activity.

Another application of landscape mapping in marine spatial planning at South Georgia is the ability to identify and thus maintain habitat heterogeneity in the region. Habitat heterogeneity is well established as a useful proxy for species diversity at multiple spatial scales (Williams, 1943; Hewitt et al., 2008; Foley et al., 2010). As such it is often adopted in marine conservation as a mean of identifying and maintaining species-level diversity (Roberts et al., 2003; Mumby et al., 2008). Landscape mapping provides a framework by which to map and protect regions of high habitat heterogeneity. Habitat heterogeneity can also help us identify regions of high functional diversity (diversity in functional traits), which in turn has been linked to ecosystem functioning (Zeppilli et al., 2016), and to greater provision in ecosystem services (Tilman et al., 1997; Barnes and Sands, 2017).

VLMPAs by nature adopt a 'cover as much as possible-protect as much as possible' model to conservation and management of marine resources. Landscape mapping can be used in synthesis with predictive modelling approaches, across spatial scales, to identify important, vulnerable or unique habitats that may warrant enhanced protection and also provide a better understanding of the habitats and their functions that are currently being protected.

5.5 Conclusions

We demonstrated a statistically significant relationship between environmentally derived landscape mapping clusters at South Georgia (Hogg et al., 2016), and the composition of presence-only species data from the region (Hogg et al., 2011). This relationship reveals a distinct biological signature in the faunal composition of individual clusters, and as such, attributes ecological relevance to South Georgia's environmentally derived landscape mapping clusters. This correlation was evident across three hierarchically nested spatial scales, from very large regional clusters (10^4 km^2) to much smaller spatially constrained features (10^1 km^2).

In order to demonstrate this relationship however, required specific treatment of the data to remove biological rarity, biological cosmopolitism, range restricted sampling of specific taxa, and fine-scale heterogeneity between sampling stations. The need for such iterative cleaning and re-sampling of the biological data highlighted the problematic nature of analysing historical data (in this case representing over 130 years of polar exploration), specifically in accounting for spatial and taxonomic biases not always explicit in the data without knowledge of the provenance and collection protocol applied during data collection. Furthermore, it was indicative of the high degree of heterogeneity in the biological data, presumably reflecting fine-scale heterogeneity in the environment not accounted for in relatively broad-scale, top-down approaches to habitat classifications.

Analysis identified some clusters as more biologically distinct than others. Where environmental conditions were distinct from geographically neighbouring regions, a corresponding distinctiveness in faunal composition was often recorded. Functional traits of South Georgia's benthic fauna correlated well with certain landscape mapping clusters, for example, representing a good surrogate for distribution patterns of reef-building corals.

Marine habitat mapping has been suggested as representing an effective tool in addressing the mismatch between large-scale marine spatial planning and paucity in biological data. One of the challenges facing marine spatial planners at the broad spatial scales of VLMPAs, is paucity in biological data at a scale relevant to planning decisions. There is however, also a disparity between rigid habitat classification systems, and the reality in which habitats are not delineated by abrupt boundaries, but rather a continuum of gradual biotic and abiotic change. In this study, by smoothing out this boundary effect, mapping clusters are shown to be biologically distinct. By extension therefore, the use of environmental clustering as a management tool can, we argue, represent an effective means of ensuring a degree of representative protection of benthic habitats.

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Chapter 6: An ensemble modelling approach to conservation prioritization at sub-Antarctic South Georgia

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Abstract

This study adopts a bottom-up approach to habitat mapping at the large marine protected area of South Georgia and the South Sandwich Islands. As such, we assess the application of an ensemble approach to habitat suitability modelling in informing on the spatial distribution of biotic attributes of the benthic environment of importance to regional conservation planning.

A range of faunal metrics were used to provide a holistic overview of the benthic environment, these included taxonomic classification, classification based on functional traits, and the presence of vulnerable marine ecosystems (VME). This analysis provided the first bio-physical assessment of the benthic environment around South Georgia, inferring distinct coastal, shelf, shelf-edge, slope and deep water communities which corresponded with changing physical conditions. The analysis identified a mixture of hydrodynamic and terrain-based variables as ecological drivers of regional biogeographical patterns. The use of an ensemble approach to habitat suitability modelling allowed assessment of variance in modelling performance between response variable, modelling algorithms and separate modelling runs. This provided a measure of confidence associated with each distribution model.

Modelled distributions were assessed in the context of the current zoned MPA in place at South Georgia. Spatial distributions of VME taxa and regions of high functional group diversity demonstrated the highest likelihood within the current open fisheries zone. As such, we question whether the current spatial configuration of the MPA is best placed to protect benthic functional and taxonomic diversity.

6.1 Introduction

The benthic environment represents a habitat for the majority of marine life. Of the 34 marine phyla, 11 are exclusively benthic, with all 34 represented in the macrobenthos (Steele et al., 2009). Universal paucity in regional marine biological datasets however, means our spatial understanding of benthic biogeography at scales relevant to marine conservation is significantly constrained. This study adopts a bottom-up approach to habitat mapping at the large-scale marine protected area of South Georgia and the South Sandwich Islands, in order to assess the application of habitat suitability ensemble models in informing on the spatial distribution of biotic attributes of the benthic environment of importance to regional conservation planning.

Habitat suitability modelling, also known as ecological niche modelling or species distribution modelling, is a method for predicting the suitability of a location for a certain species or taxon based on the observed relationship between their presence or abundance and the corresponding environmental conditions. This analysis of the interaction between physical and biological variables helps create a more comprehensive spatial and temporal understanding of how biodiversity is structured across a region, and helps constrain what processes are driving this structuring.

Different habitat suitability modelling algorithms do not perform equally in predicting distribution patterns, with the potential for contrasting predictions based on model parameterization and model selection criteria or data characteristics such as sample size and data type (Segurado and Araújo, 2004; Elith et al., 2006; Pearson et al., 2006; Graham et al., 2008; Elith and Graham, 2009; Qiao et al., 2015). Ensemble modelling avoids such dependence on single model types (Araújo and New, 2007; Buisson et al., 2009; Robert et al., 2016), incorporating multiple modelling outputs with different underlying assumptions into a single prediction whilst also providing an assessment on inter-model variance.

Habitat suitability modelling has application in mapping distributions of potentially important or vulnerable taxa (Tittensor et al., 2009; Rowden et al., 2017), particularly when they are data-deficient (Bland et al., 2014); mapping invasive species (Václavík and Meentemeyer, 2009); conservation prioritisation and reserve selection (Araújo et al., 2004; Moilanen, 2007; Guisan et al., 2013); assessing temporal change in response to stressors such as the impact of climate change on marine communities (Araújo et al., 2004; Wiens et al., 2009; Porfirio et al., 2014), and modelling hotspots of species diversity (Ferrier, 2002).

The prioritised protection of species-level diversity, and in particular hotspots of species richness and endemism is a well-established paradigm in conservation biology (Myers, 1990; Prendergast et al., 1993; Pressey et al., 1993; Myers et al., 2000; Roberts et al., 2002; Orme et al., 2005). Increasingly however ecologists and conservation managers are recognising that species do not contribute evenly to ecosystem services and processes (Luck et al., 2009). It is therefore important to account for the range of things that organisms do in communities and ecosystems, rather than just considering their abundance, diversity, and evolutionary history (Petchey and Gaston, 2006; Stuart-Smith et al., 2013).

A set of taxa can be taxonomically unrelated yet have evolved similar biological adaptations and thus be considered phenotypically similar. These taxa can be defined as sharing functional traits. The functional structure of a community and its effect on other aspects of the ecosystem can be represented by a number of traits such as mobility, feeding strategy, reproductive strategy and physical size. These traits and their interactions can help inform on the functioning and stability of an ecosystem, with functionally similar taxa having an analogous effect on ecosystem processes (Cadotte, 2011).

Trait diversity and variability relate to changes in ecosystem processes and function (Gagic et al., 2015). Behavioural traits related to bioturbation, for example, affect sediment stability and biogeochemistry (Bremner et al., 2006); growth size and structure, such as with reef-building benthic invertebrates, provide physical structures for colonisation (Jones et al., 1994) and modify water currents and boundary layer conditions (Reidenbach et al., 2006); feeding strategies control energy transfer and nutrient cycling across trophic levels. Furthermore, diversity in functional traits is shown to influence productivity (Tilman, 2001, Hooper et al. 2005) and regulate compensatory responses to environmental change (Mouillot et al., 2013b).

Ecosystem functions provide ecosystem services on which human survival depends (Millennium Ecosystem Assessment 2005; Barbier, 2017). These services range from storm protection and erosion control to food provision and carbon sequestration (Worm et al., 2006; Barnes and Sands, 2016). Measuring an organism's function in the ecosystem and its influence on ecosystem processes can relate directly to the ecosystem services it provides. This can therefore link ecosystem management with aspects of the ecosystem for which there is the strongest economic incentives to conserve (Costanza et al. 1997). The adoption of functional indices as a conservation metric can, in many instances, be considered more informative than taxonomic-based metrics as they are better at predicting community response and resilience to disturbance (Mouillot et al., 2013b; Gagic et al., 2015). As such, species that contribute a large amount of functional diversity may be considered more valuable for conservation (Fonseca and Ganade, 2001). Despite the potential of trait-based approaches in marine conservation (Robinson et al., 2014; Stuart-Smith et al., 2013, 2015; D'Aloia et al., 2017), its application in this field remains in its infancy and its inclusion in marine habitat suitability modelling largely untested.

A more established metric by which conservation and remediation practices are prioritised is the degree to which benthic ecosystems are vulnerable to disturbance, especially when that vulnerability coincides with regions of high diversity or distinctiveness (i.e. rare or endemic species). Vulnerable marine ecosystems (VMEs) are generally defined as assemblages of marine benthic organisms which are susceptible to anthropogenic disturbance, typically through impact from fishing gear. In many cases, the slow growth rates and fragility of the species associated with such ecosystems (i.e. VME taxa) make the organisms particularly vulnerable to adverse impacts of bottom fishing (FAO, 2009; CCAMLR, 2009). VME taxa include species that form complex biogenic structures such as coral reefs and sponge gardens. These three-dimensional structures provide habitats for epifaunal communities and are often associated with regions of high diversity (Jones et al., 1994).

International commitments passed through the United Nations General Assembly resolutions require nation states to identify VME within their jurisdiction and take measures to protect them (see Ardon et al., 2014). CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) defines VME risk areas under Conservation Measure 22-07 (2013) and Conservation Measure 22-06 (2017). VME closure is designated when 10 or more VME indicator units are recovered within a single line segment. Under this definition a VME indicator unit is defined as equal to either 1 litre of VME fauna when placed in a 10-litre container, or 1 kg or VME fauna. Line segment is defined as a 1,000 hook section of line or 1.2km of line whichever is shorter. On meeting this somewhat arbitrary 'risk threshold' a closure area of 1 nautical mile from the mid-point of the line recording the VME is enforced until the region can be scientifically assessed.

The need to rank and prioritise regions vulnerable to anthropogenic threats is well established (e.g. Halpern et al., 2007), as such it has increasingly been included in habitat suitability models within the context of marine conservation. This includes the predictive modelling of specific VME taxa such as cold water corals (Rengstorf et al., 2013; Taylor et al., 2013), sponges (Knudby et al., 2013) and more recently modelling of VME communities using indicator species (Rowden et al., 2017).

This study aims to model the spatial distribution of taxonomic groups, functional traits and management-specific metrics such as vulnerable marine ecosystems around the sub-Antarctic island of South Georgia. In doing so we aim to (i) bio-physically characterise the benthic environment around South Georgia; (ii) analyse how taxonomic and trait-based faunal groups are distributed in the region; (iii) assess how modelled spatial data can help inform on marine spatial planning for the South Georgia region, and in doing so, (iv) assess the application of ensemble modelling in large-scale MPA design more generally.

6.2 Methodology

6.2.1 Study area

This study focuses on a contiguous region around South Georgia within a depth range between 0 and 3,000m. This includes the continental shelf of South Georgia and the Shag Rock shelf (to the west of

South Georgia) and the surrounding continental slopes (Figure 6.1). The study region covers an area of 134,239 km^2 of which 35,105 km^2 constitutes the zone between 700 and 2250m depth, which through the current management plan is open to licenced long-line fishing. This geographical delimitation was selected based on the spatial extent of the environmental datasets (see section 4.2.1) and significant paucity in deep-sea biological samples beyond the South Georgia slope (Figure 6.1). A depth of 3000m provided analysis across the entire South Georgia shelf and slope, in addition to a spatial window beyond the current permissible fishing zone.

Bottom fishing has a negative impact on benthic diversity and abundances (Kaiser et al., 2002; 2006). This is potentially compounded at South Georgia because the benthic fauna is typically Antarctic in character (Barnes et al., 2006; Griffiths et al., 2009). As such it is characterised by slow growth rates, increased longevity and deferred sexual maturity (Peck, 2002). This delays and potentially reduces recovery in the benthic community from damage (Parker and Bowden, 2010).

Bottom fishing at South Georgia is restricted to bottom longlining between 700 and 2250m, using Spanish and autoline systems (see Benedet (2017) for detailed descriptions). Longlining allows fishing in regions of rough topography and steep slope angles due to the fact that it does not involve active trawling or dredging along the seabed, but rather the laying of long lengths of hooked lines. As such it known as a passive fishing method (Benedet, 2017), and considered to have comparatively low impact on benthic fauna (Pham et al., 2014). Nonetheless there is an increasing body of research highlighting the negative impact that longlining has on cold-water corals (Orejas et al., 2009) and VME habitats (Durán Muñoza et al., 2010) often as a result of gear entanglement (Clark and Koslow, 2007; Bo et al., 2014) and damage from weighted lines (Reed, 2002). The demersal longline fishery has been operating at South Georgia targeting Patagonian toothfish (Dissostichus eleginoides) since the late 1980s. Between 2014 and 2017 an average of 9.5 million hooks were set annually by six vessels at South Georgia (Benedet, 2017).

6.2.2 Biological data

Biodiversity data for South Georgia were obtained from a 2011 baseline assessment of the region's benthic environments (Hogg et. al., 2011), combined with more recent BAS research cruises to the region in 2011 (JR262 Science Cruise Report, 2011) and 2013 (JR287 Science Cruise Report, 2013). These data represented a comprehensive review of reports and papers spanning 140 years of polar exploration. Combined this included 31,197 unique biological records from 6593 sampling stations and 1748 species across 51 classes and 22 phyla.

The scientific cruises, from which the data were drawn, differed in collection techniques and sampling protocol. Most commonly Agassiz trawl and epi-benthic sledges were used, but benthos was also collected using inshore SCUBA surveys, fisheries bycatch collection and dredges. Here we report these findings in a standardized format, recording all scientific classification to species level and the location at which the specimens were found with the geo-reference linked to a Geographical Information System (ArcGIS 10.4.1). Synonyms in species classification were reconciled using the World Register of Marine Species (http://www.marinespecies.org). Data management was undertaken using R version 3.4.1 (R Core Team, 2017).

To assign functional trait information to South Georgia's benthic species, species lists were created for each higher level taxonomic group (typically phyla or class), and sent out to taxonomic experts at universities and research institutes around the world (see acknowledgments). Data were collected on development types, reproductive modes, feeding strategies, mobility, lifestyle, affinity to specific substrata, reef-building capacity, whether they were considered habitat forming, whether they were associated with a certain stage of ecological succession and how fragile they are to physical impacts. A breakdown of these traits and their definitions are summarised in Chapter 5 (Table 5.1) and Hogg et al. (2018). Fourteen functional groups were assigned based on these ten functional traits, in line with previous research on functional traits at South Georgia (Barnes & Sand, 2017). These groupings are summarised in Table 6.1.

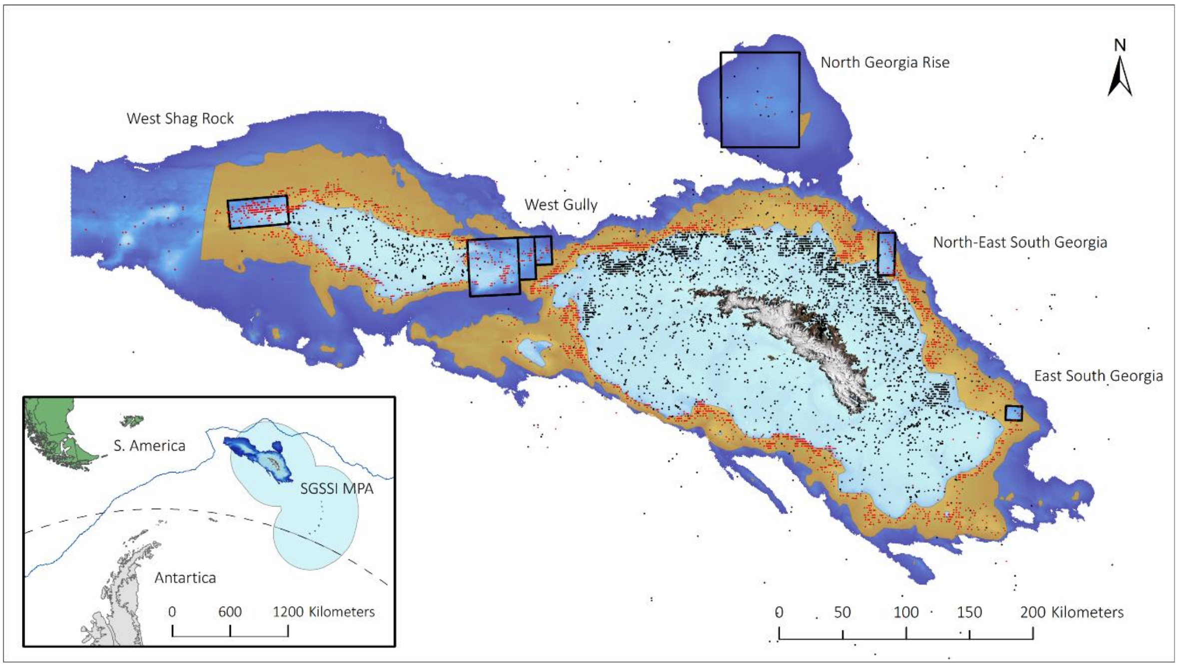


Figure 6.1. South Georgia study region delineated by 3000m depth contour. Black points denote biological sampling stations. Orange polygons denote regions between 700m and 2250m which are currently open to a licenced long-line fishery. Inset provides geographical context to the study region and the South Georgia and South Sandwich Islands marine protected area (SGSSI MPA). The black dashed line denotes 60°S Latitude and the blue line the path of the Polar Front.

Fauna were categorised as constituting vulnerable marine ecosystems (VME) based on inclusion in The Commission on the Conservation of Antarctic Marine Living Resources (CCAMLR) VME registry (CCAMLR, 2009). Fauna were categorised as reef-building species based on expert assessment of their propensity to create a massive biogenic physical structure raised above the surrounding seabed creating a consolidated habitat for epibenthic species.

6.2.3 Environmental data

Environmental data for the region includes: (i) a 530,000 km^2 bathymetry dataset gridded to 100m spatial resolution covering the entire study region (Hogg et al. 2016); (ii) an oceanographic dataset modelled at 2.8km resolution (Young et al., 2011) and interpolated to 100m resolution (Hogg et al., 2016); and (iii) satellite-derived primary productivity data obtained through Oregon State University (http://www.science.oregonstate.edu/ocean.productivity/). The productivity data were extracted as monthly means over a five year period (2010–2014) with a grid cell resolution of 1/12 degree of latitude (~9275 m) by longitude (~5465 m), then interpolated to 100m spatial resolution (see Hogg et al., 2016).

From these three datasets, 19 environmental data layers were included in the analysis, to characterise physical geomorphology (depth, slope, rugosity, topographic position, aspect and curvature), surface productivity (net surface chlorophyll) and physical oceanography (temperature, salinity, current magnitude and velocity). All input variables are summarised in Table 6.4, and discussed in further detail in Chapter 4 (section 4.2.2) and Hogg et al. (2016).

To balance the computational requirements of modelling whilst ensuring robustness of the modelling process (i.e. multiple model runs) and the intended use of the data (i.e. a scale relevant to marine spatial planning) the environmental input variables were re-gridded to 500m spatial resolution using the re-sampling bilinear interpolation in ArcGIS.

To reduce errors in the models associated with multi-collinearity of the environmental predictors (Legendre & Legendre, 1998), principal component analysis (PCA) was conducted on the 19 environmental input variables using the Factoextra R package. The use of PCA also acts as an objective means of data reduction, and as such a means of addressing problems associated with large-numbers of predictor variables reducing the accuracy of the model (Porfirio et al. 2014). The input variables were all standardised to have zero-means and unit variance, thus giving them equal weight in the PCA. We followed the Kaiser-Guttman criterion (Legendre & Legendre, 1998) retaining only principal components (PCs) with Eigen values greater than one. In order to simplify the interpretation of the factor loading pattern, a promax oblique rotation of the PCs was computed using the Psych R package.

6.2.4 Environmental niche modelling

Modelling protocol

Habitat suitability models were used to estimate the distributions of 23 biological response variable data layers: (i) five individual phyla (Cnidaria, Bryozoa, Echinodermata, Annelida and Porifera), (ii) taxa considered by CCMLAR as VME, (iii) taxa considered to be reef-building (see Chapter 5, Table 5.1), (iv) taxa associated with specific habitat characteristics (namely species with exclusive affinity to hard or soft substrate), and (v) 14 functional groups based on categorisation of South Georgia's benthic fauna into 10 functional traits. Biological point data for each of these data layers were converted to a presence-only raster grid in ArcGIS (version 10.4.1) and imported into R.

Habitat suitability models were run using the BIOMOD framework (Thuiller et al. 2009) through the R package: Biomod2. Biomod2 is a species distribution modelling method that utilises ten common modelling techniques and creates an ensemble model of projected current and future distribution based on model fit. Biomod2 accounts for inter-model variability by fitting ensembles of forecasts by simulation across more than one set of initial conditions (i.e. using different algorithms, model parameters, and iterations) (see Araujo and New 2007). Biomod2 analyses the resulting range of uncertainties, assessing predictive consensus and probabilistic density functions and summarises the likelihood of a species presence estimated from an ensemble of different models (Araujo and New 2007; Thuiller, 2003, 2009, 2014).

All ten modelling algorithms included in Biomod2 were employed in this study. These algorithms can be classified in four categories: regression, machine-learning, classification and enveloping, and are summarised in Table 6.2.

Habitat suitability models require presence-absence (PA) data or presence-background (PB) data. Given the predominantly trawl-based approach to South Georgia's historic benthic sampling and the unknown taxonomic bias associated with some of the earlier samples, species absence from any given was not treated as proof of absence. As such, without true absence data, pseudo absences were generated within Biomod2.

The output of the different habitat suitability models has been shown to vary widely depending on how many pseudo-absences are used and how they were selected (Barbet-Massin et al. 2012) with different models sensitive to different treatments. Random generation of pseudo-absences has been shown to be the best strategy for regression and enveloping modelling techniques (see Table 6.2 for model classifications) whilst for classification and machine-learning techniques, absence generation method had little influence (Wisz & Guisan, 2009; Barbet-Massin et al. 2012). As such this analysis employed random pseudo-absence selection across all ten model algorithms.

Table 6.1. Functional group categories modelled in BIOMOD ensemble analysis. Descriptions adapted from Barnes & Sands (2017) with trait categorisation based on assessment by 10 taxonomic experts (see acknowledgements).

Functional Group	Record Count	Description	Example taxa
1	359	Pioneer sessile suspension feeders	Encrusting bryozoans, ascidians, some polychaetes
2	449	Climax sessile suspension feeders	Demosponges, glass sponges, brachiopods
3	123	Sedentary suspension feeders	Basket stars, valviferan isopods, some polychaetes
4	172	Mobile suspension feeders	Some brittle stars, crinoids
5	151	Epifaunal deposit feeders	Sea cucumbers, some polychaetes
6	123	Infaunal soft-bodied deposit feeders	Echiurans, sipunculans, some polychaetes
7	60	Infaunal shelled deposit feeders	Bivalves, irregular sea urchins
8	27	Grazers	Regular sea urchins, limpets
9	559	Soft-bodied, sessile scavenger or predators	Sea pens, soft corals, anemones, hydroids
10	86	Hard-bodied, sessile scavenger or predator	Cup corals, whip corals, hydrocorals
11	361	Soft-bodied mobile scavenger or predator	Some polychaetes, nemerteans, octopus
12	1965	Hard-bodied mobile scavenger/predator (inc. fish)	Fish, sea stars, gastropods, some brittlestars
13	607	Hard-bodied mobile scavenger/predator (ex. Fish)	Sea stars, gastropods, some brittlestars
14	2290	Jointed legged, mobile scavenger or predator	Sea spiders, shrimps, amphipods

The optimal number of pseudo-absences varies significantly with regression models performing best with large pseudo-absence numbers (e.g. 10,000) or multiple runs with fewer pseudo-absences (e.g. 1000PA with 10 runs). Other models such as MARS are better suited to lower numbers of pseudo-absences over multiple runs (e.g. 100PA with 10 runs) whilst CTA, BRT and RF perform best with the same number of presences as absences (Barbet-Massin et al. 2012).

In this analysis the number of pseudo absences was set to a lower threshold of 500, or equal to the number of presences, whichever was greater. Five different pseudo-absence distributions were randomly generated for each model and each pseudo-absence distribution was replicated 10 times. 10 replicates was adopted as a compromise between testing model robustness and limiting computational time. This replication enabled us to account for variability resulting from random sampling of pseudo-absence data and variability in model accuracy between multiple runs. In total 50 replicates were performed for each algorithm for each combination of parameters. Thus in total 500 models were run per response variable and 11,500 models were run through the course of the study.

Regression-based models build linear or non-linear relationships between species presence and their environmental space. Machine-learning methods extract the environmental space of the species presence directly from the training data. Classification methods employ successive data partitions creating homogeneous groups of responses. The enveloping method, defines the environmental conditions of the species presence and extrapolates the results to similar areas based on shared environmental conditions. These modelling techniques are described in more detail in the references provided in Table 6.2.

This study used the default settings of the Biomod2 R-package version 3.4.2 (Phillips et al., 2006; Thuiller et al., 2009).

Table 6.2. The ten biomod2 modelling algorithms used in this study.

Code	Model	Model Category	References
GAM	Generalised additive models	Regression	Hastie (1986); Guisan et al. (2002)
GLM	Generalized linear models	Regression	McCullagh (1984); Guisan et al. (2002)
ANN	Artificial neural networks	Machine-learning	Ripley (1996); Lek and Guegan (1999)
BRT	Boosted regression trees	Machine-learning	Ridgeway (1999); Elith et al. (2008)
MARS	Multivariate adaptive regression splines	Machine-learning	Friedman (1991)
MaxEnt	Maximum entropy	Machine-learning	Phillips et al. (2006)
RF	Random forest	Machine-learning	Breiman (2001)
CTA	Classification tree analysis	Classification	Elith et al. (2008); Breiman (1984)
FDA	Flexible discriminant analysis	Classification	Breiman (1984); Trevor et al. (1994)
SRE	Surface range envelope/ BIOCLIM	Enveloping	Busby (1991)

Modelling performance

In order to quantitatively evaluate the quality of model predictions, each biological dataset was randomly split into two subsets. 70% of the data were used to calibrate (train) the models, with the remaining 30%, used to evaluate (test) model predictions (see Fielding & Bell, 1997). This data split represents a trade-of between the amount of data used for the construction of the model and the accuracy of the evaluation measure (Arajo et al. 2005; Guisan & Thuiller, 2005).

Two metrics were used to test the performance of each model run: TSS and ROC. Both record occurrences where the test model equals the evaluation model (hits & correct negatives) and where the test model does not equal the evaluation model (misses & false alarms).

The TSS or true skill statistic metric (Allouche et al., 2006; Somodi et al., 2017) normalises the overall accuracy of a distribution model by the accuracy that might have occurred solely by random chance. TSS accounts for both omission (misses) and commission (false alarms) errors as well as success as a result of random guessing:

$$TSS = \frac{hits}{hits + misses} - \frac{false\ alarms}{false\ alarms + correct\ negatives}$$

Output scores range from -1 to 1, where a value of zero or less indicates the predictive ability of the model is no better than random, and a value of 1 indicates a perfect model. TSS has increasingly been applied in species distribution modelling as it is not affected by prevalence or by the size of the validation dataset, thus unlike other commonly employed methodologies such as kappa (Cohen, 1960), with TSS, two models of equal performance will have equal TSS scores (Allouche et al., 2006).

ROC or receiver operating characteristic (Lusted, 1971) measures the ability of the model to discriminate between two alternative outcomes, thus measuring resolution. ROC plots model sensitivity (the proportion of observed positives that were predicted to be positive) against the inverse specificity (1 minus the proportion of observed negatives that were predicted to be negatives):

$$Sensitivity = \frac{hits}{hits + misses} \qquad Specificity = \frac{correct\ negative}{false\ alarms + correct\ negative}$$

The line y=x indicates a completely random relationship (i.e. equal modelling hits to false alarms). Using a series of increasing probability thresholds (e.g. 0.05, 0.15, 0.25, etc.) a curve of the model data is plotted from the bottom left to top right. The area under the model curve is then used as a score to assess the predictive ability of the model. Output score range from 0.5 to 1. A value of 0.5 (as with y=x) indicate an equal probability of successfully prediction as not (i.e. no better than chance). An AUC value of say 0.9 indicates that 90% of the time a random selection from the positive group will have a score greater than a random selection from the negative group (Fielding & Bell, 1997).

AUC values of 0·5–0·7 are typically taken to indicate low accuracy, values of 0·7–0·9 indicate useful applications and values of > 0·9 indicate high accuracy (Swets, 1988). TSS values ranging from 0.2 to 0.5 were considered poor, from 0.5 to 0.8 useful, and values larger than 0.8 were considered good to excellent (Coetzee et al., 2009).

Both AUC and TSS values were plotted for each individual modelling run, providing a comparative assessment of model performance. TSS was used as the a priori threshold measure for inclusion of models in the ensemble as it is viewed as the more rigorous measure of model performance (Allouche et al., 2006). Models with TSS values >0.5 were retained for inclusion in the ensemble model.

Ensemble modelling

Individual model runs above the TSS 0.5 threshold were used to produce a single ensemble model using the unweighted mean (all) consensus method. The mean (all) consensus method was used because it provides more robust predictions, reducing model errors and uncertainties associated with single-models or other consensus methods (Araújo, et al. 2005; Marmion et al. 2009). The unweighted mean gives equal probability to each model above the a priori selection threshold.

The CV or coefficient of variation (i.e. standard deviation/mean) was plotted for each ensemble model to provide a measure in environmental space of the uncertainty associated with the modelling predictions of each ensemble forecast. High CV evaluation scores demonstrate that uncertainty in the model prediction is high. The lower the CV score, the lower the uncertainty and better the model.

Ensemble models means and Coefficient of variation were converted to raster format and exported to ArcGIS to map spatial distributions.

6.3 Results

6.3.1 Principal component analysis

Retaining only PCs with Eigen values greater than 1, PCA resulted in seven Principal components, explaining 78.6% of the total variance. The components matrix (Table 6.3) shows the factor loads which explain the correlation between Promax rotated PCs (with Eigen values > 1) and the original environmental input variables. It excludes any factor loads < 0.3 (see Figure 6.2 for graphical biplots representation). Assessment of the rotated components matrix showed no variable had a high factor load for multiple PCs, thus each variable had an exclusive relationship with each specific PCs. PC 1 had high loads ($r < -0.6$ or $r > 0.6$) for the variables depth, seabed temperature range and seabed salinity; PC 2 for current magnitude (specifically on an easterly axis); PC 3 for current on a northerly axis; PC 4 for seabed temperature; PC 5 for slope gradient and terrain ruggedness; PC 6 for curvature and topographic positioning and PC7 for primary productivity and northerly aspect. A high degree of collinearity was recorded between certain environmental variables, most notably between seasonal comparisons of the same abiotic variable, such as summer and winter temperatures, salinities and currents. Collinearity was also high between curvature and topographic position; and between slope and rugosity. This is demonstrated in Figure 6.2 by the similarity in the variable's loadings. Other variable such as geomorphological curvature and topographic position as well as slope angle and terrain rugosity were also shown to be highly correlated.

6.3.2 Model performance

Model performance varied between models (Figures 6.3 and 6.4; Appendix D Supplementary materials Figure 6.1 and 6.2). Universally SRE, the only enveloping method employed, performed poorly (TSS $\bar{x} = 0.30$, $\sigma = 0.09$; ROC $\bar{x} = 0.64$, $\sigma = 0.09$) with only 6.7% of model runs meeting the a priori 0.5 TSS threshold. There was less variation between the performances of the other nine models (TSS $\bar{x} = 0.53$, $\sigma = 0.08$; ROC $\bar{x} = 0.80$, $\sigma = 0.05$). However GAM, and in some instances CTA, tended to perform more poorly modelling response variables with lower record counts (e.g. functional groups 7, 8 and 10 (see Table 6.1 and Figure 6.3). Averaged across all response variables in the study, 52.37% (6023) of models meet the 0.5 TSS threshold level and thus were included in ensemble modelling. The best performing models for TSS and ROC were artificial neural networks (ANN), boosted regression trees (BRT) and flexible discriminant analysis (FDA). Multivariate adaptive regression splines (MARS) also performed well for TSS and had the highest percentage of models included in the final ensemble (Table 6.4).

Table 6.3. Component matrix showing correlation between the promax-rotated PCs and the original input variables. High factor loads (r < -0.6 or r > 0.6) are highlighted in bold; Low factor loads (r < -0.3 or r > 0.3) are omitted.

Abiotic Variables	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Depth	**-0.897**	-	-	0.314	-	-	-
Slope	-	-	-	-	**0.937**	-	-
Terrain Ruggedness Index	-	-	-	-	**0.928**	-	-
Curvature	-	-	0.310	-	-	**0.804**	-
Topographic Position Index	-	-	-	-	-	**0.823**	-0.349
Aspect: Northness	-	-	-	-	-	-	**0.719**
Aspect: Eastness	-	-	-	-	-	-	-
Primary Productivity	-	-	-	-	-	-	**0.714**
Summer Seabed Temperature	-	-	-	**0.861**	-	-	-
Summer Seabed Salinity	**0.938**	-	-	-	-	-	-
Summer Seabed Current U	-	**0.808**	-	-	-	-	-
Summer Seabed Current V	-	-	**0.974**	-	-	-	-
Summer Seabed Current Magnitude	-	**0.939**	-	-	-	-	-
Winter Seabed Temperature	-	-	-	**0.970**	-	-	-
Winter Seabed Salinity	**0.911**	-	-	-	-	-	-
Winter Seabed Current U	-	**0.806**	-	-	-	-	-
Winter Seabed Current V	-	-	**0.975**	-	-	-	-
Winter Seabed Current Magnitude	-	**0.933**	-	-	-	-	-
Seabed Temperature Range	**-0.733**	-	-	-	-	-	-
Variance Explained (%)	16.50%	16.2%	11.6%	10.8%	10.2%	7.1%	6.3%
Cumulative Variance (%)	16.50%	32.7%	44.3%	55.1%	65.2%	72.3%	78.6%
Eigenvalues	3.144	3.070	2.199	2.048	1.931	1.353	1.190

Model performance also varied significantly between response variables (Figures 6.3 and 6.4). For the best performing model (FG4) 95.6% (478) of model runs had TSS values >0.5 whilst for the worst performing model (T13) only 12% (60) reached the same threshold. Model performance did not obviously correspond with the sample size of each response variable. Of the five worst performing models four were functional groups characterised by mobile predator or scavengers (FG1, 9, 11, 13). This is perhaps not surprising given mobile animals are not spatially confined to a specific locality and as such more difficult to model spatially. Annelida was the only taxonomic group modelled to perform consistently poorly.

6.3.3 Sampling bias

Benthic biological collections at South Georgia can be broadly split into two categories: bycatch from long-line fisheries vessels and scientific specimen sampling predominantly from trawling. There was a distinct spatial bias to these collections (Figure 6.5) with 81.40% of the bycatch data collected (n=10,194) in the licenced fishing zone (Figure 6.1) between 700 and 2250m. Conversely 80.18% of the scientific data (n=9,306) were collected between 0 and 699m depth (the majority occurring in shelf waters of <400m). 11.55% of scientific sampling occurred deeper than the fishing zone (>2250m).

The nature of the capture method in longline fishing, i.e. by lines of baited hooks suspended just above the seabed, makes it a far more selective means of sampling benthic fauna than scientific trawling.

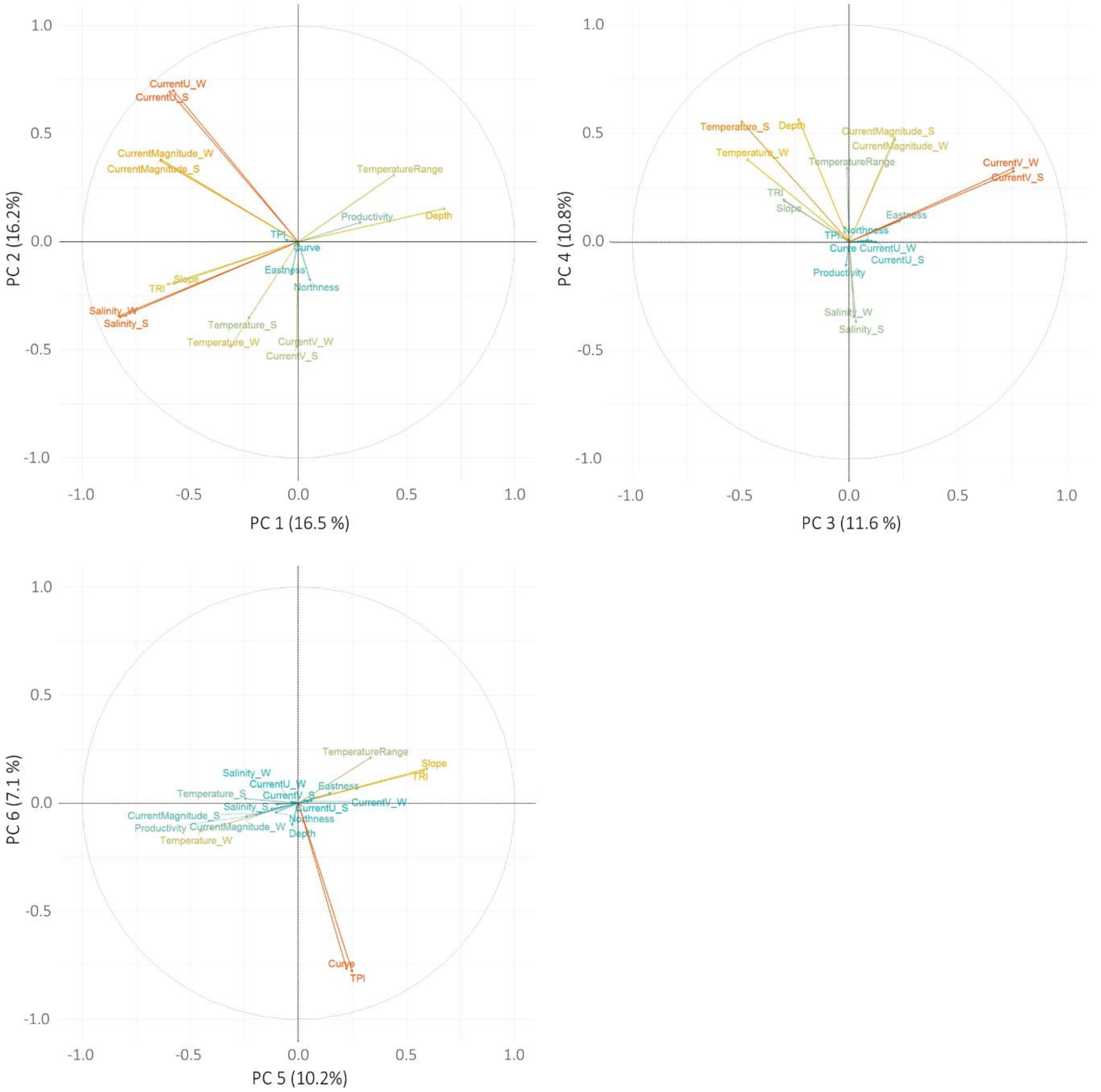
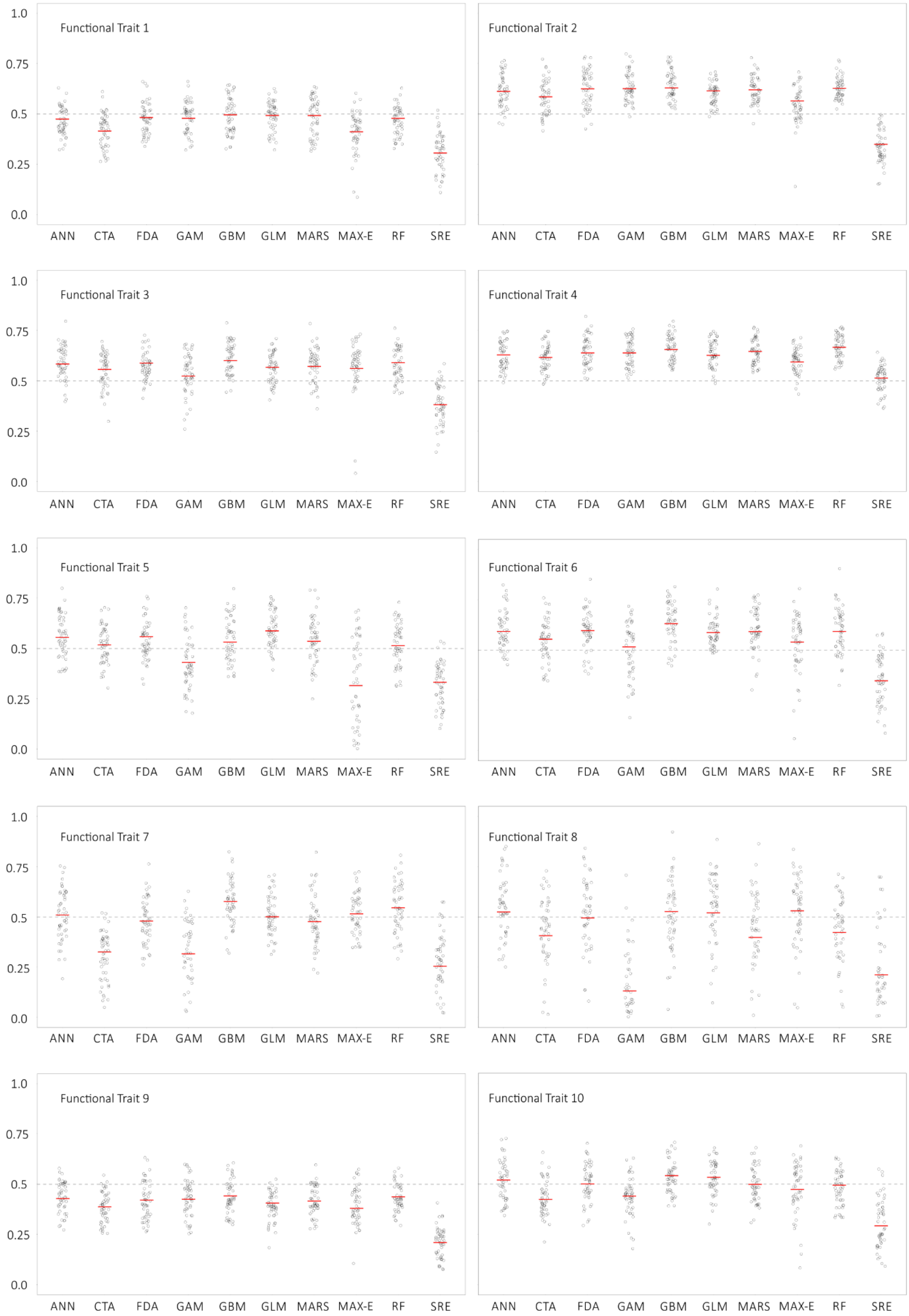


Figure 6.2. PCA biplots showing correlation between environmental variables and Principal components 1-6 (explaining 72.3% of total variance). The plot illustrates which variables are driving the PCs. The longest arrow in the plot represents the most prominent environmental variable driving each principal components. Arrows are also colour graded from red (most prominent variables) to blue (least prominent variables). The distances between arrows describe their correlation to one another, the closer the arrows, the greater the correlation.


Functional Trait 1
Functional Trait 2
Functional Trait 3
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Functional Trait 6
Functional Trait 7
Functional Trait 8
Functional Trait 9
Functional Trait 10
1.0
0.75
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MAX-E
RF
SRE

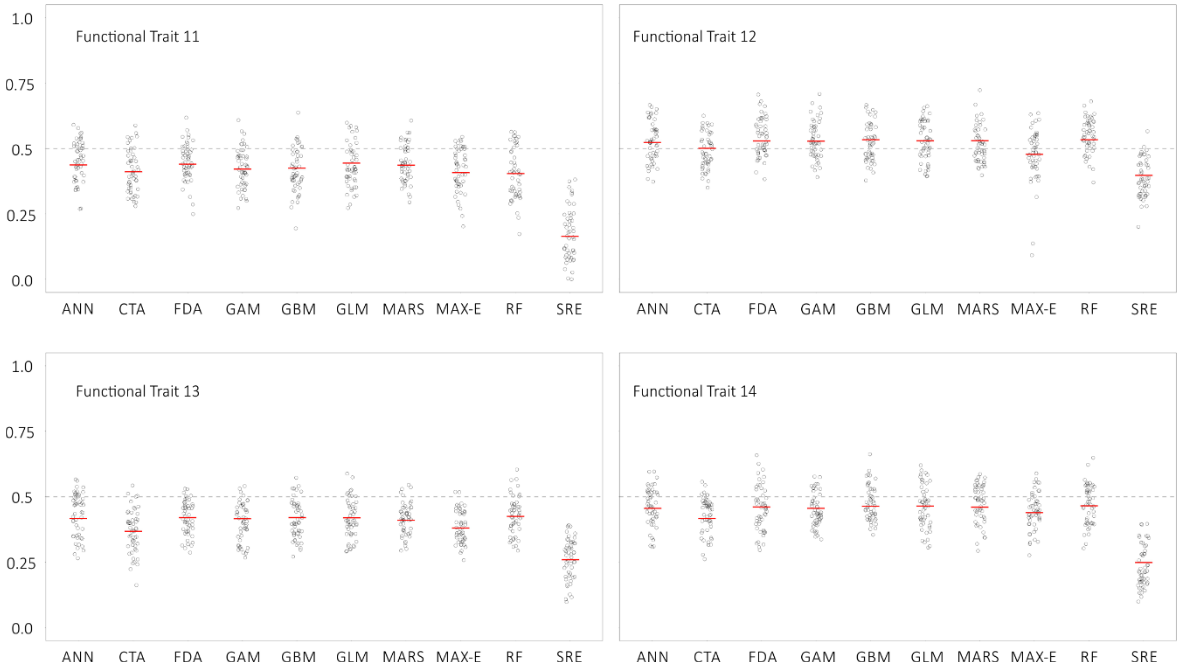
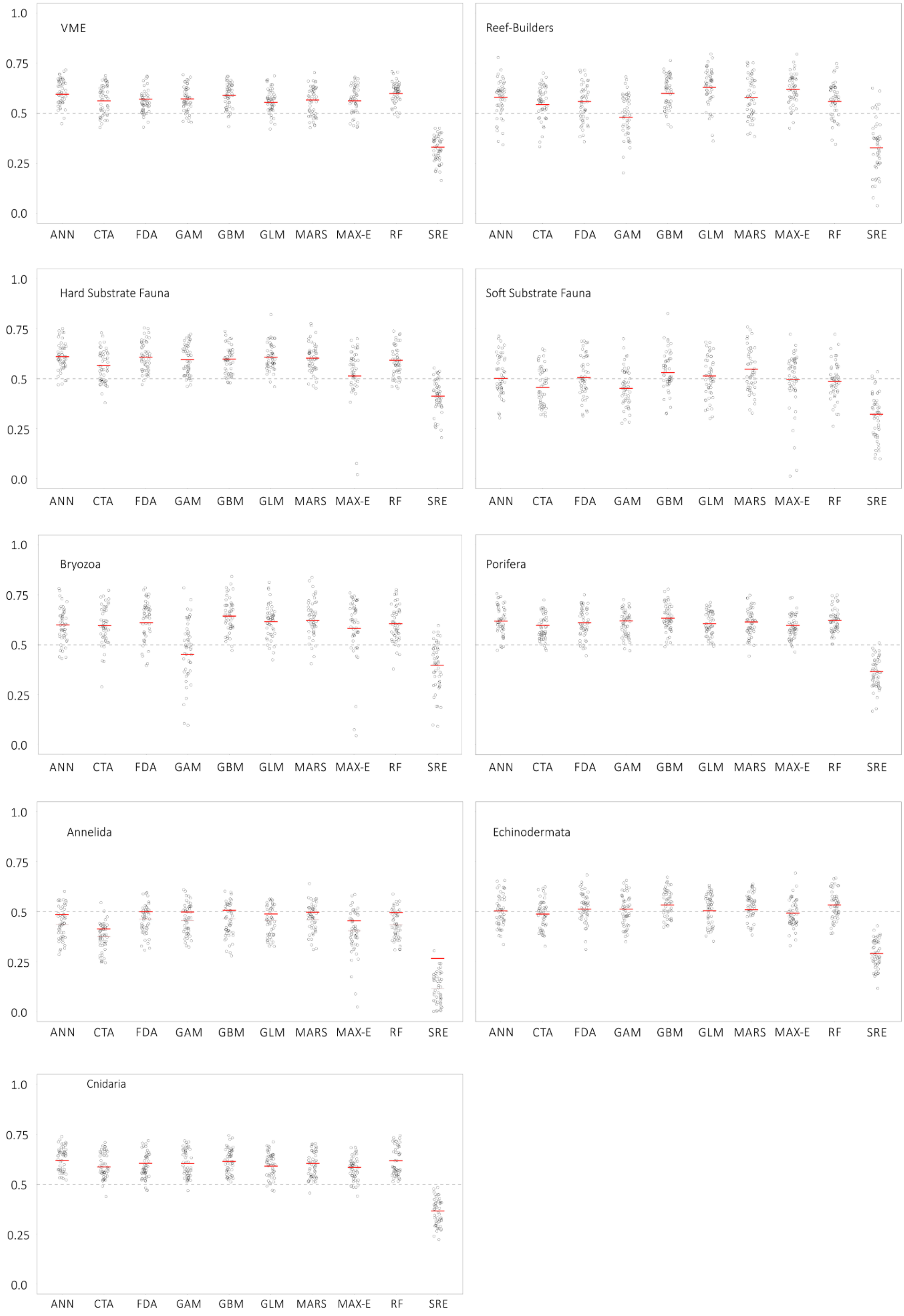


Figure 6.3. True skill statistic (TSS) plots for 14 modelled functional traits (Figure 6.4) showing model performance of each run of the 10 modelling algorithms summarised in Table 3. Mean TSS value for each algorithm is shown as a red bar. The TSS cut-off value of 0.5 used in the ensemble modelling is shown as a dashed grey line.

Figure 6.4 (page 117). True skill statistic (TSS) plots for trait and taxa-based models in Figure 6.5 showing model performance of each run of the 10 modelling algorithms summarised in Table 3. Mean TSS value for each algorithm is shown as a red bar. The TSS cut-off value of 0.5 used in the ensemble modelling is shown as a dashed grey line.


VME
Reef-Builders
Hard Substrate Fauna
Soft Substrate Fauna
Bryozoa
Porifera
Annelida
Echinodermata
Cnidaria
1.0
0.75
0.5
0.25
0.0
ANN
CTA
FDA
GAM
GBM
GLM
MARS
MAX-E
RF
SRE

Longline hooks select for easily 'hookable' items such as brittle branching corals, soft fleshy animals projecting into the water column such as sponges and soft corals as well as active predators that are lured to the baited hooks. They rarely catch, smaller animals (except as epifaunal specimens), infaunal animals, flexible taxa that bend out of the way of hooks or friable taxa which tend to disintegrate before collection. Scientific trawl data conversely, whilst also not good at collecting very small or infaunal species, is far less selective in what it samples. As such our data demonstrates a taxonomic bias in sampling between fisheries dominated regions and non-fisheries dominated regions. Fisheries data was restricted to seven phyla, with Cnidaria (50.7% of records), Arthropoda (24.5%) and Echinodermata (18.3%) constituting the majority of samples (after the exclusion of fish). This compares to sampling across the entire study region which included representation from 21 phyla. In samples from non-fisheries regions Arthropoda was the dominant phylum (55.5%) followed by Echinodermata (15.3%). Cnidaria made up a much smaller proportion of records (3.68%).

Table 6.4. Model performance averaged across all response variables and all model runs. TSS and ROC values are the median value for each model and inclusion percentage relates to the proportion of model runs where TSS > 0.5 and thus the proportion of the total runs for each model included in the ensemble models. Top performing models for each metric are displayed in bold.

Code	Model	TSS	ROC	Inclusion
GAM	Generalised additive models	0.48	0.79	**63.57%**
GLM	Generalized linear models	**0.53**	0.81	45.65%
ANN	Artificial neural networks	**0.53**	**0.82**	59.39%
BRT/GBM	Boosted regression trees	**0.54**	**0.83**	49.83%
MARS	Multivariate adaptive regression splines	**0.54**	0.80	**65.57%**
MaxEnt	Maximum entropy	0.51	0.79	**63.74%**
RF	Random forest	**0.53**	0.81	56.35%
CTA/CART	Classification tree analysis	0.50	0.76	52.78%
FDA	Flexible discriminant analysis	**0.53**	**0.82**	60.17%
SRE	Surface range envelope/ BIOCLIM	0.33	0.66	6.70%

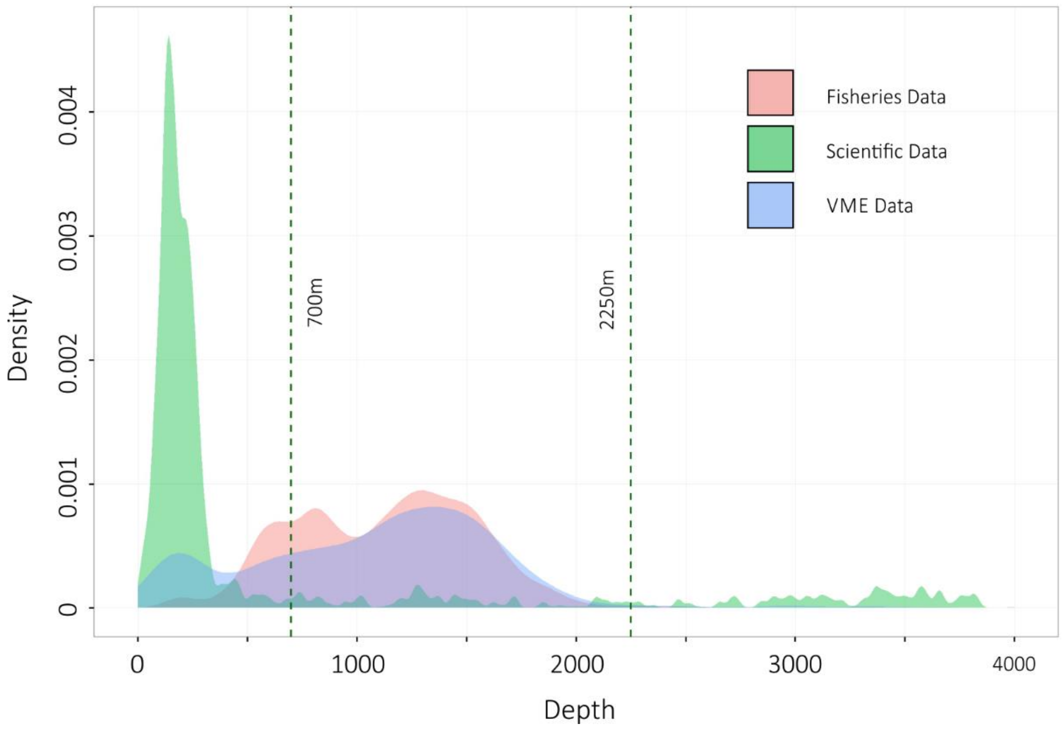


Figure 6.5. Kernel density plot of sampling effort by depth at South Georgia. Sampling effort is defined as the number of unique records. Scientific data collection is symbolised in green (n=11,377) and fisheries bycatch data in red (n=12,523). VME species records are recorded in blue (n=1,798). Dashed green lines at 700 and 2250m denote the upper and lower limit respectively of the open fisheries area.

6.3.4 Modelled functional characterisation of South Georgia

Based on ensemble modelling of functional groups (Table 6.1; Figure 6.6; Figure 6.7), South Georgia can be broadly characterised into several distinct functional regions:

The coastal environment demonstrates higher likelihood of early successional pioneer communities (FG1) represented by animals such as encrusting bryozoans and ascidians; a high prevalence of deposit feeding epifauna (FG5) and infauna (FG6/7) such as sea cucumbers, irregular sea urchins, bivalve molluscs and certain polychaete worms. Grazing species (FG8) such regular sea urchins were predicted in many coastal locations as were mobile hard-bodies predators (FG12/13) such as fish, brittlestars, gastropods and sea stars. A notable absence in these coastal waters were sessile predators and scavengers (FG10) such as cup corals, hydrocorals and whip corals.

The mid shelf demonstrated the highest modelled occurrences of sedentary suspension feeding organisms (FG3) such as basket stars and valviferan isopods (e.g. Antarcturidae). Mobility appeared to be a dominant trait on the mid shelf with high occurrences of mobile suspension feeders (FG4) such as brittle stars and crinoids, mobile scavengers and predators (FG12/13) such as fish, sea stars and gastropods, and jointed legged predators (FG14) such as sea spiders and amphipods. At the lip of some cross shelf troughs a mix of pioneer (FG1) and climax suspension feeding communities (FG2) was predicted.

The outer shelf and slope environments (typically starting at depths of around 250m and extending down to 2500 - 3000m) were characterised by a very high likelihood of climax sessile communities (FG2) such as demosponges, glass sponges and brachiopods. The highest probabilities of occurrence of climax communities were seen in the depth range 400 – 2000m. At the shallower end of the range (300-1200m) climax communities coexisted with pioneer sessile communities (FG1). The slope region also saw a prevalence of mobile predators and scavengers (FG12/13 & 14) and sessile scavengers, typically corals including sea pens, soft corals, anemones, hydroids, cup corals, whip corals and hydrocorals.

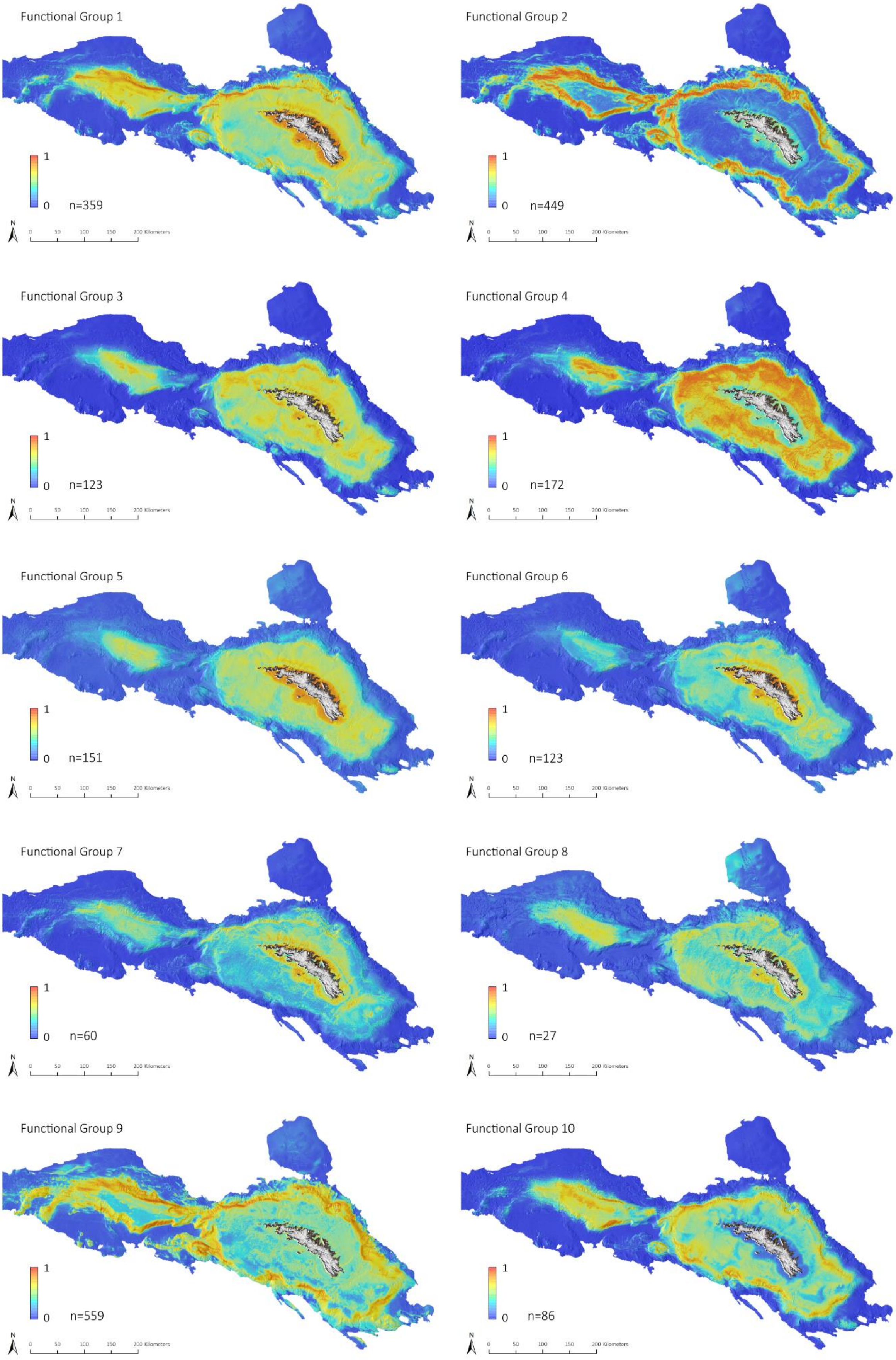
The deep sea recorded low modelled occurrences across all functional groups, though with low sampling effort for this region, variance in models was also higher than elsewhere (Figures 6.8 and 6.9). The predicted distributions of some soft-bodied sessile scavengers/predators, and mobile hard bodied and jointed legged predators extended into the deep sea from the continental slopes. Grazing animals (FG8) and infaunal deposit feeders (FG6/7) were seen at 2000m depth on the Georgia Rise plateau to the north of the South Georgia northern continental slope (see Figure 6.1 for location).

Shag Rocks exhibited similar predicted functional distributions to the main South Georgia shelf. Climax suspension feeding communities were most likely on the slope and shelf edge region, whilst pioneer communities were more likely on the outer shelf. Mobile scavengers and predators were present across Shag Rocks whilst infaunal animals (FG6/7) were uncommon. Grazers and epifaunal deposit feeders were most dominant on the inner shelf.

6.3.5 Modelled taxonomic characterisation of South Georgia

Modelled distributions of South Georgia's taxonomic groups are presented in Figure 6.7. The highest likelihood of occurrence for vulnerable marine ecosystems (VME) was constrained to a narrow band around the South Georgia and Shag Rocks continental slope. There was also a high probability of occurrence in inshore locations and along the margins of cross shelf troughs. The rest of the shelf and deep sea regions exhibited low probabilities of occurrence.

Benthic fauna with exclusive affinity to either hard or soft substrata were most common in overlapping distributions in inshore locations of the South Georgia shelf.


Functional Group 1
1
0
n=359
Functional Group 2
1
0
n=449
Functional Group 3
1
0
n=123
Functional Group 4
1
0
n=172
Functional Group 5
1
0
n=151
Functional Group 6
1
0
n=123
Functional Group 7
1
0
n=60
Functional Group 8
1
0
n=27
Functional Group 9
1
0
n=559
Functional Group 10
1
0
n=86
N
0 50 100 150 200 Kilometers

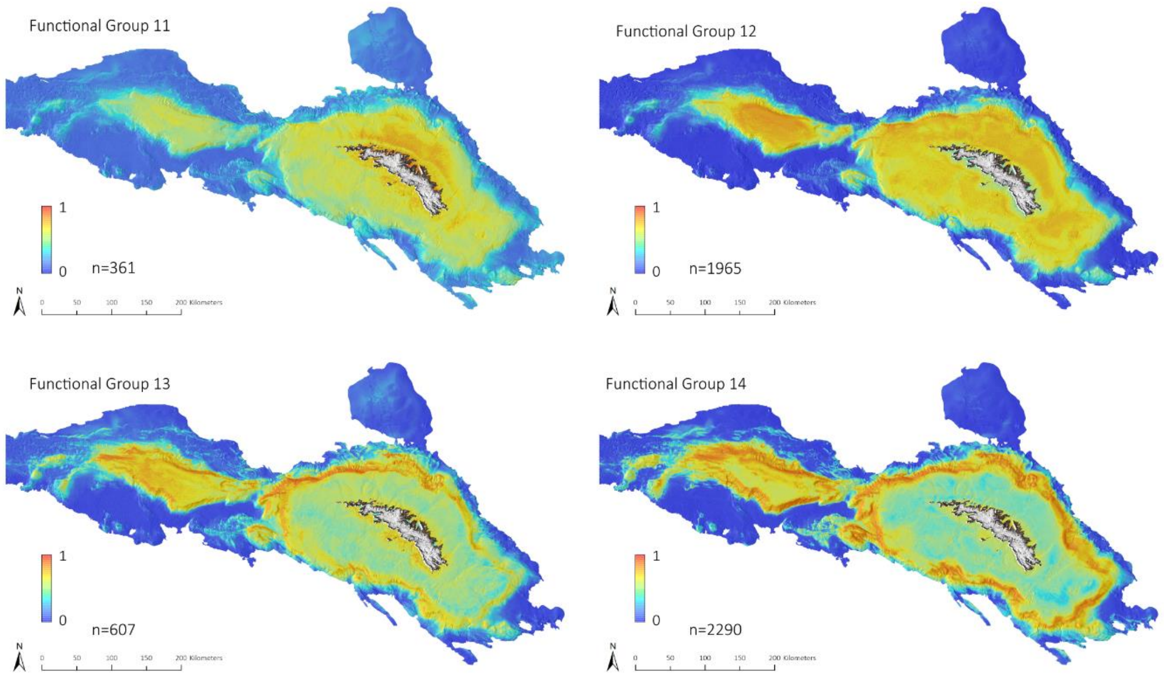
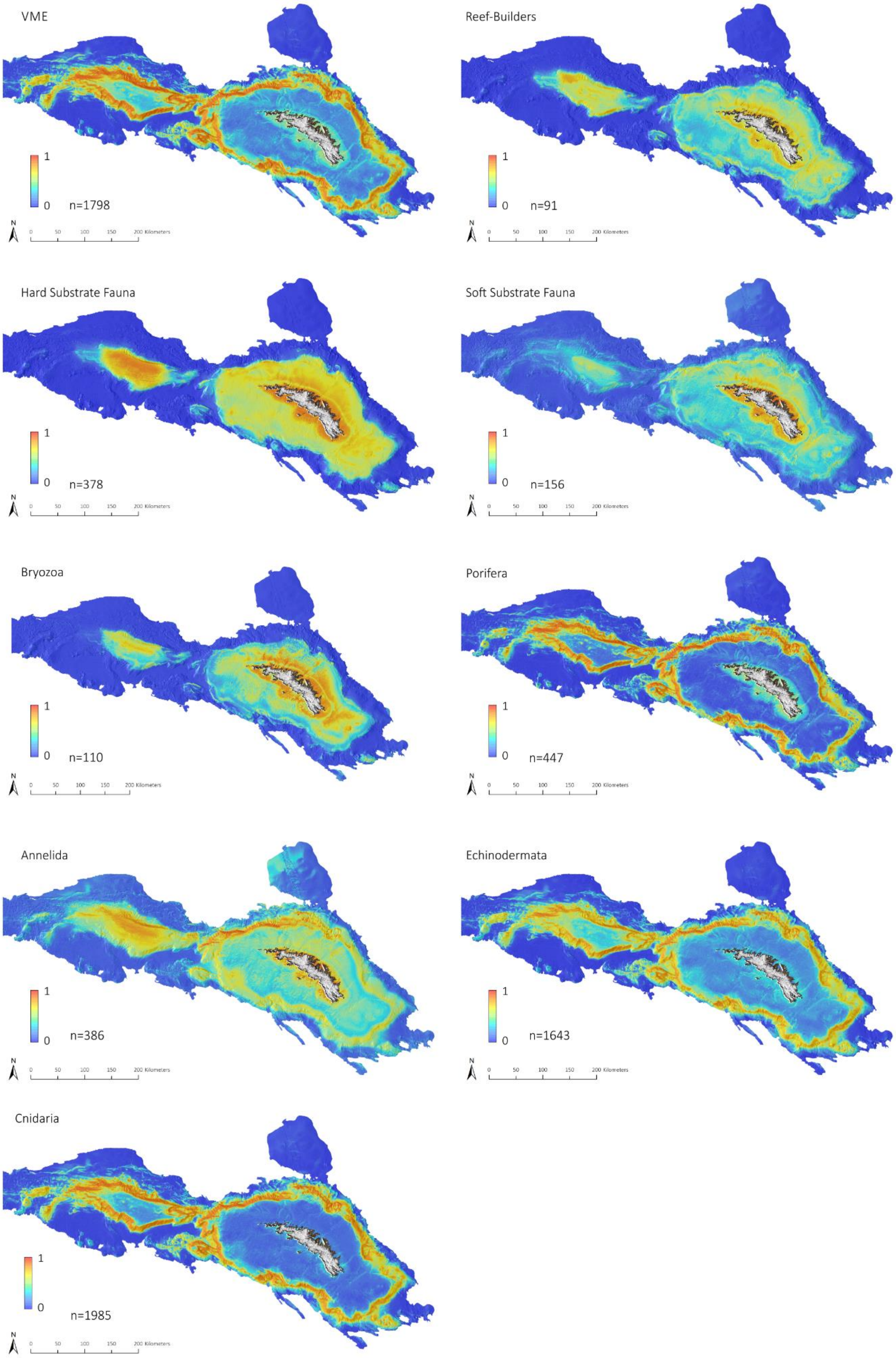


Figure 6.6. Ensemble models of the predicted spatial distribution of 14 functional groups (see Table 1) around South Georgia between 0 and 3000m depth. Areas in red show high probability of occurrence and blue show low probability of occurrence. The number of response variable records used in each ensemble is indicated by the 'n' number in each plot.

Figure 6.7 (page 123). Ensemble models of the predicted spatial distribution of taxa and trait-based variables. Distributions are modelled between 0 and 3000m depth for: (i) five key phyla; (ii) taxa considered to constitute vulnerable marine ecosystems; (iii) reef-building species; and (iv) species with exclusive affinity to hard or soft substrate around South Georgia. Areas in red show high probability of occurrence and blue show low probability of occurrence. The number of response variable records used in each ensemble is indicated by the 'n' number in each plot.

This corresponded with the depth distributions of records for fauna with exclusive affinity to both hard and soft substrata (Supplementary materials Figure 6.3). Shag Rocks was almost exclusively associated with hard-substrate fauna. The entire shelf of South Georgia demonstrated relatively high likelihood of occurrence for hard substrate fauna with low or zero predicted occurrences in slope and deep-sea environments. Soft-substrate fauna demonstrated patchy occurrences across the South Georgia shelf and slope with a greater likelihood of distributions extending into deeper water than hard substrate fauna.

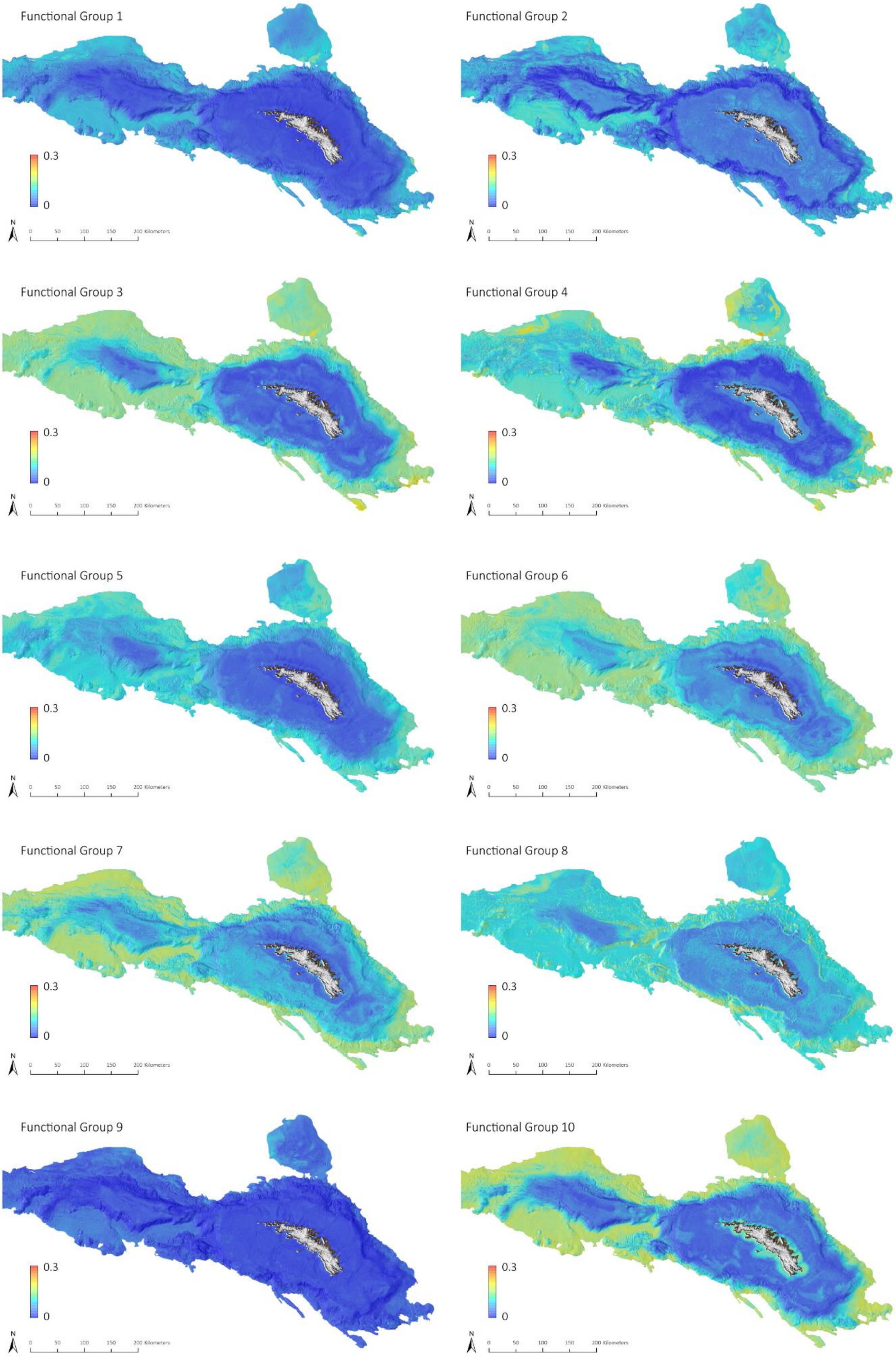
Reef-building fauna demonstrated highest likelihood at Shag Rocks and inshore South Georgia. Distribution across the South Georgia shelf was patchy with few or no predicted occurrences in slope or deep-water environments. Sampling of reef-building fauna was however notably low (n=91).


VME
1
0
n=1798
Reef-Builders
1
0
n=91
Hard Substrate Fauna
1
0
n=378
Soft Substrate Fauna
1
0
n=156
Bryozoa
1
0
n=110
Porifera
1
0
n=447
Annelida
1
0
n=386
Echinodermata
1
0
n=1643
Cnidaria
1
0
n=1985
N
0 50 100 150 200 Kilometers

Annelida demonstrated the highest likelihood of occurrences along the north-west South Georgia shelf break and across most of the shelf area of Shag Rocks. Inshore South Georgia especially within the fjord systems was shown to present high probability of occurrence, whilst distribution on the South Georgia shelf was high in places but patchy. Presences were also predicted in some deeper water environments. Cnidaria demonstrated an almost identical predicted spatial distribution to VME (of which it forms a major constituent) with a narrow band around the South Georgia and Shag Rocks continental slope. Porifera had a similar distribution pattern but in addition was also predicted in the coastal waters around the South Georgia landmass. Echinoderms also demonstrated affinity with the slope environment, but unlike Porifera and Cnidaria the predicted distribution was less spatially constrained and extended to shelf and deeper water environments, albeit with lower probability than the adjacent slope. Bryozoa demonstrated an inshore distribution around South Georgia and extending into the middle of the continental shelf and the northern section of Shag Rocks. Probability of occurrence then reduced to zero in slope and deep-sea environments.

6.3.6 Modelling confidence

Modelling confidence calculated as the coefficient of variation (i.e. standard deviation/mean) is shown in Figures 6.8 and 6.9 for each response variable. The lowest coefficients, and thus highest confidence in modelling output were seen in functional groups 1,9,11 and 13 and for the phyla Bryozoa and Annelida. These groups however also represented the same groups that performed worst in modelling performance (section 4.3.1), and as such contained amongst the lowest number of model runs included in each ensemble model by which to calculate variation in mean. All other models demonstrated highest confidence in model predictions for the shelf region at both South Georgia and Shag Rocks and lower confidence in deeper-water regions (>2000m). This spatial trend corresponded with regions of higher sampling effort (shelf) and low or no sampling effort (the deep). Higher uncertainty, notably in slope and deep sea regions and also patchily in deeper shelf sites, was shown to be particular apparent in the modelled distributions of response variables with lower record counts. These included functional groups 10 (86), 7 (60) and 8 (27), as well as soft-substrata fauna (156), hard-substrate fauna (378), reef building fauna (91) and the phylum Bryozoa (110). The highest confidence levels were seen in spatially constrained high probability regions such as the South Georgia slope for taxa such as Cnidaria, Porifera and VME species. This coincided with high sampling densities (see Figures 6.1 and 6.9).


Functional Group 1
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Functional Group 2
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Functional Group 3
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Functional Group 4
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Functional Group 5
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Functional Group 6
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Functional Group 7
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Functional Group 8
0.3
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N
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Functional Group 9
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N
0 50 100 150 200 Kilometers
Functional Group 10
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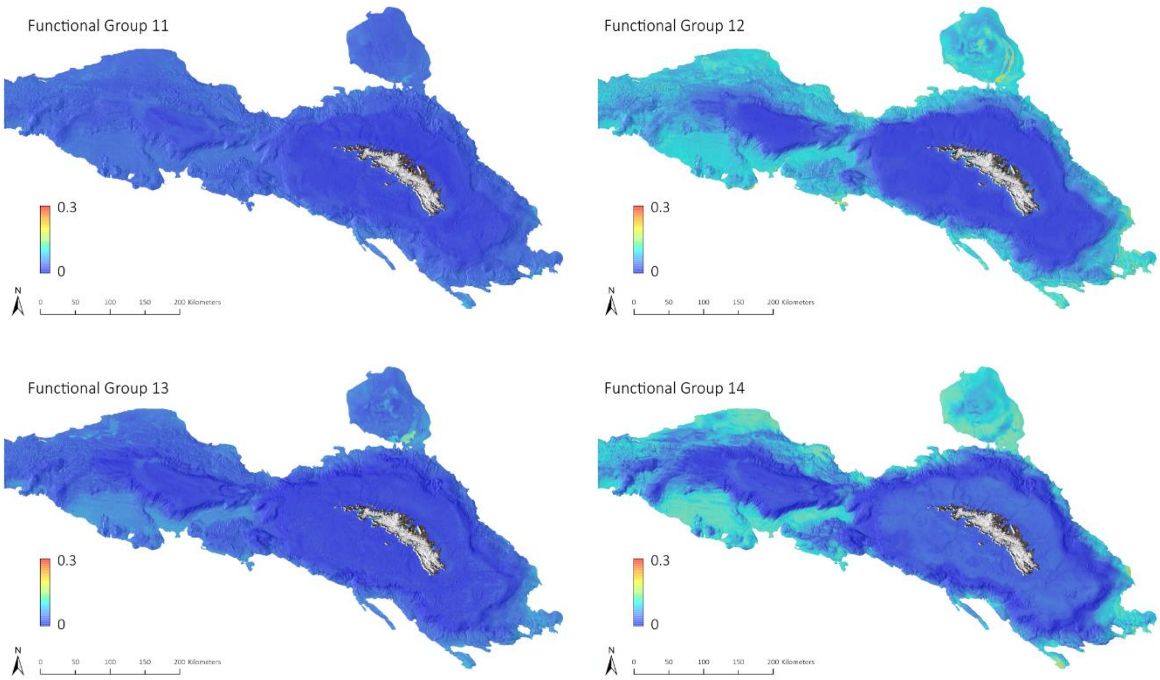

Figure 6.8. Coefficient of variance plots symbolising uncertainty associated with the functional group modelling predictions of each Figure 6.4 ensemble forecast. High CV evaluation scores demonstrate high uncertainty (red) in the model prediction. Lower CV scores (blue) denote lower uncertainty and thus a better model.

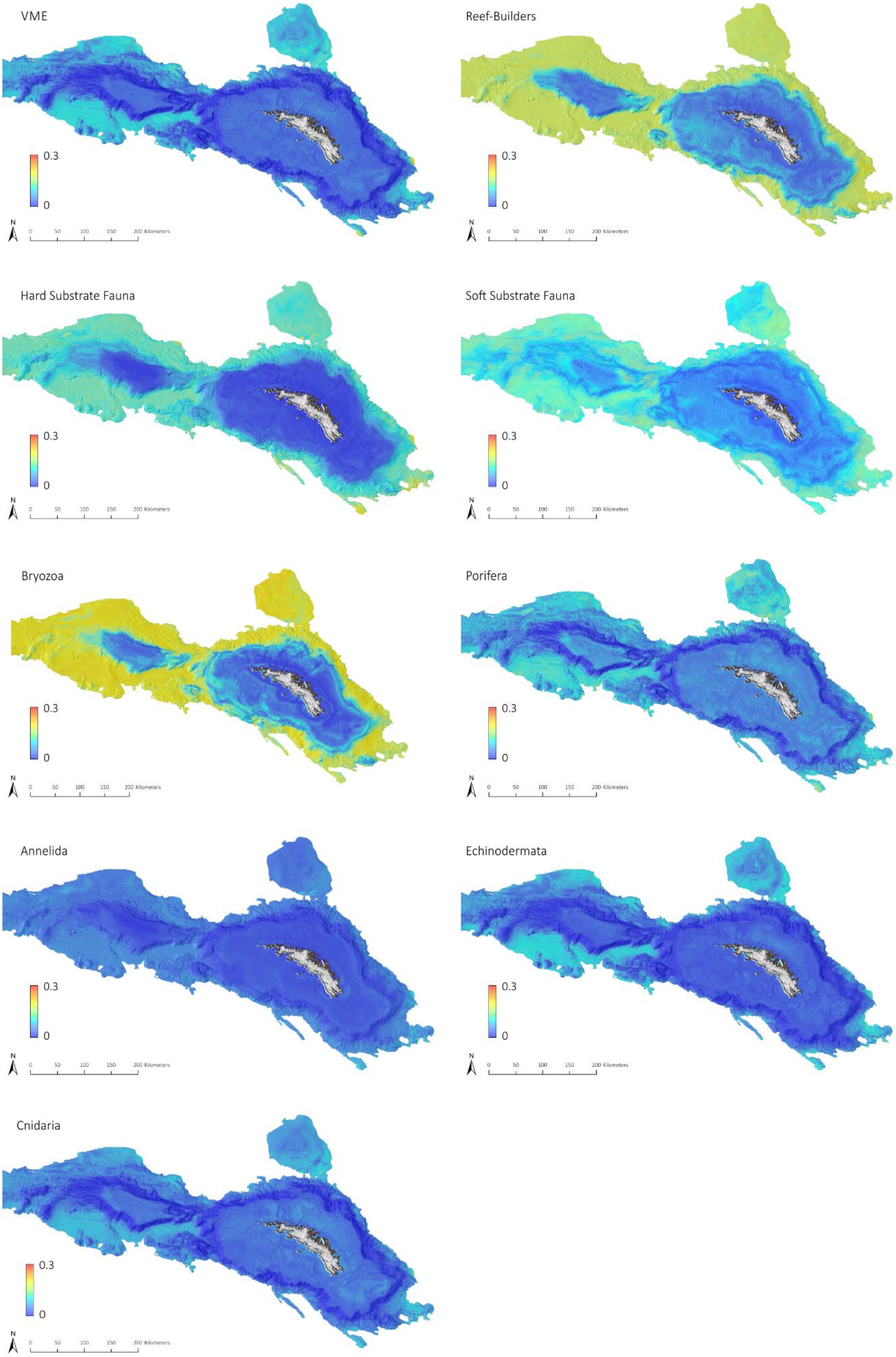

Figure 6.9. Coefficient of variance plots symbolising uncertainty associated with the modelling predictions of each Figure 6.5 ensemble forecast. High CV evaluation scores demonstrate high uncertainty (red) in the model prediction. Lower CV scores (blue) denote lower uncertainty.

6.3.7 Predictor influence

Of the seven principal components used to build the ensemble models, 16 of the 23 models were driven principally by just one - PC1 (Appendix D Supplementary materials Tables 6.1 and 6.2). PC1 was characterised by depth, temperature range and salinity. Across the functional groups, exceptions to this were seen in FG2 which was split between PC4 (seabed temperature) and PC5 (slope and terrain rugosity) and FG14 which was primarily driven by PC5. FG8 appeared to be driven by several PCs, principally PC1 but also several models identified PC3, PC4, PC5, PC6 and PC7 as important drivers.

Across taxonomic groupings the Bryozoa distribution was driven by PC1 with several models also identifying PC5. Cnidaria was principally driven by PC5 with only two models not supporting this and loading more heavily on PC1. Annelida was also riven by PC5 and in some models also PC1. Echinodermata were almost universally driven by PC5 and Porifera by PC4 and PC5. The spatial distributions of the environmental variables underpinning the three main principal components (PC1, PC4 and PC5) are presented in Figure 6.10.

Across all groups, if there were a clear principal factor driving the model then this was often universal across the ten modelling algorithms. Secondary driving factors however often varied between models.

6.3.8 Mapping VME habitat and functional group diversity

VME

The distribution of VME species predicted by ensemble modelling demonstrates a strong bias towards the continental margin and slope of South Georgia and Shag Rocks (Figure 6.11; Figure 6.7). Probability of VME presence was low or zero in most deep water regions (>2250m). In shallower waters VME presence was most likely in deeper shelf waters (300-500m), along the flanks of glacial troughs and at inshore locations (see also Figure 6.5). Principally VME was not modelled to occur across the rest of the South Georgia shelf.

Figure 6.12 and Table 6.5 summarise the proportion of 500m grid cells for which VME species are modelled to be present, with 50% probability (VME-50) and 70% probability (VME-70). The study area was split into: (i) waters open to benthic longline fishing (i.e. the fisheries zone); (ii) waters within the fisheries depth zone but closed to fisheries (i.e. benthic closed areas) and (iii) the remainder of the study area outside the fisheries zone and predominantly inside the MPA (see Figure 6.1).

The probability of VME occurrence was over twice as high inside the fisheries zone than across the rest of the MPA. Within the five benthic closed areas (see Figure 6.1 for locations) probability of occurrence was highest at West Shag Rocks with almost 90% of the area predicted as VME-50 and 60% as VME-70. Probabilities were also high at East South Georgia closed area (albeit with a much lower VME-70 and across a relatively small area (143 km^2). The West Gully closed area exhibited similar VME probabilities as the fisheries area more generally. The large North Georgia Rise closed area demonstrated zero likelihood of VME presence. Sampling in this region (as other deeper and offshore regions) was however very low (Figure 6.1; Figure 6.5).

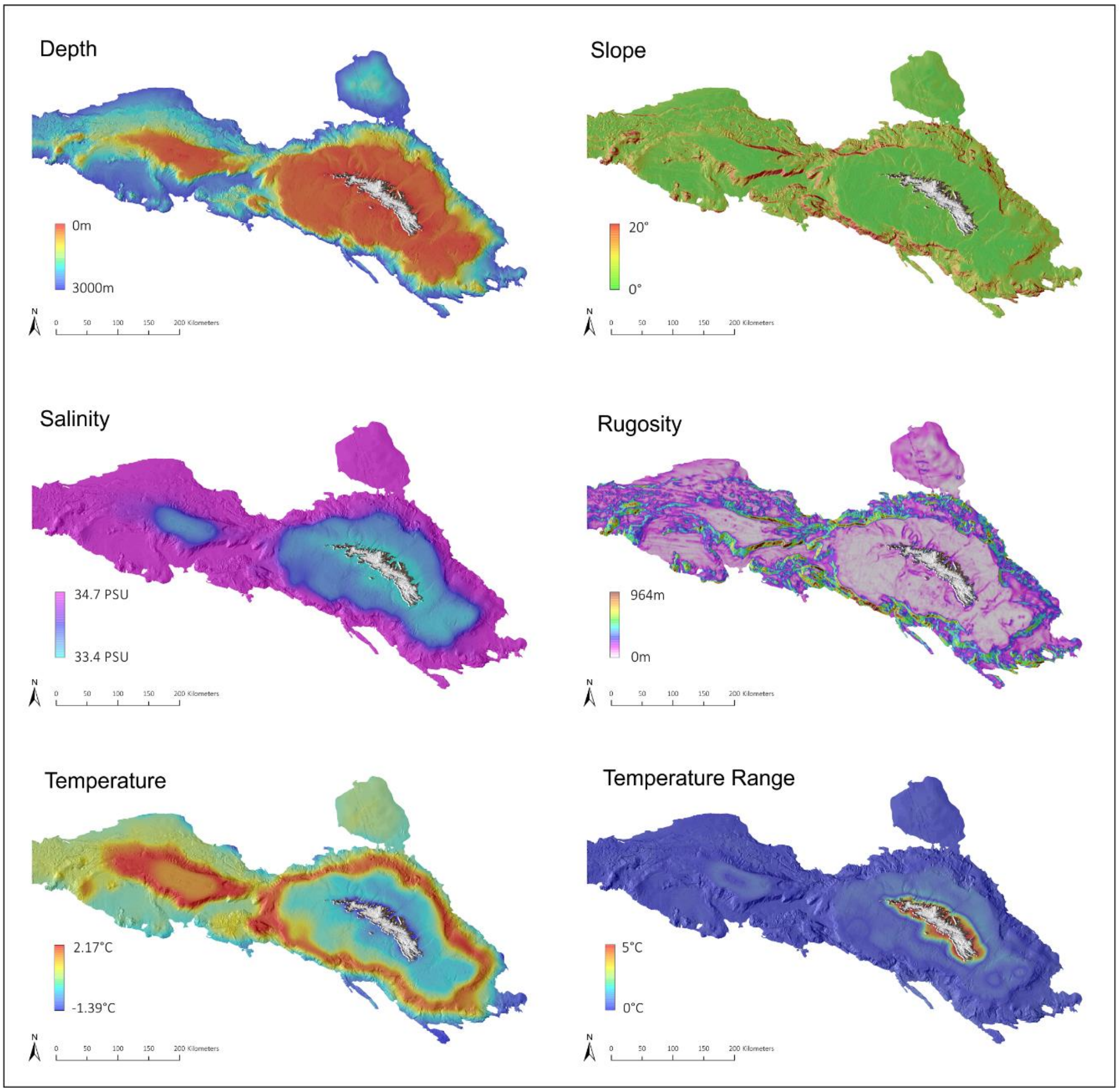

Figure 6.10. Environmental variables driving the three main principal components (PC1, PC4 and PC5) in the ensemble modelling. PC1 was primarily driven by depth, salinity and temperature range; PC4 by seabed temperature; PC5 by slope angle and rugosity.

Despite constituting only 26% (35,105 km^2) of the total study area, 65% of grid cells which had a greater than 50% probability of VME presence (VME-50) occurred in the fisheries zone. At 70% probability of VME (VME-70), this proportion increased to 70.7%. 6.5% of the study area (8,711 km^2) fell within the benthic closed areas (Figure 6.1). 9.5 % of VME-50 sites and 10.7% of VME-70 sites occurred in these areas. The remaining 67.5% of the study area (91,462 km^2) constituted only 25.5% of VME-50 sites and 18.6% of VME-70 sites. Of this final category most VMEs (18.1% and 10.8% respectively) were predicted in the narrow 550-700m depth band on the continental slope just above and adjoining the fishing zone.

The narrow depth between 550 and 700m on the upper part of the continental slope just above the fishing zone exhibited high modelled likelihood for VME species, second only to West Shag Rocks (Figure 6.12; Table 6.6). At the lower limit just below the fishing zone (2250-2500m) however VME presence was shown to be unlikely.

To assess the impact of sampling effort on the probability of modelled VME presence and thus discount this as a driving influence on VME dominance in slope environments we sub-divided the study region using a hexagonal grid. Each grid cell measured 10km on along each side thus represented an area of 260km^2. Grid cells were categorised as shelf if they occurred within the 0-499m depth range, slope within the 500-2250m depth range and deep sea if greater than 2250m. Grid cells that straddled two regions were excluded from the analysis. The total number of sampling stations was calculated for each grid cell as a measure of sampling effort per unit area and plotted against the median modelled VME value for each grid (Figure 6.13). Whilst increased sampling of slope environments increased probability of VME occurrence (dark blue points), for the shelf environment occurrence probability was much lower irrespective of sampling effort (light blue points). Indeed most of the high VME occurrence grid squares on the shelf were those adjoining the slope environment.

As such it seem likely that low VME occurrences on South Georgia's shelf was a true reflection of the regions biogeography and not an artefact of sample. Conversely the fact that increased sampling on the slope equated to higher probability of VME species was unlikely to represent bias in the model, but rather an underlying interaction between favoured fishing grounds and VME presence.

Functional group diversity

Functional diversity was modelled as a composite of 13 functional groups (Table 6.1) using an *a priori* probability threshold cut-off of 0.7 (FD-70). In no regions of South Georgia were all 13 functional groups recorded together. FD-70 was highest along upper sections of the region's continental slopes (Figure 6.10). Most notably this was apparent on the slopes of the north and west of South Georgia, some spatially constrained areas of the southern slope and along the northern margin of the Shag Rocks slope. These functional diversity hotspots centred along or just above the 700m depth contour (Figure 6.11). FD-70 was also high across parts of the central shelf area of Shag Rocks and also inshore along the northern coast of South Georgia and to the south of the island around Annenkov Island. The deep sea demonstrated low functional diversity. Within the fisheries zone, most regions of higher functional diversity were constrained to above around 1500m. Functional diversity was also modelled using a probability threshold cut-off of 0.5 (FD-50). FD-50 demonstrated the same hotspots as FD-70. In addition larger areas along the upper slope and shelf break particularly to the north-west of South Georgia were shown to have high functional group diversity (Figure 6.11). The shelf regions of Shag Rocks' inshore region of South Georgia also demonstrated diversity not apparent using FD-70. The majority of the fisheries zone and the entirety of the deep-sea zone showed low or zero functional diversity.

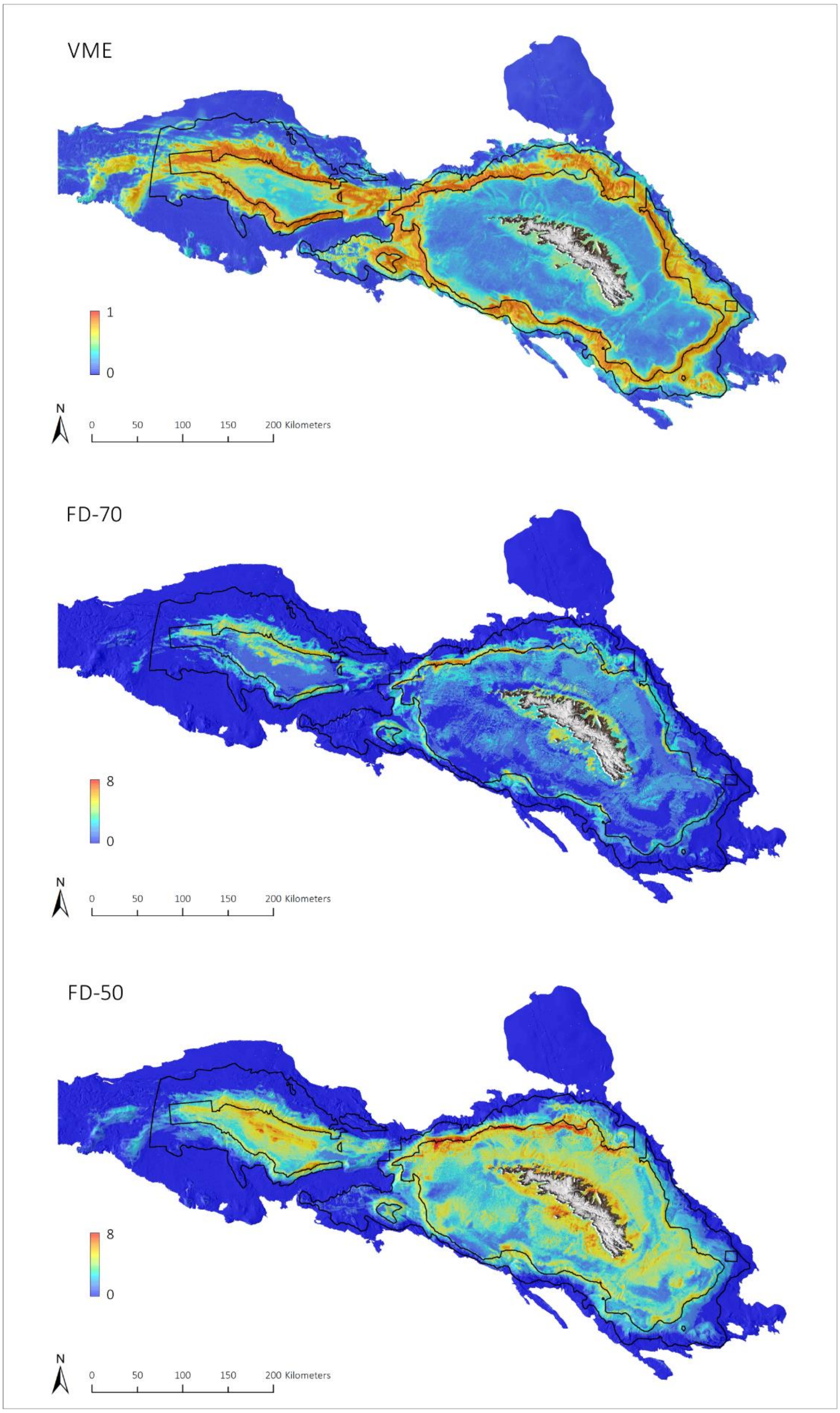

Figure 6.11. Ensemble model of vulnerable marine ecosystems and functional group diversity at South Georgia. Functional group diversity maps are based on a 0.7 probability cut-off (FD-70), and a 0.5 probability cut-off (FD-50). Black lines demark the limit of the licenced fishery zone around the island. Functional group diversity is calculated across all groups in Table 6.1 (except group 13).

Table 6.5. Proportion of study region with a 50% and 70% probability of VME species presence. The fisheries zone is defined by a depth range of 700m-2250m, the benthic closed areas represent current additional closures to fisheries (see Figure 6.1). The depth extension zones represent the region above and below the current fisheries zone in which fishing could be allowed in the future.

Regions	Total area (km^2)	>50% probability of VME habitat	>70% probability of VME habitat
Study Area	**134,239**	**21.99%**	**12.41%**
Fisheries Zone	35,105	54.66%	33.56%
Benthic Closed Areas			
West Gully	2,494	58.32%	37.93%
North Georgia Rise	4,594	0%	0%
East South Georgia	143	83.52%	27.03%
NE South Georgia	441	67.83%	40.57%
West Shag Rock	1,039	88.69%	59.26%
Depth Extensions			
550-700m	2,112	85.72%	53.27%
2250-2500m	9,022	4.14%	1.8%

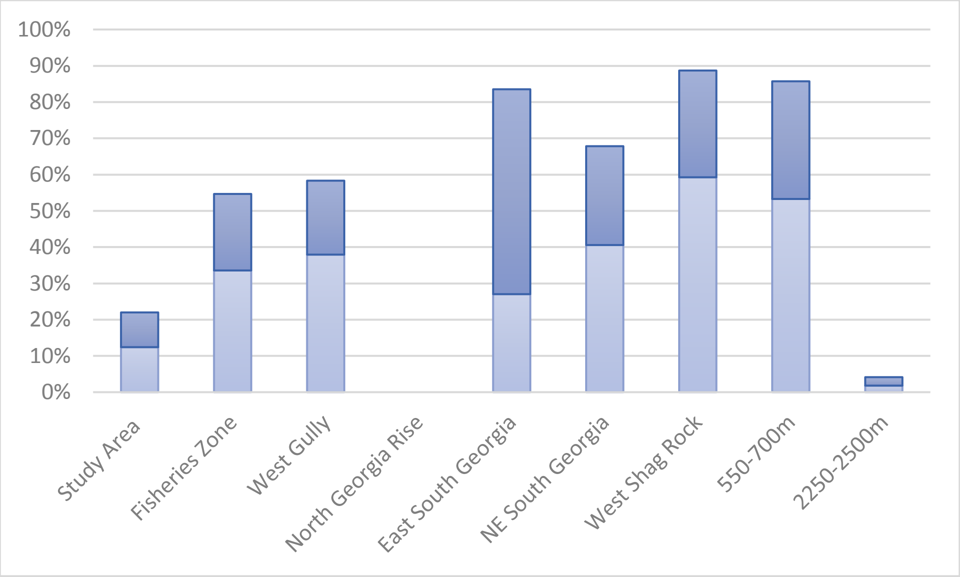

Figure 6.12. Stacked proportion of study region with a 50% (dark blue) and 70% (light blue) probability of VME species presence. The fisheries zone is defined by a depth range of 700m-2250m, the benthic closed areas represent current additional closures to fisheries (see Figure 6.1). The depth extension zones represent the region above and below the current fisheries zone for which future fishing could be opened to.

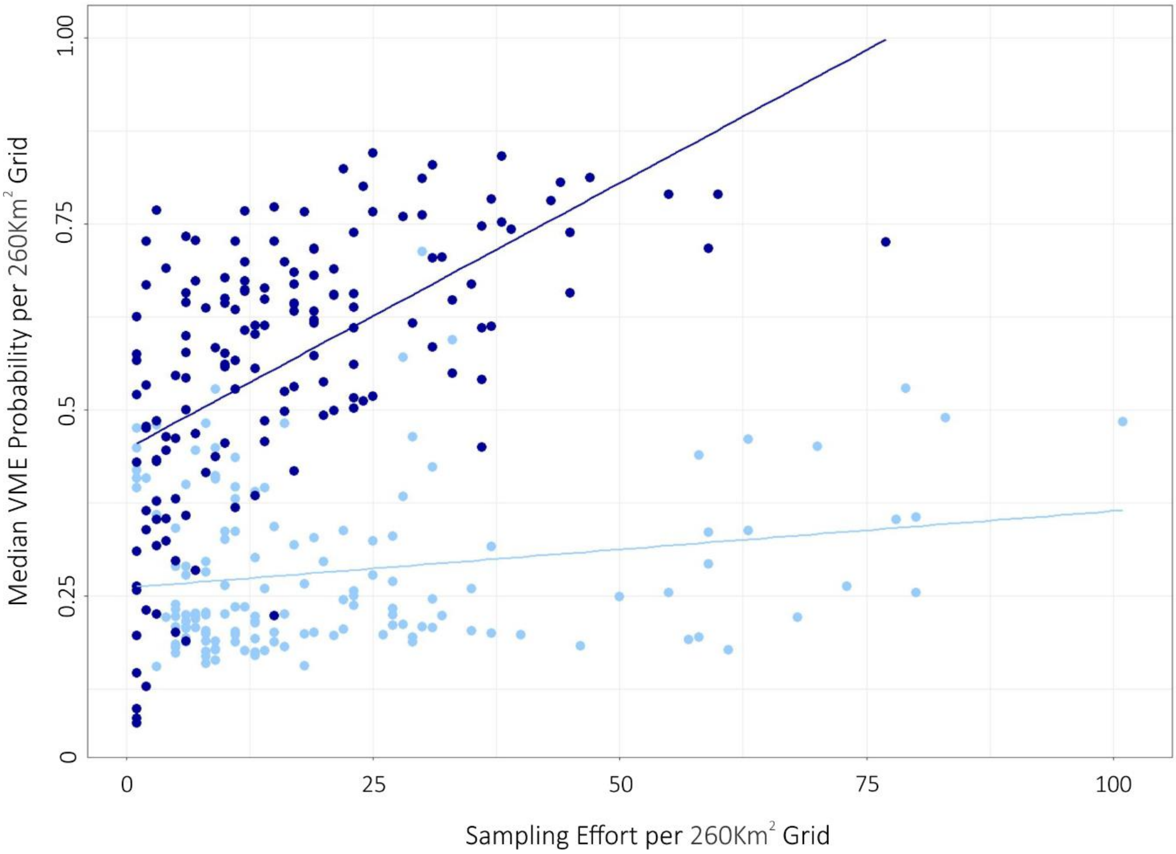

Figure 6.13. Relationship between sampling effort and the modelled probability of VME occurrence. Shelf-based samples (0-499m) and associated regression line are denoted in light blue; slope-based samples (500-2250m) and regression line in dark blue. Deep-water samples are excluded from analysis. The study region was divided into 10km-sided hexagons (260km^2). Sampling effort is defined as the number of distinct sampling locations within each hexagonal grid. VME probability is defined as the median modelled probability occurrence value for each grid cell which included >1 sampling station.

6.4 Discussion

6.4.1 Model-based bio-physical characterisation of South Georgia

The results of this study contribute to a growing body of work describing the physical and biological character of South Georgia's marine environment (Barnes, 2006, 2011; Graham et al., 2008, 2017; Young et al., 2009; Hogg et al., 2011, 2016, 2018; Taylor et al., 2011, 2013; Benedet, 2017).

The analysis in this study was conducted at a relatively broad spatial scale with environmental variables gridded to 500m. Broad spatial analysis was necessitated by the resolution of oceanographic data for the region and the computational requirements of ensemble modelling over large spatial scales. The primary environmental drivers of the modelled distributions for the taxa and trait-based response variables in this study were depth, slope, rugosity, temperature and salinity (Figure 6.10). These were summarised by two principal components (PC1 and PC5 – Figure 6.2). This mixture of hydrodynamic and terrain-based variables as ecological drivers builds on the findings of previous higher resolution studies (Rengstorf et al., 2014), that the inclusion of hydrodynamic components improves model accuracy both at fine, and in this case, broad spatial resolution. Many of the significant environmental predictors for the response variables in this study were consistent with those in previous studies (see Harris and Baker, 2011; Howell et al., 2011; Rengstorf et al., 2013; Rowden et al., 2017). It is notable that the suite of driving factors was not more varied or nuanced amongst the 23 different biological response variables modelled. Given the spatial scale of the analysis however, the environment of an oceanic island is arguably relatively simplistic in character. Through the spatial descriptions of functional and taxonomic groups, our analysis highlighted five major bio-physical environment types – the coastal environment, the main shelf, the shelf edge, the slope and the deep sea.

The **coastal environment**. This environment is dominated by glacial fjords which exhibit strong environmental gradients over relatively small vertical and horizontal spatial scales (Hop et al., 2002; Wlodarska-Kowalczuk and Pearson 2004). Complex topography is manifest in a mixture of steeply sloped glacial flanks, highly rugose coastal rocky shores and deep, flat glacial basins. This is reflected in the modelled faunal composition of the region, with animals demonstrating exclusive affinity to either hard or soft substrata shown to co-exist in the inshore zone (Figure 6.7; Appendix D Supplementary materials Figure 6.3). The deep basins experience high sedimentation rates and seasonally high suspended sediment loads from glacially-derived particles (Farrow et al. 1983; Blanchard et al., 2017). Modelled high prevalence in deposit feeding epifauna and infauna such as sea cucumbers, irregular urchins (FG 5, 6 & 7, Figure 6.6) and polychaete worms (Figure 6.7) are likely associated with this aspect of the inshore environment. Shallower waters of the inshore zone occur within the photic zone. As such there is increased dominance of multi-storied epiphytic algal communities (Brewin and Brickle, 2010) and grazing animals (FG8, Figure 6.6). Seasonality is a key factor in the complex inshore environment, with large seasonal shifts in temperature and salinity (Figure 6.10). South Georgia's waters are characterised by three distinct water masses: Surface Antarctic Water (SAW; 0-90m depth), Winter Water (WW; 90-150m) and Circumpolar Deep Water (CDW >150m). SAW typically reaches a summer maximum of 5°C and winter minimum of -1; the CDW ranges from 1–3°C, whilst the intermediate layer of WW maintains temperatures as low as -0.5°C (Brandon et al., 2004; Barnes et al., 2006; Whitehouse et al., 2008; Morley et al., 2014). As such, both seasonally and bathymetrically, the inshore environment experiences benthic temperature ranges in excess of 5°C (see Appendix D Supplementary materials Figure 6.4). Such variable conditions require sessile benthic fauna to exhibit a high degree of thermal plasticity, or would favour animals with the ability to move laterally or vertically. Whilst we cannot report on the former, there was a modelled prevalence of mobile predators and scavengers such as fish, gastropods and sea stars (FG12/13, Figure 6.6) in the coastal environment with a notable absence of sessile predators and scavengers (FG10, Figure 6.4) such as cup corals, hydrocorals and whip corals. The significant depth gradient in temperature could also act as a key driver to higher diversity in this region due to increased niche variability (see Hogg et al., 2011). Terrestrial influences play an important role in the inshore environment. The region sees low seabed salinity (Figure 6.10) on account of seasonal fluxes in turbid glacial melt water and surface runoff from the land. These seasonal processes also feed nutrients into the marine environment including iron enrichment from runoff (Schmidt et al., 2016; Bohrmann et al., 2017) and suspended particulates in the form of glacial flour (Farrow et al., 1983; https://earthobservatory.nasa.gov/IOTD /view.php?id=80994). Such sediment loading in the near-shore could restrict the distributions of certain climax filter-feeding fauna (FG2, Figure 6.6) such as sponges (Strehlow et al., 2017). Notably the coastal environment demonstrated much higher likelihood of early successional pioneer communities, with encrusting life forms such as bryozoans and ascidians, than climax communities (FG1 and FG2 respectively, Figure 6.6). Predators such as fur seals and penguins aggregate in vast coastal colonies of hundreds of thousands of individuals (Rogers et al., 2015). As such the environment is likely subject to a high degree of top-down control on trophic structure from higher predators through foraging activities and nutrient cycling (e.g. Smetacek and Nicol, 2005; Baum and Worm, 2009). With many inlets and channels, the coastal environment has complex water currents as well as influence from the tidal activity driving changes in faunal composition.

The **main shelf environment** is entirely contained within the CDW zone and as such has relatively seasonally stable water temperature at a relatively constant depth of 200m (Figure 6.10). The shelf is punctuated by several glacially derived cross-shelf troughs which provide some isolated complexity in topography (see Graham et al., 2008; Hogg et al., 2016). Along the margins of many of the troughs, modelled probabilities of both pioneer and climax suspension feeding communities (FG1 & 2, Figure 6.6) were notably higher than the surrounding shelf or trough basins demonstrating the importance the ensemble models placed on slope angle as an environmental driver. Otherwise the slope angle and rugosity across the shelf more generally remained consistently low. Historic glaciation in the region also adds complexity to the benthic ecosystem through the deposition of glacial dropstones representing islands of hard substrate in a sea of mud (Meyer et al., 2016; Meyer, 2017). Glacial environments also cause environmental perturbation through benthic impact from iceberg scouring (Gutt, 2001; Gutt and Starmans; Barnes, 2017). The general fauna of the shelf appeared to be dominated by mobile animals such as demersal fish, sea stars, gastropods, sea spiders and amphipods (summarised by FG4, 12/13 and 14, Figure 6.6). The basins of cross-shelf troughs represent a comparatively sediment-laden benthic environment to the trough flanks and main shelf above, across which many isolated hard rock communities exist. Many of the trough basins have active biogenic methane seepage (Römer et al., 2014; Bohrmann et al., 2017), often with anoxic sediments.

The **shelf edge** sees the transition from a predominantly soft-sediment shelf environment to one dominated by hard rock. Hard rock features such as terminal moraine fields form at the end of cross shelf troughs (Graham et al., 2008; Graham et al., 2017). At around 400-500m depth, the shelf edge falls within a band of the CDW mass that is both seasonally stable and relatively warm at approx. 2°C (Appendix D Supplementary materials Figure 6.6). The shelf edge region also has stronger currents than the main shelf. At the shelf edge topography changes sharply with a marked increase in slope angle, rugosity and curvature (Figure 6.10). The shelf edge and upper slope environments have also been suggested as potential refugia for South Georgia's fauna during the last glacial maxima with a reported line of discontinuity in benthic richness with higher richness (notably in brooding species) occurring on the shelf edge and slope (Barnes et al., 2016). Ensemble modelling supports this discontinuity, with shelf-edge and upper slope environment demonstrating high functional diversity (Figure 6.11) and a high probability of the presence of both climax (FG2) and pioneer sessile (FG1) communities represented by animals such as demo and glass sponges, ascidians and bryozoans. Sessile scavenging fauna (FG9) was also commonly predicted with the presence of a diverse range of corals such as sea pens, soft corals, anemones, cup corals, whip corals and hydrocorals. Distinctly lacking were exclusively soft-sediment dwelling infaunal animals such as certain bivalves and polychaetes (Figure 6.7). Whilst further down the slope this absence could be argued as a shift in collection gear towards long-line collection not suited to record infauna (see section 6.3.3), the upper slope and shelf break saw an overlap in the spatial distribution of both scientific data and fisheries data (Figure 6.5). As such infauna if present would likely be represented at least in the scientific element of the data, suggesting its absence is not an artefact of sampling. Conversely however Annelida were modelled to be particularly prevalent on the north-west South Georgia shelf break.

The **slope** environment has a stable annual temperature of 2°C to a depth of approximately 1500m. Deeper than 1500m the temperature drops steadily to a minimum of 0.3°C at 4000m. The slope and shelf edge environment can be characterised by a relatively warm water mass sandwiched between the cooler waters of the shelf and the deep sea. The defining feature of the slope is the dominance of a high slope gradient, high rugosity and changing depth profile indicative of an environment consisting of hard substrate. This zone is also dominated by some of the strongest currents around South Georgia, particularly towards the bottom of the slope. Parts of the slope show evidence of slope instability, with the seabed often formed of small to medium-sized rocks and cobbles (Bohrmann et al., 2017). The fauna associated with the slope is similar to that of the shelf break but with an increased predictive dominance of climax suspension feeding communities (FG2) over pioneer communities (FG1). The phyla Porifera, Cnidaria and Echinodermata exhibited particularly high predictive values in the slope environment. The slope was notable by the absence of exclusively infaunal and soft-sediment fauna likely indicative of a predominantly hard substrate environment. As on the shelf-edge, Annelida were modelled with high likelihood particularly along parts of the upper slope and to the north-west South Georgia slope. Given the taxonomic resolution of many of the slope biological records this distribution is not reconcilable against predictive distributions of functional groups that include polychaetes (e.g. FG 3, 5, 6, 11) that do not occur on the slope. It seems probable however that recorded slope annelid communities may consist of free-living epifaunal/commensal species (e.g. some Polynoidae) or those associated with hard substrata (e.g. Sabellidae or Serpulidae).

The **deep sea** is a stable cold environment (approximately 0.5°C). We define it as the environment beyond the bottom of the slope environment (i.e. the bathymetric profile is generally exhibits slope angles < 2°). At South Georgia this occurs at a minimum depth of 2500m. The deep-sea environment is characterised by relatively higher but stable salinity levels (Figure 6.10) and low nutrient levels. It is dominated by fine particulate substrata. This region's benthic fauna remains largely unknown. Model outputs demonstrate low occurrences across all functional and taxonomic groups, albeit in an environment with significant paucity in sample data and higher modelling uncertainty. The only groups to extend into the deep, albeit at lower occurrence probabilities, were sessile soft-bodied predators and scavengers (FG9) such as sea pens.

The bio-physical descriptions outlined above correspond with the unsupervised landscape classifications defined in the previous two chapters. Landscape mapping of the region also identified a distinct coastal, main shelf and shelf break environment (Chapter 4; Figure 4.5b) with distinct biological signatures (Chapter 5; Figure 5.6). In addition landscape mapping classified the slope environment as a distinct unit with regions of high slope angle and rugosity as a further separate cluster (cluster 4). Comparison between landscape mapping and ensemble modelling approaches to habitat mapping demonstrated a significant overlap between regions classified as Cluster 4 (Figure 4.5a) and regions of high VME and particularly functional diversity (Figure 6.11).

Based on these broad-scale habitat descriptions, the current configuration of the South Georgia section of the marine protected area would appear to be representative (as per CBD, 2010). All but the slope environment are currently afforded 100% benthic protection, with an additional 24.8% (with the inclusion of the North Georgia Rise) of the slope environment protected through benthic closed areas.

This type of predictive modelling compliments the top-down approaches to habitat mapping adopted in Chapters 4 and 5, providing a more in-depth assessment of faunal distributions and potential associations with spatial clusters than possible through the use of point-based biological sampling alone (Chapter 5).

6.4.2 Ensemble modelling

Ensemble approaches to modelling avoid dependence on a single habitat suitability modelling algorithm (Araújo and New, 2007; Buisson et al., 2009; Robert et al., 2016). This study incorporated ten distinct modelling algorithms, with different underlying assumptions, into a single ensemble prediction. The benefit of this approach is that it allows the assessment of variance between models. The low variance between models in this study, particularly in non-deep sea environments (Figures 6.8 and 6.9), inferred a degree of confidence in the accuracy of the study's model outputs, something which would not necessarily be quantifiable with single-model distribution modelling.

The degree to which the model output reflects the real-world environment at South Georgia was assessed through a split-sample approach to quantifying modelling performance. This necessitated retaining part of the biological data in order to then use it to test the accuracy of the prediction. Alternatively (or in addition), it would be beneficial to test modelled distributions against an independently sampled biological dataset. Whilst no such dataset was available for the region, previous work in the region supports some of the biological characterisation described in section 6.4.1. This includes the reported dominance of octocorals (Taylor et al., 2013) alongside sponges, anemones, ascidians and hydroids (Clarke et al., 2004; Barnes et al., 2006; Griffiths et al., 2008) in deeper areas of the shelf and slope. Studies from north of South Georgia (between 200 and 1500m depth) showed that Cnidaria were the most abundant taxa and had the highest biomass at depths of 1000 and 1500 m (Griffiths et al., 2008). Analysis of the South Georgia shelf fauna using a camera lander system paired with trawl samples (Barnes et al., 2016), identified a discontinuity in benthic structure and diversity. The outer shelf, moraine fields and shelf break were shown to be rich in benthic diversity (particularly in brooding species), compared to a relatively impoverished inner shelf. Barnes et al. (2016) argued that this trend demonstrated that re-colonisation following the last glacial maxima (LGM) was still occurring at South Georgia. This recolonisation he argued was emanating from refugia on the slope and outer shelf from regions that remained ice-free during glaciation (Graham et al., 2008, 2017). Whilst our analysis did not model the distribution of brooding vs. non-brooding species, the relatively high modelled probabilities of complex climax communities in self-break and slope environments (Figure 6.7), goes some way to supporting the trends reported in Barnes et al. (2016), if not the underlying cause.

The spatial scale (134,239 km^2) and spatial resolution (500m) of analysis is an important consideration in interpreting the model outputs. One likely effect of analysis at 500m spatial resolution, for example, is the underestimation of maximum environmental values (particularly in terrain-based variables). Previous studies have demonstrated the effect of scale of analysis on model output, reporting an 80% underestimation in maximum slope value when moving from a 50m grid size to 1000m grid size (Rengstorf et al., 2012). As such for a taxa, traits or faunal aggregations that may be driven by slope angle, rugosity of topographic position, a modelled predicative distribution is likely to be far more spatially constrained under the high resolution model where distributions may associate with small areas of very steep or rough terrain. By contrast, under a lower-resolution model, distributions would likely be associated far more generally with regions of higher slope values. Another example of this can be seen when comparing the results of this study to that of previous modelling of coral communities around South Georgia (Taylor et al., 2013). Taylor et al. (2013) utilised an ENFA (Ecological Niche Factor Analysis) model using 150m resolution environmental data in contrast to our coarser 500m resolution analysis. In comparison the 150m ENFA model identified smaller scale features (notable the flanks of the cross shelf troughs) as important potential octocorals environments. Our ensemble models do not identify these spatial patterns nearly so prominently (Figure 6.6 and 6.7), likely on account of the flanks of each trough falling beyond the resolution of our analysis.

A further example of scale-dependent analysis and interpretation can be seen in anecdotal examples of fine-scale VMEs not included in the biological datasets for the region and subsequently not predicted in model outputs. These included the presence of reputably large sponge gardens inshore off the south-east tip of South Georgia (Cape Vahsel) (personal communication Mark Belchier, BAS); Spirulid reef near Clerke Rock on-shelf and adjacent to the East South Georgia benthic closed area (Marine Protected Areas Order, 2013) and tectonically uplifted vertical hard rock walls in Annenkov trough (Bohrmann et al., 2017). Whilst these features were not included in the biological datasets, even if they were, in the case of the latter example (and perhaps the others) it is likely local-scale factors such as substrate type and geomorphology that drive these isolated, abundant and biodiverse communities.

Another consideration in interpreting model outputs is understanding why certain environmental variables drive distribution patterns the way they do. In doing so variables should not be viewed in isolation. Instead composite effects should be considered whereby factors or combinations of factors may represent proxies for others that are not explicitly included in the analysis. For example our study lacked input data on substrate type. Nonetheless it is possible that in shallow coastal waters, salinity acted as an inadvertent proxy for fjordic environments given their overlapping spatial distribution. More ostensibly, combinations of rugosity, TPI and slope angle could act as proxy for hard substrate environments.

Habitat suitability modelling helps to address the disparity between the specificity of point-based biological samples and the generality needed to describe regional distribution patterns at a scale relevant to marine spatial planning. The tripartite approach to modelling taxonomic, trait-based and conservation-based metrics provided both a holistic bio-physical categorisation of South Georgian waters (section 6.4.1), and the distinct distribution trends in individual taxa and functional classes. There are also clear advantages and disadvantages to each metric. In some instances, for example, functional groups are easier to categorise than species identification, especially if that functional trait is characteristic of a higher taxonomic division (e.g. phylum or class). In other cases very little is known about the functionality of some species so this type of analysis leaves large gaps in functional datasets. VMEs represent a management-centric metric. VME taxa are easily categorised given a number of easy to use identification guides, the fact that they tend to be morphological distinctive and charismatic and their management importance makes them a priority to recognise and record. In modelling their distribution however it should be considered that VME taxa as a group are only grouped together on the basis of their perceived vulnerability. As such they span a wide range of higher taxonomic groups and likely exhibit a wide range of different functional traits. There is no *a priori* reason therefore why such a group should necessarily exhibit the same habitat preferences. For this reason modelling the spatial distribution is often done by proxy (e.g. Rowden et al., 2017) rather than inclusive of all VME taxa. Our modelling of VME, though inclusive of all VME species, nonetheless demonstrated robust predictions with high confidence (Figure 6.9) and low number of model exclusion (Figure 6.4). This is likely on account of Cnidarians representing a large constituent proportion of the VME taxa around South Georgia and thus acting as *de facto* indicators for other VME species. That said, given that many VME taxa are often associated with climax communities which include Cnidarians, brachiopods, sponges and stalked crinoids our results should still stand as a robust assessment of VME spatial distribution.

6.4.3 Implications for spatial prioritisation at South Georgia

Mapping VME habitat

VME taxa are widely used as a metric by which to direct marine spatial planning and prioritise conservation efforts (United Nation Food and Agricultural Organisation, 2009; CCAMLR, 2013; Convention of Biological Diversity, 2008). We assess their distribution in respect to three management-related zones at South Georgia: (i) the zone currently open to fishing, (ii) the zone adjoining this fishing zone at its upper and lower depth limits, and (iii) the benthic closed areas.

Within the fisheries zone 84% of fisheries bycatch records collected at South Georgia between 1996 and 2014 were categorised as VME under CCAMLR categorisation (Benedict, 2017). Many records were considered reef-building or bio-constructor animals (Wakefield et al., 2006) with octocorals representing the most abundant group (Taylor, 2011; 2013). One reason for this frequency in bycatch is that VME by their very definition are vulnerable to fishing so would be expected to form a constituent part in fisheries catches. There has however been extensive sampling on the South Georgia shelf (11,377 samples; 4091 stations) with low occurrences of VME (Figures 6.11 and 6.13). This can also be seen in records of Cnidaria which represented only 3.68% of shelf samples and occurred at only 6.9% of shelf stations. Our analysis therefore identifies the present open fisheries zone as the zone most likely to include VME communities.

Our analysis does not assess weight nor abundance of VME and as such does not explicitly make recommendations on the effectiveness of current or alternative protection placed on the benthic environment at South Georgia (as per CCAMLR Conservation Measure 22-07 (2013) and Conservation Measure 22-06 (2017)). Nonetheless, with VME occurrence low in the shelf zone and VME occurrence dropping away sharply in deeper water (Figure 6.6), if a closed area based on presence of VME alone were to be designated, then the current fisheries zone would constitute the core of this closed area.

The presence of high levels of VME in the depth band 550 to 700m suggests that the additional protection currently afforded to this region by the GSGSSI beyond that of the statutory 550m requirements of CCAMLR, as per CCAMLR conservation measure 22-08 (2009), is warranted. Previous research has identified that most bycatch is concentrated in the shallower depth range of the fishing zone in depths up to 800m (Benedict, 2017) and thus an increase in the depth limit to 800m would be beneficial for protection. Our analysis supports this assessment. Beyond the lower limit of the fishing zone (2250m) VME occurrence was low. Sampling in these waters was lower however and thus uncertainty were higher for this region (Figure 6.8 and 6.9).

The current benthic closed areas are shown to provide varying protection to VME. West gully, East, NE Clerke Rocks and Shag Rock benthic closed areas are closed at least in part on the basis of the presence of vulnerable ecosystems, with the large North Georgia Rise closed area based on the potential for vulnerable environments (Appendix D Supplementary materials Table 6.3 and 6.4). Ensemble modelling provides no support for a closed area on the North Georgia Rise. However sampling is so low for this region that it is entirely possible that the region hosts extensive, and as yet, undocumented benthic biodiversity. West Shag Rocks is shown to support high occurrence of VME, as are the other two closed areas on the South Georgia slope (Table 6.5; Figure 6.12), though it should be noted that locating a closed area anywhere within the depth range of 500 to 1500 around the South Georgia or Shag Rocks shelf would likely produce similar justification for closure. The West gully region produced slightly lower occurrences of VME, though this did cover a larger area than many of the other benthic closed areas and extended into deeper water, for which modelling confidence was lower.

With the exception of the North Georgia Rise closed area, all benthic closed areas at South Georgia and included in this study (Appendix D Supplementary materials Table 6.3) were shown to have higher VME-50 and VME-70 values than the fisheries zone and study area more generally. The only region to exhibit higher VME probability was the seabed between the 550-700m depth contours (Figure 6.12).

Mapping functional diversity

Losses in both taxonomic and functional diversity could have significant consequences for biodiversity and ecosystem function (Petchey and Gaston, 2002; Diaz et al., 2007; Cadotte et al., 2011; Brum et al., 2017). Through assessing diversity in functional groups we attempt to look beyond the vulnerability of taxa at South Georgia and look also to understand the spatial distribution of different ecological, morphological, and physiological strategies within South Georgia's benthic fauna.

Highest functional diversity was modelled to occur along the shelf break and upper slope of South Georgia (Figure 6.11) particularly to the north-west of the island, North Shag Rocks as well as inshore at South Georgia. With reference to section 6.4.1 it could be argued that what characterises these specific regions is the transitional nature of the physical environment. For example the near-shore environment is a very dynamic environment with a steep gradient in environmental conditions such as temperature, depth and substrate. Likewise the shelf-edge is a zone in which the shelf environment transitions into the slope, with significant changes in depth, and geomorphology. That said, the highest values for functional diversity occurred along the 700m depth contour which falls below the shelf break (which typically occurs at approximately 350m) and on the slope itself. High functional diversity on this 700m contour did correspond with a marked increase in slope angle. Indeed every location for which high functional diversity was predicted on the South Georgia and Shag Rocks slope corresponded with slope angles of >10%. Lower functional diversity was modelled in the deeper slope environment. Data from this region was however predominantly fisheries derived (Figure 6.5). As such faunal taxonomy was often not resolved beyond phyla, class and occasionally family level, and consequently often not to the taxonomic level required for classification as a functional group or for a specific trait. Furthermore, as addressed in section 3.3, fisheries bycatch disproportionately selects for particular taxa such as soft corals that are easily hooked and solid corals that are easily snagged but not bendable or friable taxa, or small or infaunal animals. Therefore though VME and certain taxa-based models may be descriptive across environments, functional traits and derived diversity indices may not be, with significant under representation on the slope. Indeed the presence of climax communities on the outer shelf and slope would imply that by association high taxonomic diversity and functional diversity should also follow. At a lower probability of occurrence threshold (FD-50), high functional diversity was also patchily recorded across much of the South Georgia shelf and was particularly high at near-shore locations around South Georgia.

The 700m contour for which some of the highest levels of functional diversity were recorded also corresponds with the upper limit of the fishing zone. Much of the remainder of the fisheries zone exhibits medium to low functional diversity, though as discussed above this is likely an artefact of sampling. If the upper depth limit of fishing was shifted to 800m as proposed by Benedict (2017), greater protection would be afforded to these regions of high functional diversity. The benthic closed areas in the study region generally exhibited low levels of functional diversity (both at FD-50 and FD-70) with the possible exception of the West Shag Rocks closed area.

6.4.4 Applications in marine spatial planning

Few MPAs have benefited predictive distribution modelling to describe their benthic environment, not least across a range of attributes – taxonomic, functional, and management-specific metrics. This holistic approach to distribution modelling has universal application in aiding in the design and prioritisation framework of all MPAs around the World. The clear limitation to analysis however is always the biological data and corresponding environmental datasets available for the region.

The degree to which modelling outputs are informative is largely based on the quantity and quality of input data. Increasingly this has led to the acquisition of high-resolution data to build detailed models due, in-part, to the perceived ineffectiveness of coarse-resolution habitat models for management purposes (Howell et al., 2011; Rengstorf et al., 2012, 2013, 2014; Rowden et al., 2017). With a global trend in marine spatial management moving to increasingly large scales (Toonen et al., 2013; Shugart-Schmidt et al., 2015), we argue that a broad-scale, holistic and ensemble approach to modelling has the greatest relevance to informing marine reserve design. Furthermore with improvements in the resolution and coverage of global remote sensed environmental datasets such as bathymetry (e.g. Mayer et al., 2018), primary productivity (e.g. Westberry et al., 2008) and oceanography (e.g. Madec, 2015), there is increasingly application for modelling in remote, and hitherto underexplored regions.

A further application of ensemble modelling is that it offers the opportunity not only to predictively model distributions spatially, but also temporally. Near-surface waters around South Georgia, for example, represent some of the fastest warming waters on Earth (Whitehouse et al., 2008). Habitat suitability modelling offers the potential to predict future temporal changes in distribution patterns based on projected changes in environmental conditions such as sea temperature, using models such as CMIP5 (Taylor et al., 2012) or Bio-ORACLE (Tyberghein et al., 2012). With the marine environment experiencing increasing pressures from anthropogenic-driven changes, understanding of temporal changes within management areas will become ever more necessary.

6.5 Conclusions

This study adopted a bottom-up approach to habitat mapping using an ensemble of predictive habitat suitability models. Benthic fauna were categorised by taxonomic groups, functional traits and management-specific metrics such as vulnerable marine ecosystems. This analysis provided the first bio-physical assessment of the benthic environment around South Georgia, inferring distinct coastal, shelf, shelf-edge, slope and deep water communities which corresponded with changing physical conditions. The primary environmental drivers of these biogeographical patterns related to two principal components, corresponding to depth, salinity and temperature range (PC1) and slope and rugosity (PC5). This mixture of hydrodynamic and terrain-based variables as ecological drivers was relatively universal across all 23 taxonomic and functional-based response variables.

Ensemble model performance, assessed through a split-sample methodology, was shown to vary between response variables and model runs, though variance between model algorithms was generally relatively low. An exception to this was the universally poor performance of surface range envelope models (SRE). Modelled distributions were assessed in the context of the current zoned MPA in place at South Georgia, and specifically in relation to the regions open and closed to long-line fisheries. Modelled spatial distributions of VME taxa and regions of high functional group diversity demonstrated the highest likelihood of occurrence on the shelf edge and continental slope environment, compared to relatively low likelihood of occurrence on shelf and deeper water environments. As such, we conclude that if a closed area based on presence of VME alone were to be designated, then the current fisheries zone would constitute the core of this closed area. Ensemble habitat suitability modelling at South Georgia therefore brings in to question whether the current spatial configuration of the MPA is best placed to protect benthic functional diversity and ecosystems known to be vulnerable to bottom fishing. More universally, these results demonstrate the utility of modelling approaches in informing on the design on conservation zones both at South Georgia, and, given adequate environmental and biological data coverage, at other large MPAs.

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Chapter 7: Synthesis and Conclusions

7.1 Thesis summary

The overall aim of this thesis was to investigate the spatial distribution of benthic habitats and associated faunal communities at the sub-Antarctic island of South Georgia, over a variety of spatial scales. This aim was achieved through: (1) the application of an interdisciplinary methodology to marine landscape mapping with a top-down, objective, statistical approach to hierarchically partitioning and mapping the benthic environment into physical habitat types; and (2) a bottom-up approach to habitat mapping, using an ensemble of habitat suitability models to map a range of benthic faunal attributes relevant to marine management, based on taxonomic classification, functional traits and vulnerability to disturbance.

The results from both analyses were framed within the context of marine spatial planning and as such provide an assessment of the utility of habitat mapping to inform and underpin marine management both at South Georgia and more universally for large marine protected areas.

This thesis provided seven main scientific objectives:

1. Develop a methodology suitable for objectively partitioning the benthic environment based on its abiotic attributes.
2. Map the spatial distribution of these physical habitat classifications in a hierarchical framework that is able to reflect changes in environmental conditions across spatial scales.
3. Evaluate whether abiotic-derived habitat maps correlate to changes in the faunal structure of benthic communities, both in terms of taxonomic and functional metrics.
4. Produce habitat suitability models relevant to the management of the region's marine resources, including modelling of taxonomic and functional groups, and occurrence of vulnerable marine ecosystems (VMEs).
5. Quantify the respective influences of environmental predictor variables on the region's benthic fauna.
6. Compile the aforementioned analyses to address whether current marine protection at South Georgia ensures protection of benthic diversity, vulnerability and representative protection of habitats.
7. Examine how the habitat mapping approaches adopted in this study are transferable to large marine protected areas in general.

The following sections aim to address each of these objectives. Section 7.2 will focus on objectives 1, 2 and 3 relating mapping to abiotic and biotic attributes of an environment and cover material from Chapters 4 and 5. Section 7.3 will focus on objectives 4 and 5 regarding the use of habitat suitability modelling approaches and cover material principally from Chapter 6. Section 7.4 will address an overall analysis of all study results within the context of marine spatial planning at South Georgia, while section 7.5 will give an overview of the application of this research within the broader context of marine conservation globally. Finally section 7.6 will give an outlook to future directions for large-scale MPA management.

7.2 Landscape mapping

Objective statistical approaches to marine landscape mapping have previously been employed at finer scale (Verfaillie et al., 2009) and in assessing discrete topographical feature such as canyons (Ismail et al., 2015). This study is the first application of this methodology over such a large regional scale (10^5 km^2), and its first application across spatial scales, through use of a hierarchical nested clustering structure. Here, the methodology's utility is considered based on its capacity to be fully automated and objective, robust, repeatable and have potentially universal application for other proposed or established large marine protected areas.

A statistical approach to landscape mapping was demonstrably very effective at delineating the marine environment into a manageable number of discrete and stable clusters reflected in non-spatially-fragmented clusters and high confidence in the clustering results (see confusion index analysis in section 4.3.2). This is particularly beneficial in regions for which little is known about the benthic environment, notably regions that have not benefited from bio-physical classification systems such as EUNIS (Davis et al., 2004), which exist in European waters. The hierarchical structure of the protocol means it is effective at presenting, not only broad-scale spatial patterns in the physical environment, but also through iterative cycles of re-classification, characterisation of the environment at progressively finer scales. Hierarchical classification remained effective whilst clustering results remained relatively un-fragmented in nature.

The unsupervised protocol means each input variable used has equal influence in the model, with no *a priori* assessment or assumptions made on the degree to which different physical variables act as biological drivers. As such no weighting is applied in consideration that some variables might have a more acute influence on faunal distributions than others. Furthermore, given all variables are normalised as part of the landscape mapping protocol, large ranges within one variable may have the same influence in statistical partitioning, as small changes within another. Consequently, to retain ecological consideration of the clustering, the methodology must lose some of its objective autonomy. In our analysis for example, it became necessary to qualitatively assess the clustering results to ensure they stood up to logical interpretation. As such, multiple iterations were run, removing some variables such as slope aspect from the analysis on the basis of their influence on clustering results.

Two key benefits of the landscape mapping methodology are that it benefits from relative ease of use and has transferability to other environments with different data availability. The only requirements for the model are that environmental data needs to be continuous for the study region, and as such may require interpolation techniques to fill data gaps. The analysis also needs to be done in ensemble, i.e. without subsetting and reassembly. As such computational requirements (especially over the spatial scale and resolution employed at South Georgia) can be high, requiring the use of a super computer with high memory capability. A further consideration is that our model study region of South Georgia benefits from relatively comprehensive bathymetric and oceanographic data. With detailed oceanographic data lacking for many regions however, there may also therefore be a corresponding decrease in the explanatory power of habitat classifications in explaining biological distributions (e.g. Robert, 2014).

Versions of landscape mapping have been used around the World to classify both pelagic and benthic environments (Grant, 2006; Howell et al., 2010; Ierodiaconou et al., 2011; Copeland et al., 2013; Rees et al., 2014). Commonly however environmental-biological links are not usually sought, tested or demonstrated across the larger spatial scales relevant to the marine spatial planning. In addressing our third objective, we evaluate the ecological relevance of landscape maps by testing whether abiotic-derived habitat maps correlate to changes in the faunal structure of benthic communities, both in terms of taxonomic and functional metrics.

The marine environment, by its nature, is environmentally fluid and generally not delineated by abrupt boundaries, but rather by a continuum of gradual biotic and abiotic change. There is, therefore, a disparity between rigid habitat classification systems and this reality. Added to this is complexity of patterns in faunal community structure across spatial scales and across taxonomic groups. Within an individual taxa or functional grouping, the link between environment and fauna may be relatively direct, thus easier to bio-physically classify. Consideration of biodiversity as an inclusive measure of all species in the region is, however, considerably more complex. Different taxa and group distributions are controlled and driven by different environmental variables. Consequently, in assessing biodiversity as a singular unit, there is an increased likelihood of a wider variety of habitat preferences within that group of animals, and thus of higher likelihood of variability in intra-cluster community structure.

This high variability was apparent in our analysis. Random resampling of biological data however acted to smooth-out potential boundary effects at cluster margins and fine-scale heterogeneity in fauna. Consequently our analysis demonstrated a statistically significant relationship between environmentally derived landscape mapping clusters at South Georgia, and the composition of presence-only species data from the region. This relationship reveals a distinct biological signature in the faunal composition of individual clusters. This correlation was evident across three hierarchically nested spatial scales, from very large regional clusters (10^4 km^2) to much smaller, spatially constrained, features (10^1 km^2). Furthermore, results presented in Chapter 4 and 5 also demonstrate the effectiveness of this landscape mapping protocol in utilising large, historical datasets of opportunity.

7.3 Ensemble modelling

Preceding this study there was a baseline understanding of distribution patterns in benthic species richness of South Georgia (Hogg et al., 2011). This, however, was limited to the South Georgia shelf. One of the key objectives of this thesis was to produce habitat suitability models relevant to the management of the region's marine living resources. This study presents for the first time in the region, predictions of both the spatial distribution of taxonomic and functional groups, including a summary measure of functional diversity. Furthermore it builds on previous work which modelled the predictive distributions of VME octocoral communities using fisheries bycatch data (Taylor et al., 2013), by predicting distributions of all categories of VME. This analysis was based on the inclusion of scientific data from the South Georgia shelf, absent from previous analyses, and as such provides a more holistic view of regional ecosystem vulnerability.

The use of an ensemble approach provides an understanding both of predictive distribution probabilities and variance associated with each prediction. As such this avoids dependence on a single habitat suitability modelling algorithm, allows quantification of the level of concurrence between models and infers the level of confidence associated with each projection. Plotting predicted distributions of management-relevant biotic variables (i.e. VME taxa and functional diversity hotspots) together with modelling confidence enables the identification of potentially important sites to prioritise protection, or if associated with a high degree of uncertainty, identifies locations for which enhanced sampling could be beneficial.

Landscape mapping clusters were characterised by a range of abiotic variables (Chapter 4, figure 4.6). Key amongst them were depth (e.g. clusters 2, 3, 5, 7); temperature (e.g. cluster 5); topography (e.g. clusters 4, 7 and 6) and current velocities (e.g. clusters 1 and 6). Ensemble modelling identified two principal components as key drivers of faunal distributions. These encompassed many of the same variables as the marine landscape mapping clusters, namely, depth, temperature range, salinity, slope and rugosity. The exclusion of current velocities as a key driver of ensemble models was notable and potentially reflects the difference in effective spatial resolution between top-down landscape mapping and bottom-up distribution modelling.

Quantifying the respective influences of environmental predictor variables on the region's benthic fauna has particular relevance, not only in understanding potential distributions of biological attributes of the environment, but also in understanding how these distributions may change in the future with a changing environment. Waters around South Georgia are warming (Whitehouse et al., 2008; Griffiths et al., 2017). With significant elements of South Georgia taxonomic and functional diversity associated with a slope environment which has a relatively warm band of water (~ 2°C). Future increases in regional seabed temperatures could have significant implications for benthic fauna biogeography (Barnes et al., 2009b). Species at their upper thermal limits (e.g. northern range-edge species), for example, could exhibit range constriction, or a down-slope migration towards cooler deep water.

Conversely southern range-edge species at their lower thermal limits could see range expansions, with the increased probability of the propagation of invasive species. Given the large proportion of northern range-edge species present at South Georgia (Hogg et al., 2011), the net result in range-shift could be of great importance to conservation and management strategies at South Georgia.

7.4 South Georgia and South Sandwich Islands MPA

The South Georgia and South Sandwich Islands MPA covers an area of 1.07 million km^2 (excluding the region south of 60°S). The geographical extent covered by the analyses in this thesis was constrained to an area of 431,486 km^2 around the island of South Georgia (see figure 7.1). This limitation was due to data availability and the computational requirements of running multi-attribute habitat models. In total, therefore, the landscape mapping analysis covered 40.15% of the total MPA area, of which 85,715 km^2 (7.96%) was also included in the ensemble models. Both of these analyses covered almost 100% of the total area currently open to benthic fisheries in the South Georgia quadrant of the MPA. Using the analysis presented in this thesis, objective 6 addresses whether current marine protection at South Georgia ensures representative protection of benthic habitats, diversity and vulnerability.

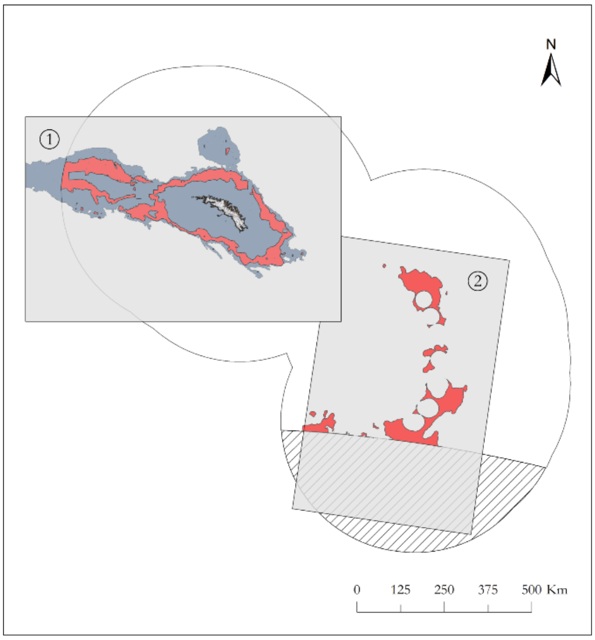


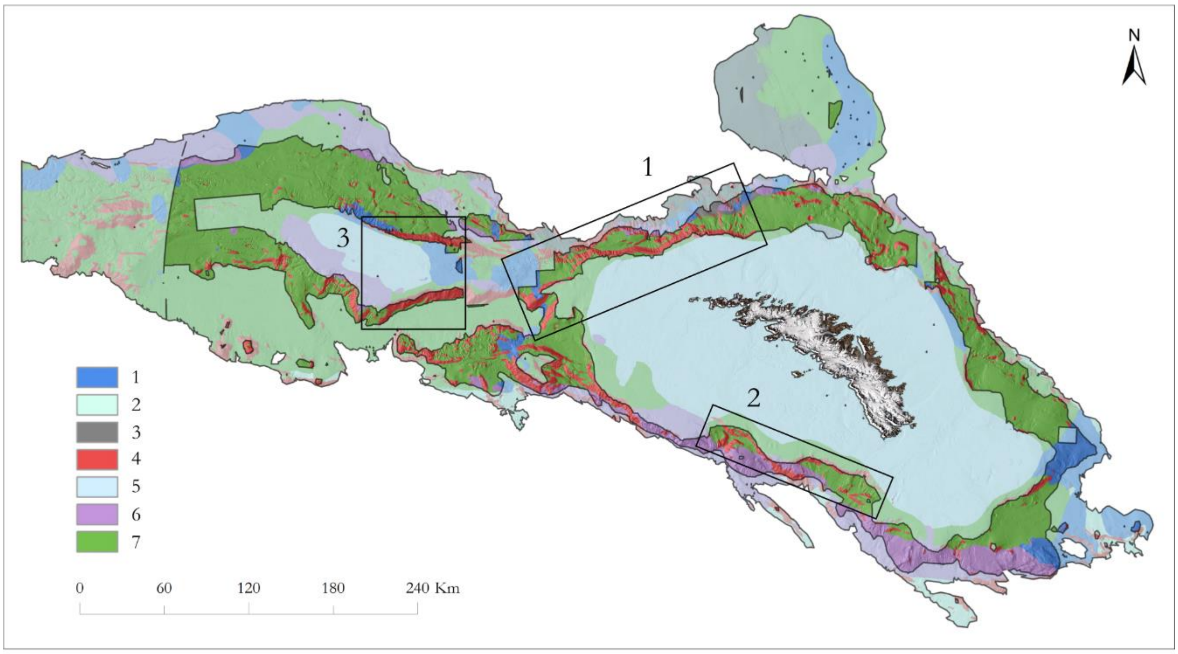
Figure 7.1. The spatial extent of data analysis undertaken in this thesis. Grey box 1 represents the coverage of landscape mapping analysis (Chapter 4 and 5); the blue polygon represents the coverage of the ensemble modelling analysis (Chapter 6). The extent of the SGSSI MPA is symbolised by the solid black line. The section of the SGSSI exclusive economic zone falling south of 60°S, and thus under the purview of the Antarctic Treaty, is symbolised by black hatching. Red polygons represent the region of the MPA open to benthic longline fishing. Grey box 2 represents the region around the SSI for which there is the potential for future habitat mapping based on a 200m resolution interpolated bathymetry dataset (Leat et al., 2014).

Spatially, there is a total ban on bottom trawling at SGSSI. The only form of permissible fishing in the region is licenced longline fisheries, which is restricted to just 8% of the MPA (~83,500 km2) occupying a zone between 700m and 2250m depth.

The entire shelf environment (<500m) is currently a benthic no-take zone, offering protection to a region of known high benthic diversity and distinctiveness (Hogg et al., 2011). Furthermore, this closure to benthic fisheries affords protection to isolated examples of vulnerable habitats such as known shallow water spirulid reef structures (Ramos and San Martin, 1999) and topographic features with high associated diversity and biomass such as sponge gardens (personal communication Mark Belchier, BAS) and diverse coral communities (Bohrmann et al., 2017). Hierarchical landscape clustering of the shelf demonstrates biologically distinct environments within the singular shelf cluster. This was also reflected in habitat suitability modelling of the region with notable differences between coastal, shelf and shelf edge communities (section 6.4.1).

The deep sea remains an environment for which very little is known. Global diversity-depth relationships demonstrate a peak in macrobenthic diversity at intermediate depths of 2000-3000m (Pineda and Caswell, 1998; Ramirez-Llodra et al., 2010). At SGSSI, 17.75% of the exclusive economic zone (figure 7.1) lies between 2000m and 3000m depth. Whilst ensemble modelling does not support a 2000-3000m peak in diversity, it must be noted that modelling result in deeper waters around South Georgia were derived from very few faunal records. Currently depths greater than 2250m are protected from benthic fisheries and based on these global biodiversity trends, it is likely a region for which it is important to take a precautionary and conservative approach to management. Landscape mapping of the deep sea demonstrated that it is not a homogenous zone but punctuated by region of topographic complexity and exposed to different oceanographic current regimes. The blanket protection in place clearly protects the range of habitats that may exist in this zone.

The slope environment is the only benthic environment at South Georgia currently open to licenced fisheries. At South Georgia the fisheries zone predominantly comprises 2 marine landscape clusters (4 and 7), characterised by topographic attributes and temperature gradients. In addition however, it also contains 5 of the 7 level-1 landscape mapping clusters, making it a relatively heterogeneous environment (Figure 7.2: main map, 1a, 2a and 3a) in comparison to large homogeneous regions on the shelf and deep sea. Given landscape mapping clusters were shown to be biologically distinct, by extension we argue the fauna of the slope environment likely reflects this heterogeneity. Habitat suitability modelling shows the shelf break and upper slope of South Georgia and Shag Rocks to exhibit peak functional diversity, the highest probabilities of VME communities and the presence of climax communities. By comparison, VME occurrence was modelled to be relative unlikely in both shelf and deep water; climax communities were almost exclusively restricted to the slope; and hotspots of functional diversity demonstrated a restricted distribution along the shelf break and upper slope (c.f. aforementioned anecdotal evidence of sponge gardens from the shelf). Consequently we conclude that,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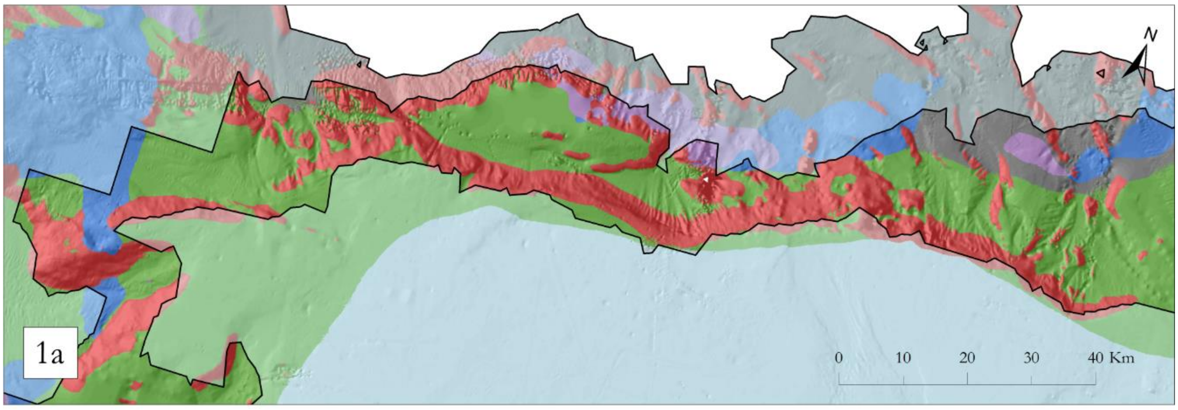
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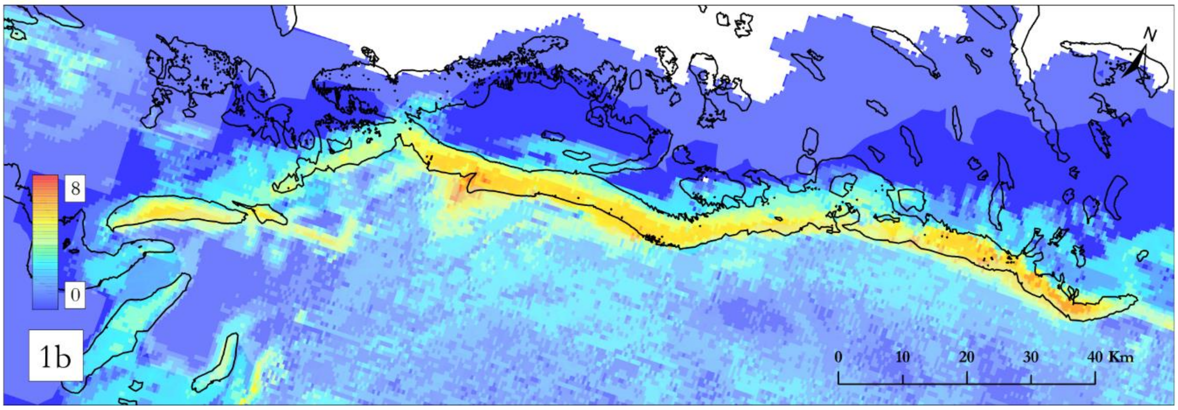
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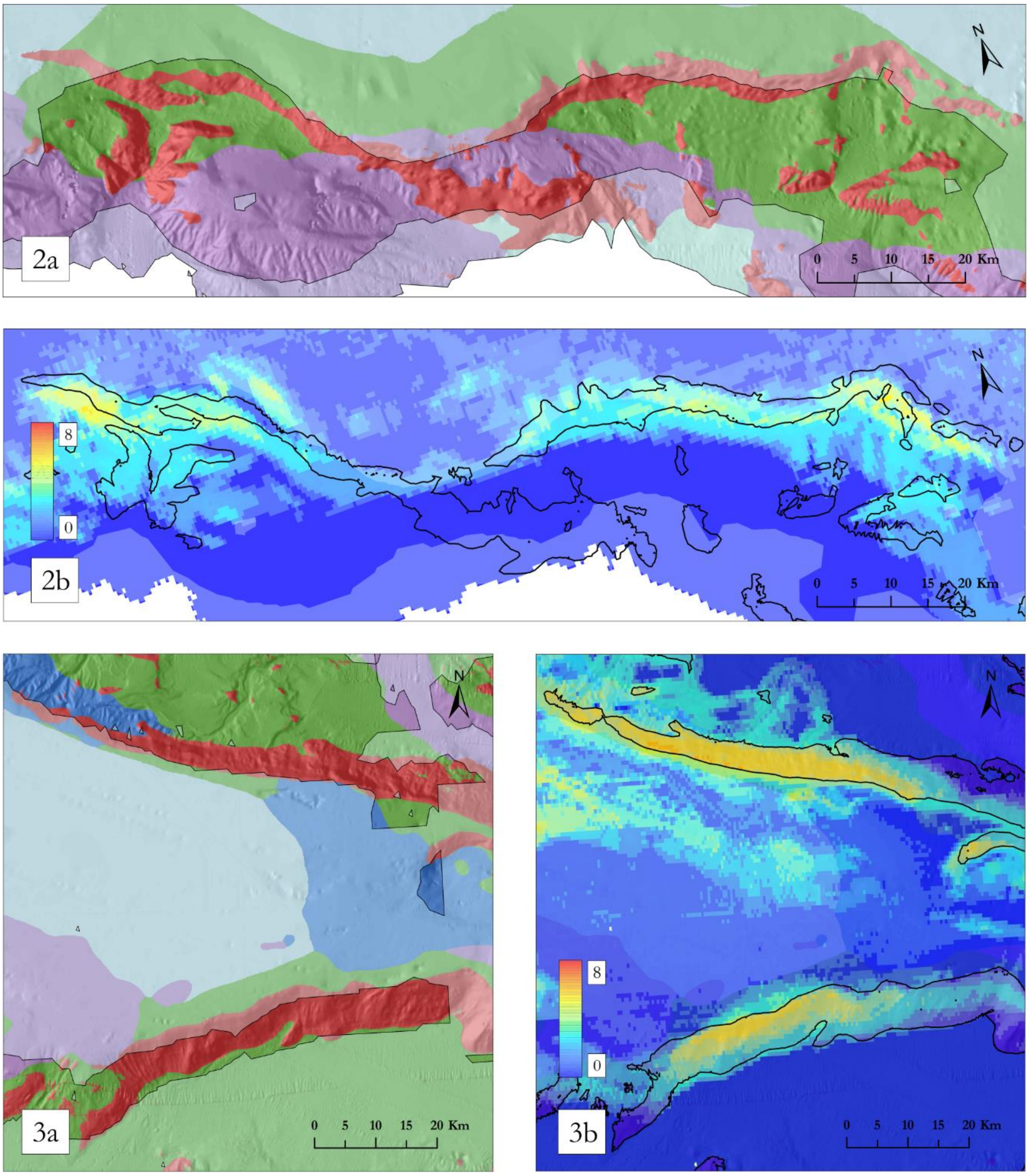


Figure 7.2. The spatial relationship between landscape mapping clusters (Chapter 4) and benthic functional diversity (Chapter 5) in the fisheries zone at South Georgia. The location of insets 1-3 are shown in the main overview map. Insets 'a' show landscape mapping clusters, with the fisheries zone delineated by solid black lines. Insets 'b' show functional diversity (FD-70), with landscape mapping cluster 4 delineated by solid black lines. Descriptions of landscape mapping clusters and functional diversity can be found in Thesis sections 4.3.2 and 6.3.7 respectively.

if a closed area were to be designated based on presence of these three management-relevant faunal classifications, then the current fisheries zone would constitute the core of this closed area.

The slope region is currently protected by a series of benthic closed areas. The largest of these, North Georgia Rise, which forms an adjunct to the northern edge of the South Georgia slope, does not represent a distinct or unique environment in terms of landscape habitat classifications. Furthermore, modelled predictions don't offer any scientific basis for its current closure. Nonetheless, minimal sampling on this plateau may suggest the precautionary principal should apply when it comes to protection. Other closed areas demonstrated relatively high likelihood of VME as well as high modelled probability of benthic climax communities. As such their protection seems appropriate. That said, positioning of a closed area on any other region of the slope environment would likely produce similar results.

Combining both landscape mapping and ensemble modelling approaches can also be informative in terms of the surrogacy value of the former. Figure 7.2, for example, overlays landscape clusters with functional diversity. This illustrates a strong relationship between steep rocky escapements (landscape mapping cluster 4) and high functional diversity. Notably, cluster 4 was also a mapping cluster associated with species with reef-building capacity (section 5.4.3). The regions of steep-sloped, high diversity environments were seen along the northern and southern upper shelves of South Georgia and Shag Rocks, both regions largely open to longline fishing.

Based on the analysis presented in this thesis, the following recommendations could be made with regards to future marine management within the South Georgia element (i.e. figure 7.1 box 1) of the SGSSI MPA:

1. Retain, as a minimum, the current zone between 550 and 700m which is closed to bottom fishing by the GSGSSI beyond the requirements of CCAMLR. This should be recognised as a region demonstrating high likelihood to VME taxa, high functional diversity and higher likelihood of the presence of climax benthic communities.
2. There should also be consideration of extension of the closed zone to the depth band between 700m and 800m, on account of peak likelihood of VME and high functional diversity occurring within this depth band, in addition to higher reported VME biomass in this zone (Benedet, 2017).
3. In addition to, or in lieu of recommendation 2, consideration should be given to the additional inclusion of benthic closed areas around South Georgia and Shag Rock. Specifically these should look to provide protection of zones of potentially high functional diversity such as those outlined in figure 7.2 1b and 3b.

7.5 Towards an integrated approach to the spatial planning of large MPAs

Many MPAs include spatial and temporal zoning, for example, the Great Barrier Reef MPA (GBRMPA zoning plan, 2003). This zoned model for marine protection is likely to become increasingly common, as more easily implemented MPAs are fulfilled, and there is increased necessity for MPA placement in more contentious national waters, waters transcending national jurisdictions and areas beyond national jurisdictions (ABNJs). Zoning in such regions aims to protect the marine environment, whilst offering ecosystem services and sustainable use of living marine resources. In order to prioritise this zonation however requires the kind of integrated analysis outlined in this thesis.

Even if the protection proposed or adopted for a region is not zoned, but rather one of blanket closure (e.g. IUCN category I), involving 100% no-take zones and strict nature reserve status across an entire region, this does not negate the need for robust scientific underpinning of the designation. The reason for this is twofold:

1. **Justifiable protection**. Societal, political and fiscal priorities change over time; geopolitics evolve; governments change, as do the commitments they have made (e.g. U.S.A. vis-à-vis Paris climate change agreement (Kemp, 2017)). MPA designations often come under review (e.g. SGSSI) or have inbuilt into them a 'sunset clause' (e.g. 35 years in the case of the Ross Sea). It is important therefore to have a robust scientific framework that can evolve with ever-increasing knowledge and that is in place for when it may be needed.
2. **Ensuring representative protection**. Working within existing frameworks such as the Convention on Biological Diversity (CBD, 2008), there is requirement to ensure representative protection of habitats and species around the World. It is however very difficult to meet these targets, or indeed assess meeting these targets of representativeness if the spaces and species currently afforded protection under the MPA network have not themselves been assessed.

The methodologies outlined in this study demonstrate how the combined approach, of top-down classification to characterise the environment (Chapter 4 and 5), and bottom up approaches to map priority taxa and communities (Chapter 6) can be effective in bio-physically mapping over large areas. Through combining hierarchical top-down and bottom-up approaches, management plans for very large marine protected areas can incorporate and reflect both broad-scale processes and finer-scale biogeographical trends. Whilst this adoption of a duel approach to habitat mapping is advantageous, in instances where there is significant paucity or a complete absence of biological data, such an approach may not be possible. In such cases, there is often still environmental data available, be it in the form of regional datasets or taken from larger global scale models. In most instances therefore, it is possible to adopt the landscape mapping approach to habitat classification. Even without biological datasets to ground-truth the physical classification this analysis can still be informative through, for example, the use of physical habitat heterogeneity as a proxy for faunal richness (e.g. Harris, 2008).

7.6 Future directions

The landscape mapping analyses described in this thesis covers an area that represents approximately 40% of the SGSSI MPA. Geographically therefore, the most immediate extension to this work would be the inclusion of the remaining 60% of the MPA. Already a large area around the SSI is covered by a 200m resolution bathymetry dataset (Leat et al., 2014). With the inclusion of this region, 66.55% of the total area of the MPA has the potential to form an integrated benthic habitat analysis. This should be considered a priority for the region given that fisheries licences are currently issued for the SSI, despite an almost complete gap in our knowledge of the benthic environment and fauna in this region. Furthermore, with the SSI inclusion in a Scotia Arc habitat map, almost 100% of the regions benthic fishing grounds would be covered and assessed for suitability.

At South Georgia there remain significant data gaps identified by our analyses. A clear case would be the need for systematic scientific sampling on the outer shelf, slope and in deep water. This would remove the reliance of management decisions on bycatch data. Furthermore, through use of camera or ROV systems the predicted distributions of some of the predicted trends reported in this thesis, such as such as outlined in section 7.4, could be ground-truthed allowing suggestions for additional or alternative benthic closed areas. A key dataset lacking from our analysis was a measure of sediment type. This is a significant omission, which if included, would likely influence our clustering and modelling results at medium to fine-scale. To a degree measures of topography likely act as effective surrogates in identifying hard-substrate environments, but the inclusion of sediment maps in the analysis would greatly enhance its value.

MPAs have increasingly become the paradigm of marine spatial protection (figure 1.1). Many recent designated or proposed MPAs, such as at Ascension Island (Nolan et al., 2017); Tristan da Cunha (JR287 Science Cruise Report, 2013) and the proposed Weddell Sea MPA (Teschke et al., 2017) represent regions that include available geophysical data, and in the case of the Weddell Sea, significant bio-physical analysis and interpretation. As such, the methodologies outlined in this thesis are unquestionably of application in these, and other, very large MPAs around the World.

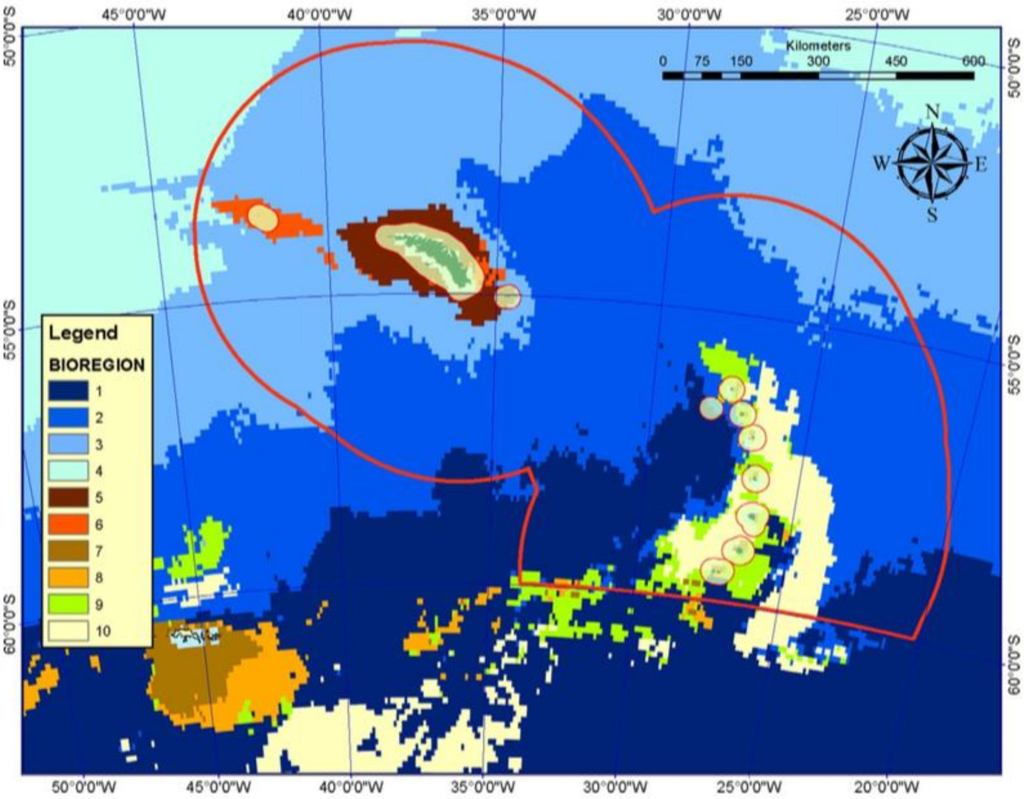
The final data chapter of this thesis explored the use of habitat suitability modelling, including not just taxonomic groups as response variables, but also functional groups. In recent years there has been increased use of functional traits as proxies for ecosystem services such as, for example, carbon sequestration (e.g. Barnes et al., 2017; also see Supplementary materials Appendix E). Functional traits and functional diversity indices are however rarely applied as a proxy for conservation importance. Habitat suitability modelling offers a methodology by which regions that provide most directly to ecosystem function and services can be identified. Considering the greater ease in which economic value can be assigned to specific ecosystem services and functions, and the direct link between services and human society, their application and the application of their modelling has potentially significant relevance to marine conservation.

7.7 Concluding remarks

Knowledge of the marine environment will, for the foreseeable future, remain patchy. Consequently marine spatial protection and frameworks for prioritising conservation will have to rely on an incomplete understanding of this environment; an understanding reliant on unsystematic records collected in a piecemeal fashion, often including historical data from grey literature for which sampling bias is unclear but inherent. Concurrently, as the World's population continues to increase, so too will pressures on the marine environment and its living resources. There is increasing need therefore for effective frameworks to help prioritise marine conservation in a manner that balances the protection of the marine environment, whilst offering ecosystem services and sustainable use of marine resources. Under such scenarios spatial and temporal prioritisation is fundamental to balancing the needs of multiple stakeholders whilst maximising conservation payoff.

Irrespective of changing conservation priorities, conservation efforts will rely on advances in habitat mapping to help inform these processes. The integrated approaches adopted in this thesis offer an applicable framework to utilise the respective benefits of top-down and bottom-up approaches to habitat mapping as a management blueprint for broad-scale informed protection of very large marine protected areas.

Appendix A: Chapter 2 Supplementary materials



Supplementary materials Figure 2.1. Bioregionalisation analysis of pelagic habitats at South Georgia and South Sandwich Islands MPA (from Trathan et al., 2014).

Supplementary materials Table 2.1. Bioregionalisation descriptions of pelagic habitats at South Georgia and South Sandwich Islands MPA (from Trathan et al., 2014).

Bioregion	Characteristics of the bioregion description	Bathymetry	Summer Chl-*a*	SST	SSH	Area (km)	Protected by the 12 nm closures (%)
1	South of SACCB	Mainly deep—4500 m	Low productivity	Coldest	Lowest	124,345.1	1.24
2	SACCB to SACCF	Mainly deep—3500 m	Mid productivity	Warmer	Mid level	471,525.7	0.39
3	SACCF to PF	Mainly deep—4000 m	Mid productivity	Warmer	High	328,471.6	0.14
4	North of PF	Mainly deep—4000 m	Low productivity	Warmest	Highest	8745.6	0.00
5	South Georgia shelf	Shelf	Productive	Warmer	High	33,026.6	31.20
6	Shag Rocks shelf	Deep shelf and shelf slope	Mid productivity	Warmer	Higher	12,005.2	26.49
7	South Scotia Arc shelf	Shelf	Productive	Cold	Low	2429.4	81.56
8	South Scotia Arc shelf slope	Shelf slope	Low productivity	Cold	Low	1156.9	22.07
9	Productive south of SACCF	Mid depth—2000 m	Productive	Cold	Low	29,348.2	20.23
10	Highly productive south of SACCF	Mainly deep—4500 m	Highly productive	Coldest	Lowest	54,324.7	9.81
	Total					1,070,266.6	

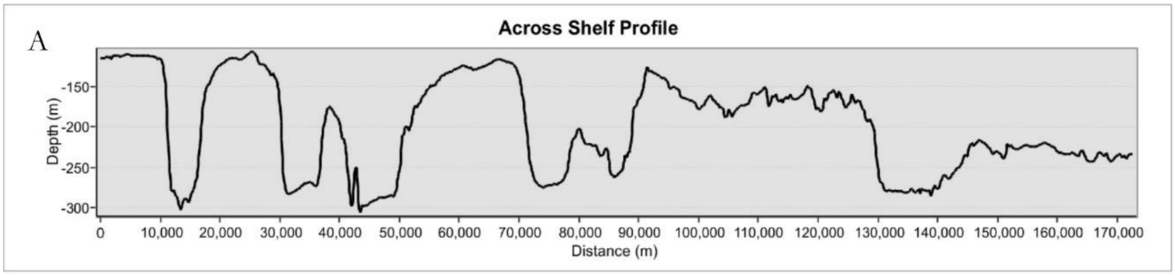
Appendix B: Chapter 4 Supplementary materials

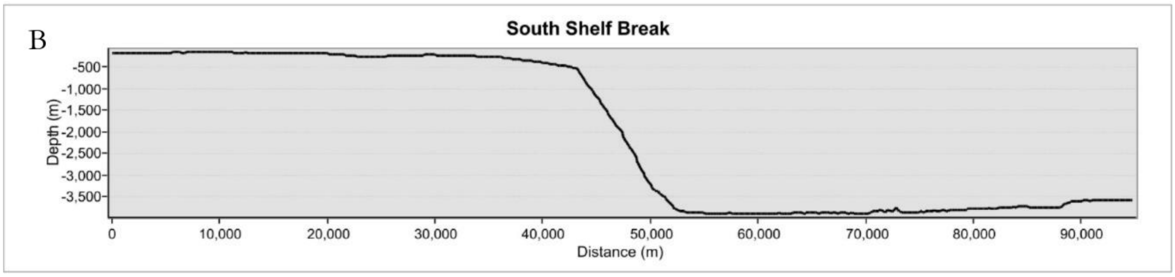
Supplementary materials Table 4.1. Data sets used in the South Georgia bathymetric compilation. BAS is the British Antarctic Survey; AWI is the Alfred Wegener Institute; UoT is the University of Texas; UKHO is the UK Hydrographic Office; GSGSSI is the Government of South Georgia & South Sandwich Islands; LDEO MGDS is the Lamont-Doherty Earth Observatory Marine Geoscience Data System; IACT is the Instituto Andaluz de Ciencias de la Tierra; GEBCO is The General Bathymetric Chart of the Oceans.

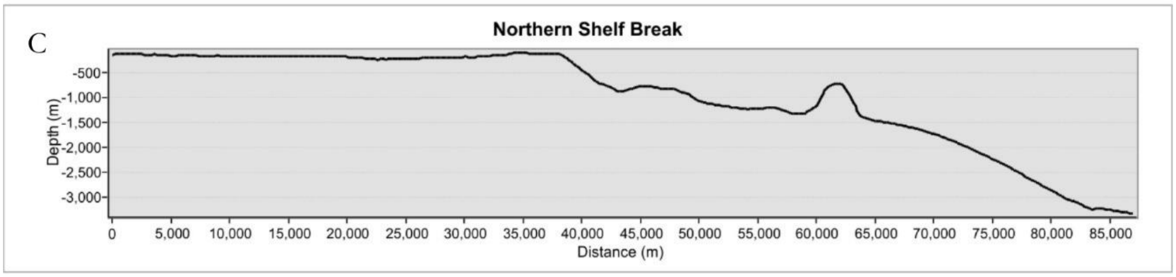
Survey ID	Data Type	Year	Source
BAS DATA			
JR287	Kongsberg EM122 multibeam	2013	BAS
JR257-272A-254E	Kongsberg EM122 multibeam	2012	BAS
JR262-260A	Kongsberg EM122 multibeam	2011	BAS
JR184	Kongsberg EK60 echo sounder	2007	BAS
JR168-167	Kongsberg EM120 multibeam	2007	BAS
JR167-168	Kongsberg EM120 multibeam	2007	BAS
JR161	Kongsberg EM120 multibeam	2006	BAS
JR152-159	Kongsberg EM120 multibeam	2006	BAS
JR149	Kongsberg EM120 multibeam	2006	BAS
JR151	Kongsberg EM120 multibeam	2006	BAS
JR134	Kongsberg EM120 multibeam	2005	BAS
JR114-121	Kongsberg EM120 multibeam	2005	BAS
JR134	Kongsberg EM120 multibeam	2005	BAS
JR130	Kongsberg EM120 multibeam	2005	BAS
JR77-78	Kongsberg EM120 multibeam	2004	BAS
JR107	Kongsberg EM120 multibeam	2004	BAS
JR109	Kongsberg EM120 multibeam	2004	BAS
JR116	Kongsberg EM120 multibeam	2004	BAS
JR82	Kongsberg EK60 echo sounder	2004	BAS
JR92	Kongsberg EK60 echo sounder	2003	BAS
JR93	Kongsberg EM120 multibeam	2003	BAS
JR100	Kongsberg EK60 echo sounder	2003	BAS
JR103	Kongsberg EM120 multibeam	2003	BAS
JR72	Kongsberg EM120 multibeam/EK500	2003	BAS
JR60	Kongsberg EK60 echo sounder	2002	BAS
JR69	Kongsberg EM120 multibeam	2001	BAS
AWI DATA			
ANT29_4	Hydrosweep DS3	2013	AWI
ANT29_5	Hydrosweep DS3	2013	AWI
ANT27_3	Hydrosweep DS3	2011	AWI
ANT23_5	Hydrosweep DS2	2006	AWI
ANT23_7	Hydrosweep DS2	2006	AWI
ANT22_4	Hydrosweep DS2	2005	AWI
ANT22_2	Hydrosweep DS2	2004	AWI
ANT19_4	Hydrosweep DS2	2002	AWI
ANT19_5	Hydrosweep DS2	2002	AWI
ANT18_4	Hydrosweep DS2	2001	AWI
ANT15_4	Hydrosweep DS2	1998	AWI
ANT14_3	Hydrosweep DS1	1997	AWI

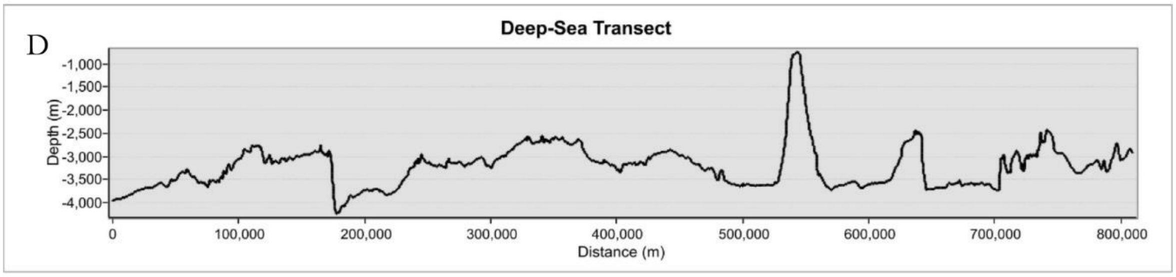
ANT15_2	Hydrosweep DS2	1997	AWI
ANT12_3	Hydrosweep DS1	1995	AWI
ANT11_3	Hydrosweep DS1	1994	AWI
ANT10_2	Hydrosweep DS1	1992	AWI
ANT10_5	Hydrosweep DS1	1992	AWI
ANT08_3	Hydrosweep DS1	1989	AWI
ANT08_5	Hydrosweep DS1	1989	AWI
ANT06_3	L3 ELAC Nautik SeaBeam	1987	AWI
ANT04_4	L3 ELAC Nautik SeaBeam	1986	AWI
ANT04_3	L3 ELAC Nautik SeaBeam	1985	AWI
OTHER CRUISES			
NBP 1408	Kongsberg EM122 multibeam	2014	UoT
BAS/UK Hydrographic Office tracks	Kongsberg EA600 single-beam	-	UKHO
HO chart no. 3596	Soundings from scanned charts	-	UKHO
HO chart no. 3597	Soundings from scanned charts	-	UKHO
Fisheries data	Single-beam echo sounders (FV Argos, Helena, FPV, Dorada)	2003-04/2015	GSGSSI
HMOI_1285	-	2009	BAS/UKHO
HMOI_1128	-	2006	BAS/UKHO
HMOI_1129	-	2006	BAS/UKHO
HMOI_1130	-	2006	BAS/UKHO
PRTR_Douglas_Strait	-	2014	HMS Protector
AMLR95	SeaBeam	1994	Surveyor
NBP9705	SeaBeam 2112	1997	LDEO MGDS
NBP0506	Kongsberg EM120 multibeam	2005	LDEO MGDS
NBP0603	Kongsberg EM120 multibeam	2006	LDEO MGDS
NBP0805	Kongsberg EM120 multibeam	2008	LDEO MGDS
Hes97	-	1996	IACT
GEBCO database	Global bathymetric compilation	2014	GEBCO [2014]

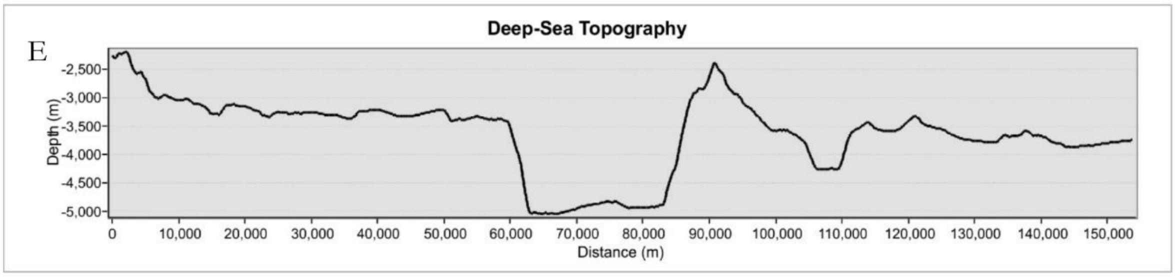
Supplementary materials Figure 4.1 (page 165). Depth profiles of new bathymetric compilation showing (A) Complex topography of the South Georgia shelf punctuated by cross shelf troughs, (B) Abrupt change in gradient of the southern South Georgia shelf break, (C) More gentle transition from shelf to slope at the northern South Georgia shelf-break, (D) Transect south of the island showing topographic complexity in the deep sea including sea mount, (E) Detail of deep-sea topographic feature, (F) Transect from Shag Rock (left) to South Georgia (right) showing deep 'Western Gully' divide between the two shelves.

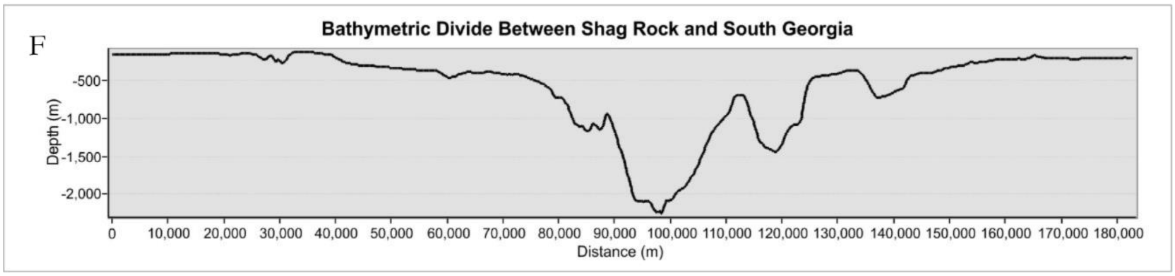

A
Across Shelf Profile
Depth (m)
-150
-200
-250
-300
0
10,000
20,000
30,000
40,000
50,000
60,000
70,000
80,000
90,000
100,000
110,000
120,000
130,000
140,000
150,000
160,000
170,000
Distance (m)

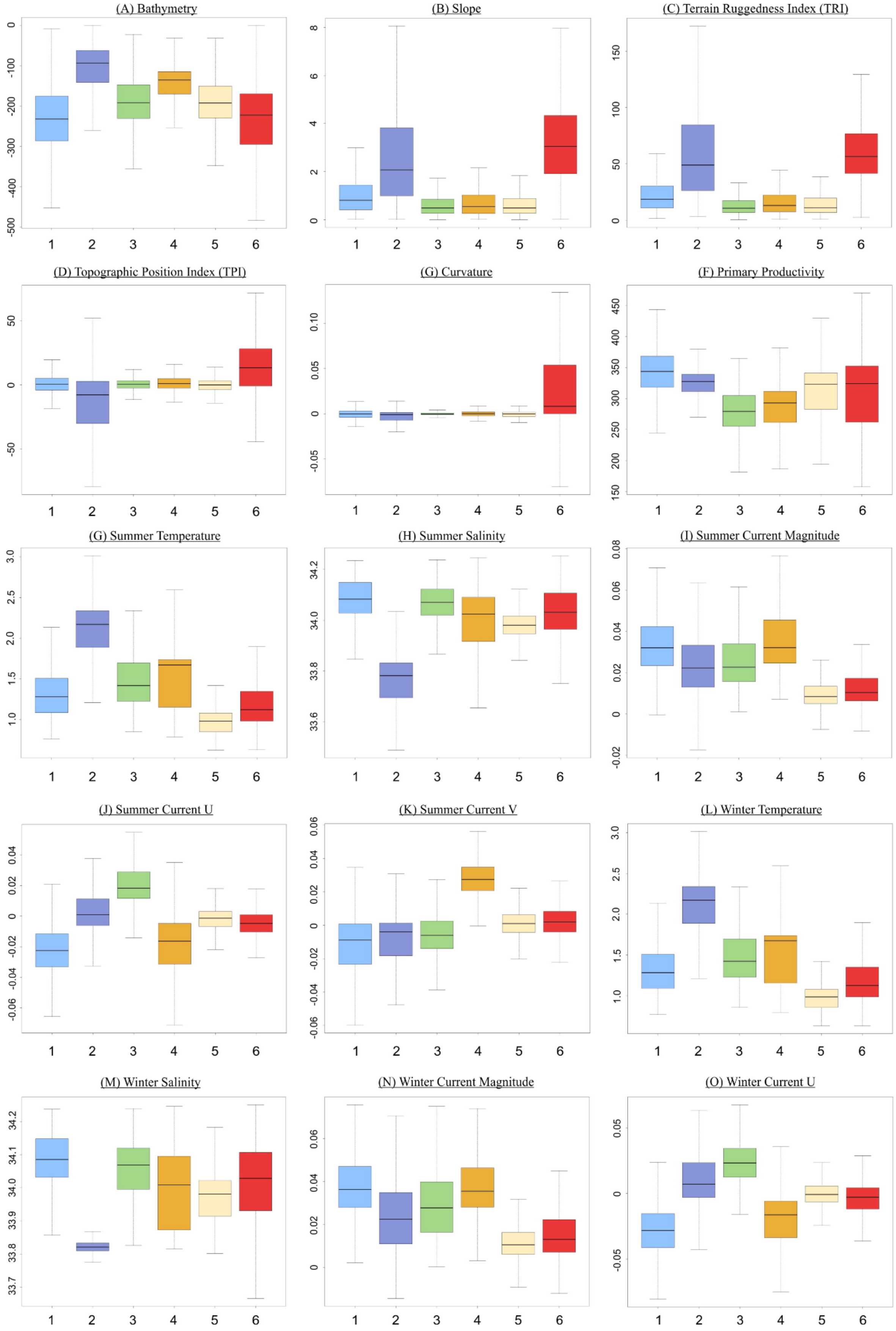

B
South Shelf Break
Depth (m)
-500
-1,000
-1,500
-2,000
-2,500
-3,000
-3,500
0
10,000
20,000
30,000
40,000
50,000
60,000
70,000
80,000
90,000
Distance (m)

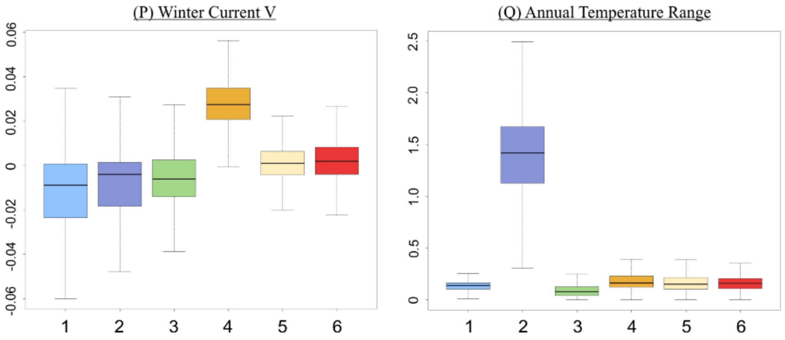

C
Northern Shelf Break
Depth (m)
-500
-1,000
-1,500
-2,000
-2,500
-3,000
0
5,000
10,000
15,000
20,000
25,000
30,000
35,000
40,000
45,000
50,000
55,000
60,000
65,000
70,000
75,000
80,000
85,000
Distance (m)


D
Deep-Sea Transect
Depth (m)
-1,000
-1,500
-2,000
-2,500
-3,000
-3,500
-4,000
0
100,000
200,000
300,000
400,000
500,000
600,000
700,000
800,000
Distance (m)

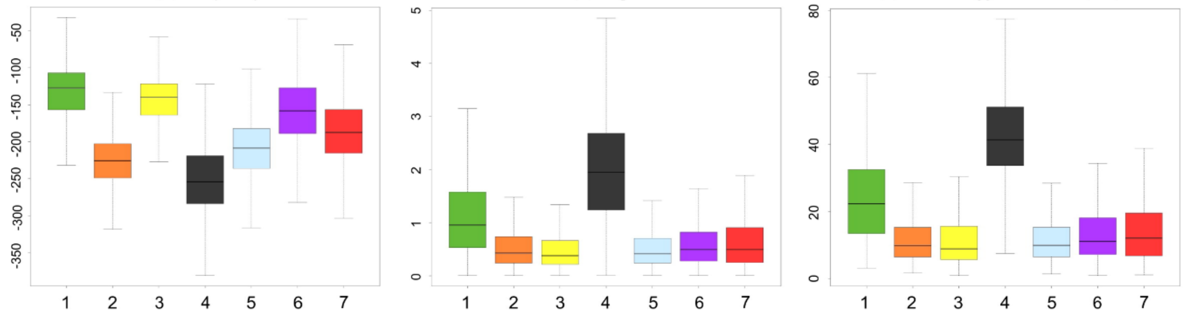

E
Deep-Sea Topography
Depth (m)
-2,500
-3,000
-3,500
-4,000
-4,500
-5,000
0
10,000
20,000
30,000
40,000
50,000
60,000
70,000
80,000
90,000
100,000
110,000
120,000
130,000
140,000
150,000
Distance (m)

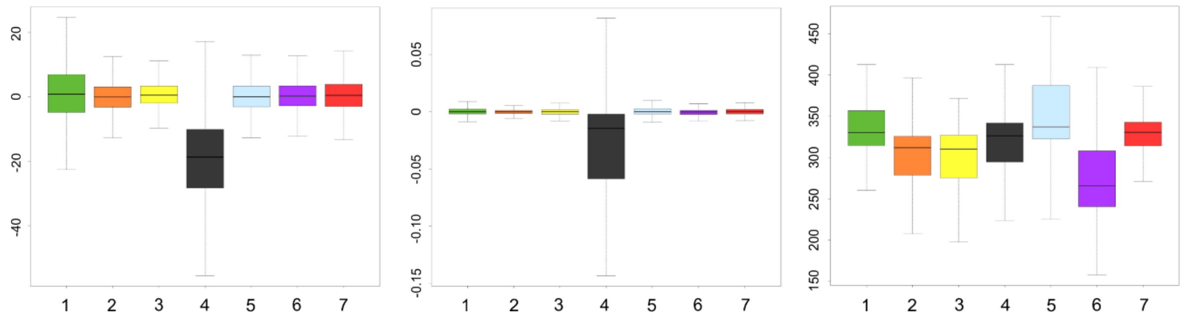

F
Bathymetric Divide Between Shag Rock and South Georgia
Depth (m)
-500
-1,000
-1,500
-2,000
0
10,000
20,000
30,000
40,000
50,000
60,000
70,000
80,000
90,000
100,000
110,000
120,000
130,000
140,000
150,000
160,000
170,000
180,000
Distance (m)

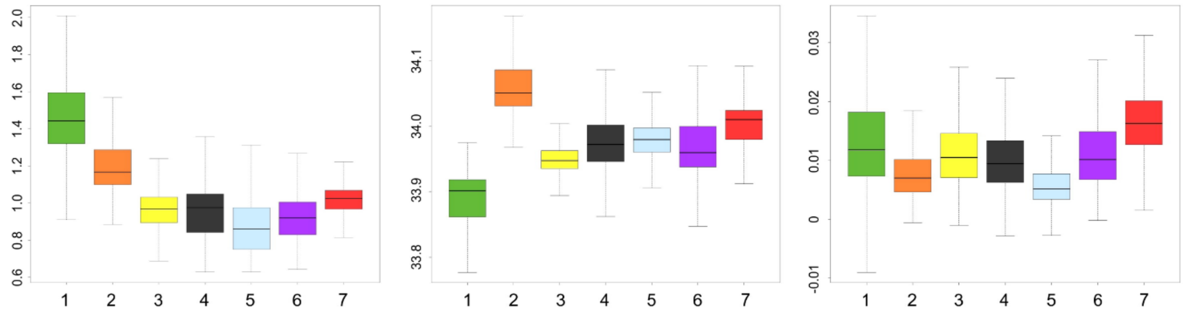

(A) Bathymetry
0
-100
-200
-300
-400
-500
1 2 3 4 5 6
(B) Slope
8
6
4
2
0
1 2 3 4 5 6
(C) Terrain Ruggedness Index (TRI)
150
100
50
0
1 2 3 4 5 6
(D) Topographic Position Index (TPI)
50
0
-50
1 2 3 4 5 6
(G) Curvature
0.10
0.05
0
-0.05
1 2 3 4 5 6
(F) Primary Productivity
450
400
350
300
250
200
150
1 2 3 4 5 6
(G) Summer Temperature
3.0
2.5
2.0
1.5
1.0
1 2 3 4 5 6
(H) Summer Salinity
34.2
34.0
33.8
33.6
1 2 3 4 5 6
(I) Summer Current Magnitude
0.08
0.06
0.04
0.02
0
-0.02
1 2 3 4 5 6
(J) Summer Current U
0.04
0.02
0
-0.02
-0.04
-0.06
1 2 3 4 5 6
(K) Summer Current V
0.06
0.04
0.02
0
-0.02
-0.04
-0.06
1 2 3 4 5 6
(L) Winter Temperature
3.0
2.5
2.0
1.5
1.0
1 2 3 4 5 6
(M) Winter Salinity
34.2
34.1
34.0
33.9
33.8
33.7
1 2 3 4 5 6
(N) Winter Current Magnitude
0.06
0.04
0.02
0
1 2 3 4 5 6
(O) Winter Current U
0.05
0
-0.05
1 2 3 4 5 6

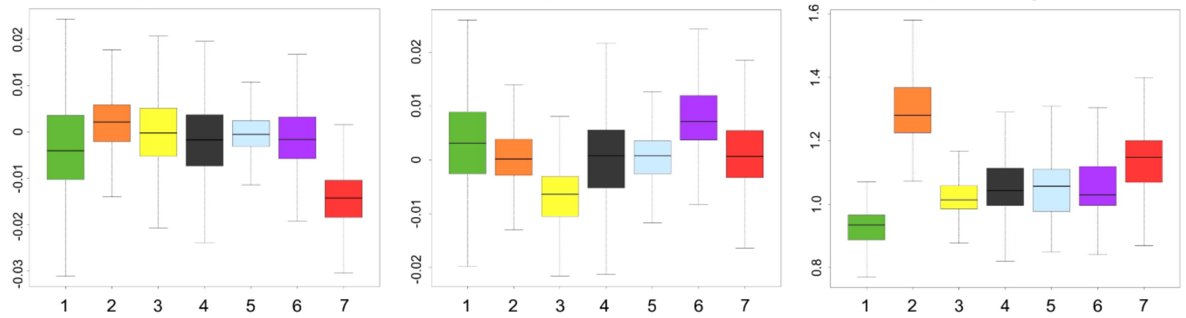


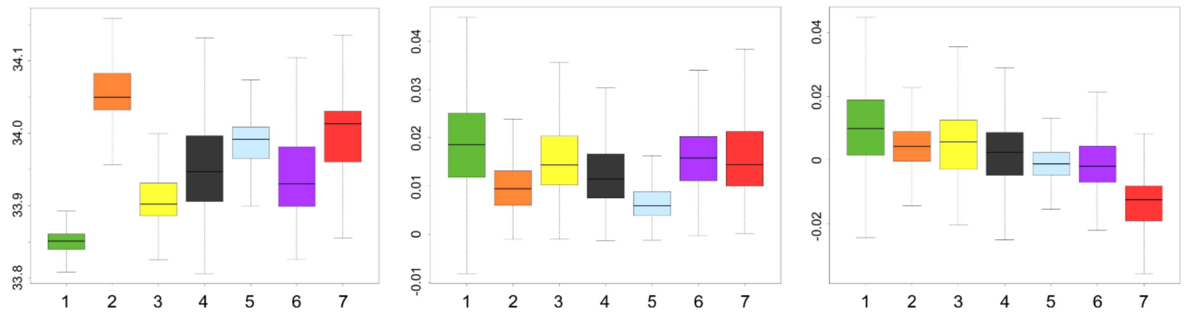
Supplementary materials Figure 4.2. Box plots of k-means derived clusters from sub-cluster 5 (Figure 4.5b) (X-axis) against the 17 original abiotic variables (excluding slope aspect) (Y-axis). Descriptions of each variable including their units are summarised in Table 4.1. In each box plot the middle line represents the median, the upper and lower extent of the box represent the first and third quartiles. The whiskers are the maximum and minimum observed values (excluding statistical outliers - values >1.5 x the interquartile range). Box plot colours denote the corresponding landscape map cluster colours from Figure 2.5b.

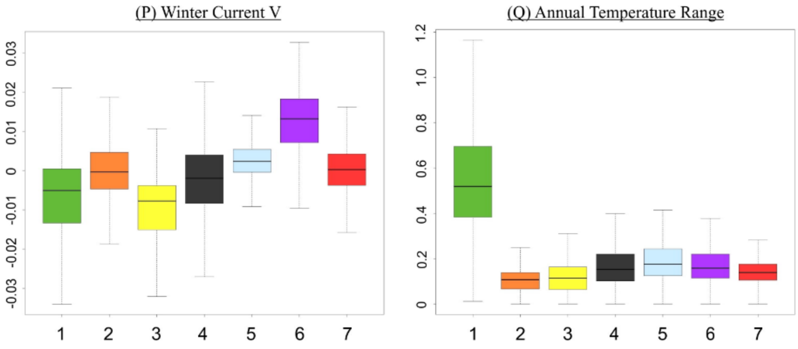

(A) Bathymetry (B) Slope (C) Terrain Ruggedness Index (TRI)


(D) Topographic Position Index (TPI) (G) Curvature (F) Primary Productivity


(G) Summer Temperature (H) Summer Salinity (I) Summer Current Magnitude


(J) Summer Current U (K) Summer Current V (L) Winter Temperature


(M) Winter Salinity (N) Winter Current Magnitude (O) Winter Current U



Supplementary materials Figure 4.3. Box plots of k-means derived clusters from re-clustering of cluster 5 of sub-cluster 5 (Figure 4.5c) (X-axis) against the 17 original abiotic variables (excluding slope aspect) (Y-axis). Descriptions of each variable including their units are summarised in Table 4.1. In each box plot the middle line represents the median, the upper and lower extent of the box represent the first and third quartiles. The whiskers are the maximum and minimum observed values (excluding statistical outliers - values >1.5 x the interquartile range). Box plot colours denote the corresponding landscape map cluster colours from Figure 5c.

Appendix C: Chapter 5 Supplementary materials

Supplementary materials Table 5.1a. Summary of biological records by level 2 cluster

Cluster	Stations	Records	Phylum	Class	Order	Family	Genus	Species
Cluster 5.1	418	1740	11	25	42	121	176	225
Cluster 5.2	318	2411	18	40	57	182	305	479
Cluster 5.3	160	1235	9	19	32	70	96	113
Cluster 5.4	215	1490	9	22	40	113	154	207
Cluster 5.5	1887	9492	14	38	74	222	368	572
Cluster 5.6	315	1309	15	35	62	165	247	352

Supplementary materials Table 5.1b. Summary of distinct taxa (cluster specific) by level 2 cluster

Cluster	Phylum	Class	Order	Family	Genus	Species	Singletons	& Doubletons
Cluster 5.1	0	0	0	1	9	20	15	28
Cluster 5.2	1	5	5	68	145	337	218	397
Cluster 5.3	0	0	0	1	1	2	2	3
Cluster 5.4	0	0	0	17	7	16	15	32
Cluster 5.5	0	3	3	3	55	152	113	251
Cluster 5.6	0	0	2	5	22	63	58	113

Supplementary materials Table 5.1c. Summary of the functional traits of biological records by level 2 cluster

Cluster	**Reef-building**		**Substrate**			**Mobility**		**Dispersal**	
	Yes	No	Hard	Soft	Cosmo	Sessile	Mobile	Pelagic	Non-pelagic
Cluster 5.1	30	288	148	18	48	133	218	191	228
Cluster 5.2	48	1234	404	198	133	341	1003	624	811
Cluster 5.3	2	274	37	5	18	22	259	69	239
Cluster 5.4	6	405	73	3	23	57	368	88	338
Cluster 5.5	131	1346	656	101	155	643	1021	775	1085
Cluster 5.6	24	434	120	42	50	108	368	164	305

Supplementary materials Table 5.2c. Summary of the functional traits of biological records by level 3 cluster

Cluster	**Reef-building**		**Substrate**			**Mobility**		**Dispersal**	
	Yes	No	Hard	Soft	Cosmo	Sessile	Mobile	Pelagic	Non-pelagic
Cluster 5.5.1	6	31	39	4	3	40	23	44	44
Cluster 5.5.2	7	135	40	4	22	38	114	58	111
Cluster 5.5.3	34	298	204	21	12	198	192	195	233
Cluster 5.5.4	6	161	62	29	17	54	126	86	101
Cluster 5.5.5	18	354	132	19	42	135	285	182	282
Cluster 5.5.6	6	116	50	4	16	48	89	60	82
Cluster 5.5.7	36	232	105	20	22	105	180	125	205

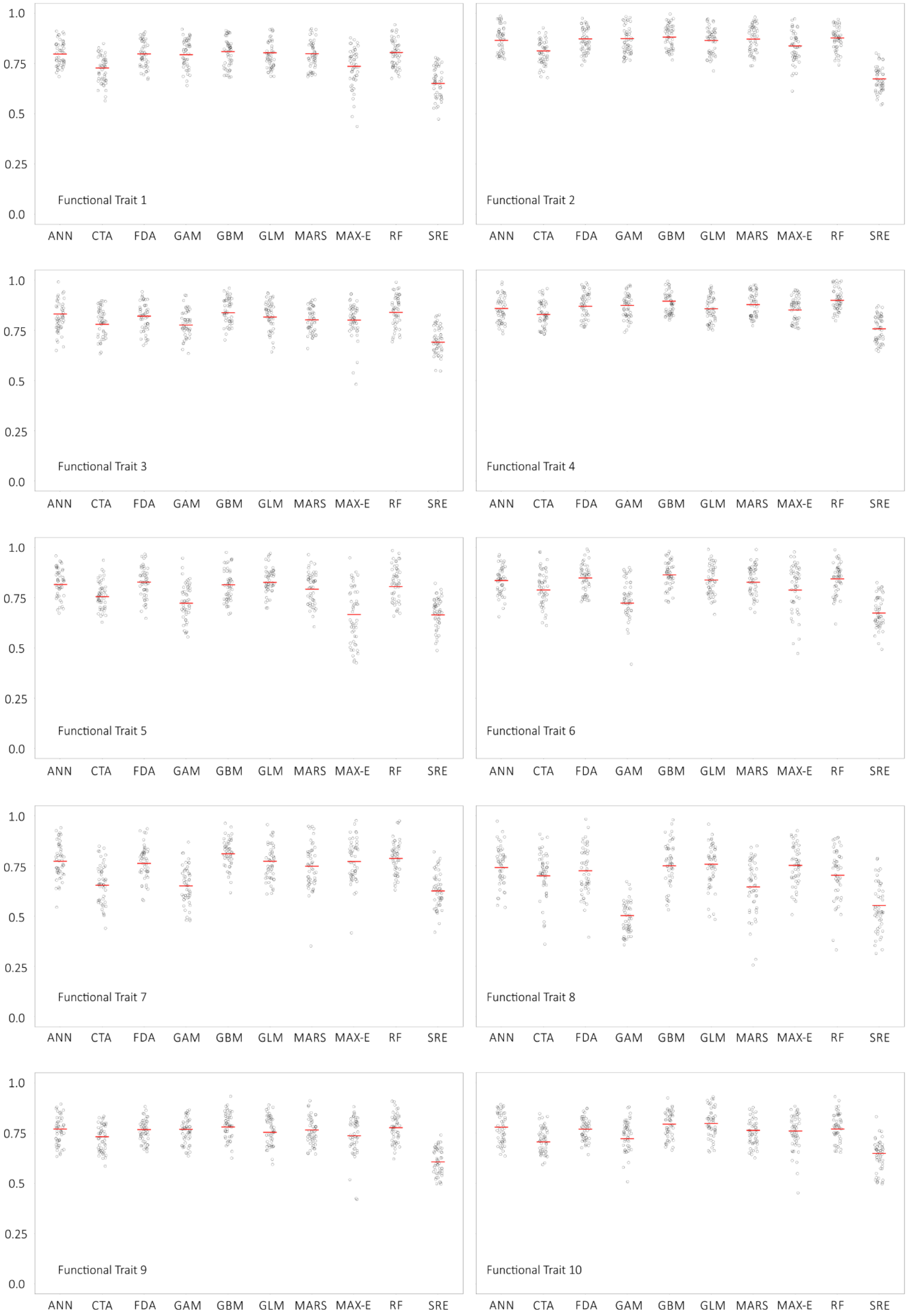
Supplementary materials Table 5.2a. Summary of biological records by level 3 cluster

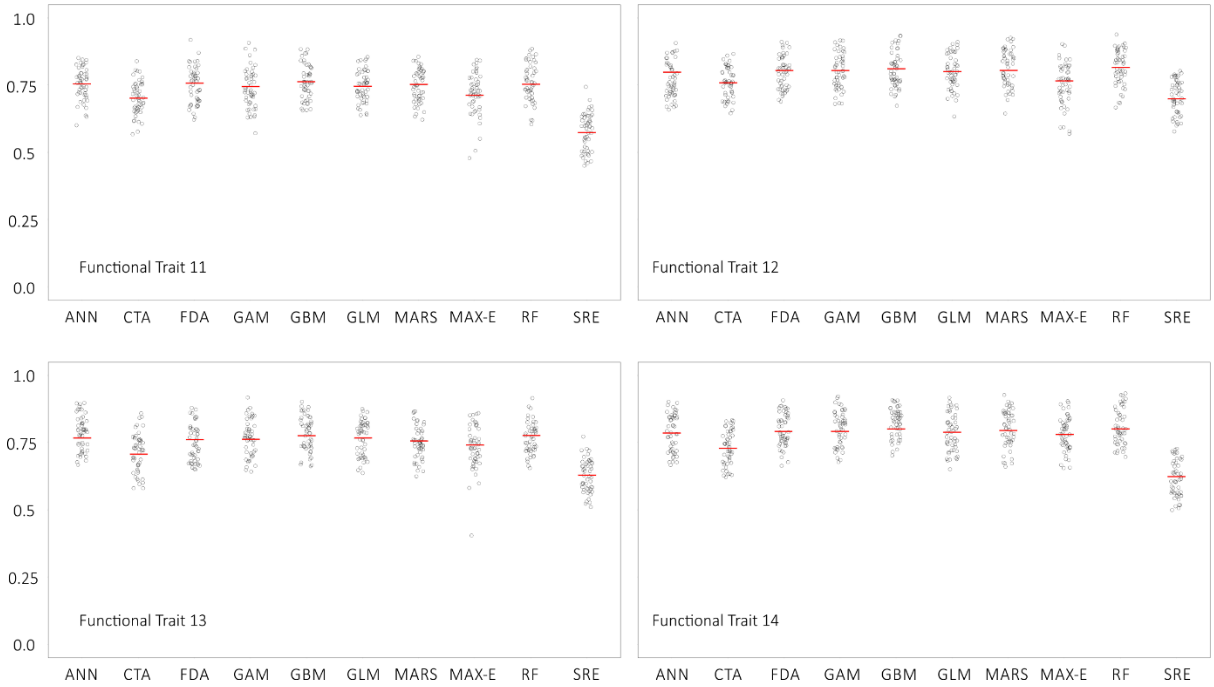
Cluster	Stations	Records	Phylum	Class	Order	Family	Genus	Species
Cluster 5.5.1	41	174	8	16	22	55	75	84
Cluster 5.5.2	191	1093	11	21	37	90	123	152
Cluster 5.5.3	209	1434	12	29	52	137	212	316
Cluster 5.5.4	109	617	13	27	48	120	163	205
Cluster 5.5.5	770	3401	13	31	51	136	213	289
Cluster 5.5.6	241	1087	10	23	38	89	118	164
Cluster 5.5.7	321	1637	11	28	51	120	177	232

Supplementary materials Table 5.2b. Summary of distinct taxa (cluster specific) by level 3 cluster

Cluster	Phylum	Class	Order	Family	Genus	Species	Singletons	& Doubletons
Cluster 5.5.1	0	1	0	1	2	2	2	6
Cluster 5.5.2	0	0	0	0	0	6	4	12
Cluster 5.5.3	0	1	1	1	7	33	39	65
Cluster 5.5.4	0	0	0	2	6	13	23	48
Cluster 5.5.5	0	0	1	2	3	11	14	41
Cluster 5.5.6	0	0	0	0	1	8	7	18
Cluster 5.5.7	0	0	1	4	9	15	21	50

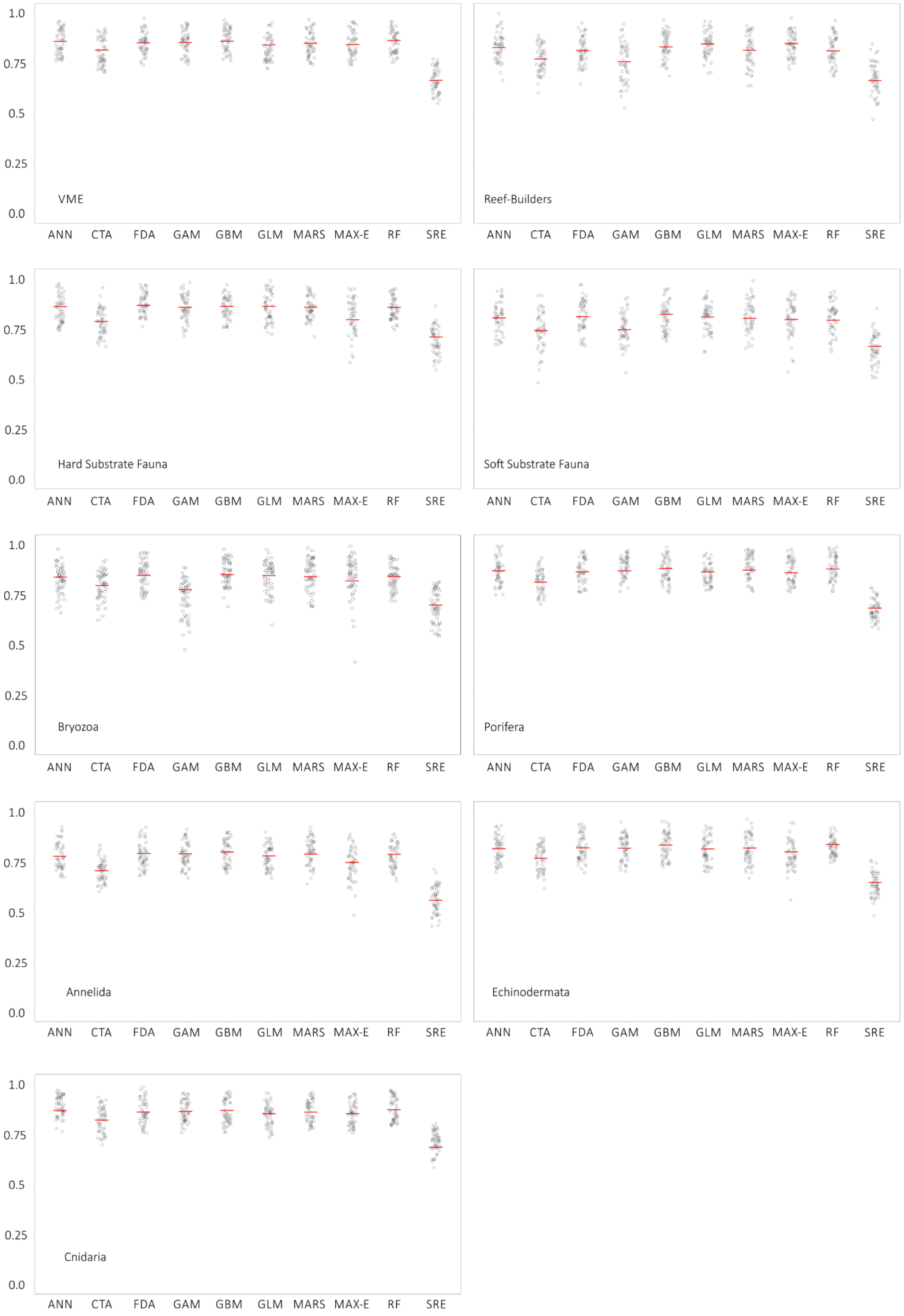
Appendix D: Chapter 6 Supplementary materials

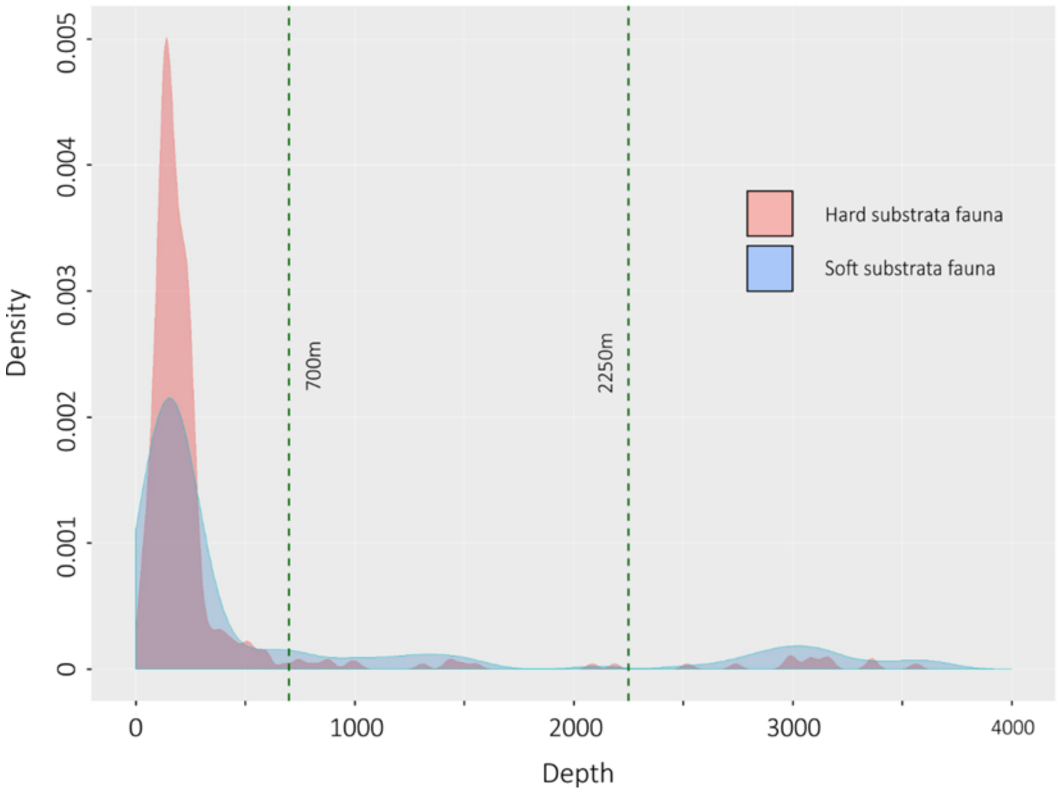




Supplementary materials Figure 6.1. Receiver operating characteristic (ROC) plots for 14 modelled functional traits (Figure 6.4) showing model performance of each run of the 10 modelling algorithms summarised in Table 3. Mean ROC value for each algorithm is shown as a red bar.

Supplementary materials Figure 6.2 (page 177). Receiver operating characteristic (ROC) plots for taxonomic and trait-based metrics (Figure 6.5) showing model performance of each run of the 10 modelling algorithms summarised in Table 6.2. Mean ROC value for each algorithm is shown as a red bar.


VME
Reef-Builders
Hard Substrate Fauna
Soft Substrate Fauna
Bryozoa
Porifera
Annelida
Echinodermata
Cnidaria
1.0
0.75
0.5
0.25
0.0
ANN
CTA
FDA
GAM
GBM
GLM
MARS
MAX-E
RF
SRE



Supplementary materials Figure 6.3. Kernel density plot of sampling distribution of benthic fauna with an exclusive affinity to hard or soft substrate at South Georgia. Hard substrate fauna symbolised in red (n=378) and soft substrate fauna in blue (n=155). Dashed green lines at 700 and 2250m denote the upper and lower limit respectively of the open fisheries area.

Supplementary materials Table 6.1. Variable importance for each model and for each functional trait response variable calculated as a mean across all model runs. PC1-PC7 refer to the principal components outlined in Table 6.4 and used in the ensemble modelling. The most significant drivers of each model are highlighted in bold green. Where a model has multiple variables driving its distribution these are also highlighted.

Trait 1	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	**0.75**	**0.69**	**0.74**	**0.79**	**0.82**	**0.69**	**0.74**	**0.72**	**0.46**	**0.82**
PC2	0.07	0.11	0.01	0.08	0.04	0.08	0.00	0.05	0.04	0.00
PC3	0.01	0.04	0.02	0.00	0.07	0.07	0.00	0.04	0.04	0.00
PC4	0.03	0.06	0.07	0.16	0.15	0.11	0.10	0.06	0.10	0.05
PC5	0.27	0.23	0.11	0.14	0.25	0.05	**0.36**	**0.31**	0.12	0.08
PC6	0.01	0.05	0.01	0.00	0.02	0.09	0.00	0.00	0.03	0.00
PC7	0.00	0.00	0.01	0.05	0.05	0.15	0.00	0.00	0.03	0.00

Trait 2	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	0.10	0.28	0.11	0.00	0.13	**0.51**	**0.21**	**0.27**	0.14	**0.22**
PC2	0.02	0.01	0.00	0.00	0.04	0.05	0.02	0.01	0.02	0.09
PC3	0.01	0.01	0.01	0.00	0.03	0.07	0.00	0.00	0.02	0.10
PC4	**0.32**	0.20	0.28	**0.49**	**0.38**	0.25	**0.22**	**0.25**	**0.21**	**0.44**
PC5	**0.39**	0.21	0.29	**0.58**	**0.38**	0.16	**0.22**	**0.27**	**0.18**	**0.23**
PC6	0.00	0.00	0.01	0.00	0.01	0.09	0.00	0.00	0.02	0.05
PC7	0.02	0.03	0.02	0.00	0.04	0.11	0.03	0.04	0.04	0.06

Trait 3	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	**0.89**	**0.70**	**0.89**	**0.99**	**1.00**	**0.66**	**0.98**	**0.87**	**0.65**	**0.96**
PC2	0.10	**0.30**	0.02	0.00	0.00	0.21	0.00	0.17	0.04	0.05
PC3	0.04	0.16	0.04	0.00	0.14	0.11	0.00	0.12	0.03	0.02
PC4	0.01	0.10	0.01	0.00	0.04	0.06	0.00	0.00	0.04	0.01
PC5	0.09	0.18	0.10	0.00	0.15	0.04	0.00	0.17	0.06	0.07
PC6	0.00	0.14	0.01	0.00	0.04	0.13	0.00	0.00	0.03	0.03
PC7	0.04	0.10	0.09	0.00	0.05	0.06	0.00	0.06	0.09	0.06

Trait 4	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	**0.80**	**0.79**	**0.85**	**0.83**	**0.76**	**0.55**	**0.85**	**0.83**	**0.68**	**0.77**
PC2	0.09	0.12	0.07	0.18	0.16	0.18	0.02	0.03	0.10	0.17
PC3	0.00	0.03	0.00	0.00	0.07	0.08	0.01	0.01	0.03	0.07
PC4	0.01	0.01	0.01	0.00	0.06	0.10	0.02	0.02	0.04	0.05
PC5	0.02	0.05	0.02	0.00	0.09	0.12	0.03	0.02	0.05	0.12
PC6	0.00	0.00	0.00	0.00	0.01	0.11	0.00	0.00	0.02	0.03
PC7	0.07	0.06	0.03	0.00	0.13	0.10	0.03	0.05	0.06	0.13

Trait 5	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	**0.79**	**0.67**	**0.89**	**0.98**	**0.91**	**0.43**	**0.92**	**0.75**	**0.61**	**0.49**
PC2	0.18	**0.33**	0.05	0.00	0.22	0.23	0.06	0.27	0.08	0.19
PC3	0.08	0.08	0.04	0.00	0.11	0.22	0.00	0.00	0.03	0.00
PC4	0.09	**0.24**	0.08	0.00	0.03	0.07	0.00	0.11	0.06	0.27
PC5	0.00	0.14	0.02	0.00	0.06	0.14	0.00	0.00	0.07	**0.41**
PC6	0.03	0.16	0.03	0.00	0.02	0.09	0.00	0.00	0.03	0.13
PC7	0.07	0.13	0.03	0.00	0.05	0.16	0.04	0.07	0.07	0.32

Trait 6	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	**0.99**	**0.85**	**0.85**	**1.00**	**0.85**	**0.54**	**0.97**	**0.89**	**0.62**	**0.66**
PC2	0.00	**0.44**	0.03	0.00	0.17	**0.33**	0.00	0.00	0.02	0.21
PC3	0.01	**0.37**	0.01	0.00	0.01	0.16	0.00	0.00	0.01	0.21
PC4	0.04	**0.42**	0.05	0.00	0.09	0.11	0.02	0.12	0.05	**0.50**
PC5	0.00	**0.35**	0.04	0.00	0.04	0.16	0.08	0.20	0.08	**0.43**
PC6	0.01	0.24	0.01	0.00	0.04	0.07	0.00	0.00	0.02	0.10
PC7	0.06	0.28	0.02	0.00	0.09	0.05	0.01	0.05	0.04	0.28

Trait 7	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	**0.81**	**0.63**	**0.68**	**1.00**	**0.84**	**0.62**	**0.80**	**0.59**	**0.53**	**0.81**
PC2	**0.30**	**0.41**	0.05	0.00	0.22	0.19	0.00	**0.34**	0.07	0.15
PC3	0.05	**0.40**	0.06	0.00	0.01	0.16	0.00	0.12	0.04	0.06
PC4	0.14	0.21	0.14	0.00	0.17	0.11	0.00	0.08	0.03	0.11
PC5	0.04	**0.50**	0.07	0.00	0.17	0.07	0.00	**0.26**	0.11	0.09
PC6	0.01	0.09	0.08	0.00	0.06	0.04	0.00	0.00	0.04	0.03
PC7	0.01	**0.35**	0.06	0.00	0.03	0.18	**0.24**	0.06	0.11	0.04

Trait 8	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	**0.79**	**0.77**	**0.67**	**1.00**	**0.71**	**0.56**	**1.00**	**0.55**	**0.30**	**0.60**
PC2	0.13	**0.41**	0.14	0.00	**0.40**	0.18	0.00	0.00	0.12	0.06
PC3	0.04	**0.51**	0.06	0.00	**0.35**	0.13	0.00	0.12	0.11	0.04
PC4	**0.38**	**0.53**	0.17	0.00	**0.39**	0.18	0.00	**0.66**	0.12	**0.29**
PC5	0.24	**0.69**	0.23	0.00	**0.48**	0.17	0.00	0.12	0.15	0.19
PC6	0.11	**0.43**	0.14	0.00	**0.32**	**0.30**	0.00	0.00	0.05	0.01
PC7	0.01	**0.72**	0.05	0.00	**0.40**	**0.27**	0.00	0.23	0.06	0.00

Trait 9	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	**0.23**	**0.34**	**0.54**	**0.59**	**0.33**	**0.50**	**0.48**	**0.63**	**0.33**	**0.42**
PC2	0.00	0.04	0.04	0.04	0.07	0.09	0.00	0.00	0.05	0.07
PC3	0.00	0.01	0.01	0.09	0.09	0.08	0.00	0.00	0.04	0.01
PC4	0.31	0.27	0.14	0.34	**0.31**	0.14	0.17	0.11	0.16	0.12
PC5	**0.42**	**0.25**	0.12	0.24	**0.56**	0.12	0.09	0.05	0.20	0.15
PC6	0.03	0.03	0.03	0.04	0.07	0.14	0.00	0.00	0.05	0.00
PC7	0.00	0.01	0.02	0.13	0.05	0.12	0.03	0.03	0.05	0.01

Trait 10	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	**0.69**	**0.64**	**0.67**	**0.96**	**0.71**	**0.75**	**0.58**	**0.79**	**0.34**	**0.58**
PC2	0.22	**0.41**	0.15	0.00	0.19	0.12	0.00	0.26	0.12	0.12
PC3	0.11	0.19	0.02	0.00	0.06	0.07	0.00	0.12	0.04	0.01
PC4	0.00	0.14	0.02	0.00	0.03	0.03	0.20	0.10	0.08	0.12
PC5	0.08	**0.24**	0.22	0.00	**0.36**	0.11	0.00	0.00	0.16	0.11
PC6	0.08	**0.24**	0.09	0.00	0.08	0.11	0.18	0.16	0.08	0.10
PC7	0.05	0.14	0.03	0.00	0.03	0.09	0.13	0.06	0.10	0.11

Trait 11	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	**0.92**	**0.88**	**0.80**	**1.00**	**0.76**	**0.24**	**0.76**	**0.91**	**0.49**	**0.73**
PC2	0.00	0.02	0.01	0.00	0.04	**0.27**	0.00	0.00	0.05	0.03
PC3	0.03	0.02	0.02	0.00	0.07	0.12	0.00	0.00	0.04	0.01
PC4	0.00	0.07	0.01	0.00	0.14	0.05	0.00	0.00	0.04	0.02
PC5	0.04	0.08	0.07	0.00	**0.30**	0.07	0.14	0.00	0.11	0.14
PC6	0.00	0.03	0.02	0.00	0.17	**0.22**	0.00	0.00	0.05	0.04
PC7	0.04	0.05	0.06	0.00	0.19	0.19	0.07	0.11	0.10	0.07

Trait 12	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	**0.94**	**0.88**	**0.89**	**0.99**	**0.82**	**0.55**	**0.92**	**0.89**	**0.67**	**0.87**
PC2	0.04	0.05	0.04	0.00	0.14	0.14	0.03	0.03	0.09	0.09
PC3	0.00	0.00	0.01	0.00	0.07	0.08	0.00	0.00	0.05	0.03
PC4	0.01	0.01	0.00	0.00	0.06	0.08	0.01	0.00	0.06	0.01
PC5	0.09	0.10	0.05	0.13	0.20	0.11	0.08	0.09	0.10	0.12
PC6	0.00	0.00	0.00	0.00	0.05	0.13	0.00	0.00	0.05	0.02
PC7	0.01	0.02	0.02	0.04	0.07	0.13	0.02	0.02	0.05	0.03

Trait 13	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	**0.60**	**0.63**	**0.59**	**0.85**	**0.48**	**0.53**	**0.50**	**0.57**	**0.37**	**0.51**
PC2	0.00	0.00	0.01	0.00	0.04	0.10	0.00	0.00	0.04	0.02
PC3	0.02	0.02	0.02	0.00	0.07	0.08	0.02	0.02	0.04	0.11
PC4	0.07	0.03	0.03	0.00	0.17	0.09	0.05	0.06	0.06	0.06
PC5	**0.30**	**0.31**	0.17	0.11	**0.47**	0.15	**0.49**	**0.35**	**0.23**	0.21
PC6	0.00	0.00	0.00	0.00	0.04	0.10	0.00	0.00	0.02	0.01
PC7	0.05	0.06	0.07	0.12	0.12	0.13	0.05	0.05	0.08	0.13

Trait 14	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	0.22	**0.35**	0.25	0.29	0.19	**0.53**	0.23	**0.38**	0.25	0.27
PC2	0.01	0.03	0.01	0.02	0.09	0.10	0.02	0.03	0.07	0.03
PC3	0.02	0.02	0.00	0.00	0.07	0.09	0.00	0.01	0.03	0.02
PC4	0.14	0.12	0.08	0.10	0.18	0.08	0.08	0.07	0.13	0.15
PC5	**0.66**	**0.46**	**0.48**	**0.58**	**0.76**	0.15	**0.59**	**0.40**	**0.35**	**0.48**
PC6	0.00	0.01	0.00	0.00	0.01	0.12	0.00	0.00	0.04	0.02
PC7	0.00	0.00	0.00	0.00	0.08	0.14	0.00	0.00	0.04	0.02

Supplementary materials Table 6.2. Variable importance for each model and for each taxa and trait-based response variable calculated as a mean across all model runs. PC1-PC7 refer to the principal components outlined in Table 6.4 and used in the ensemble modelling. The most significant drivers of each model are highlighted in bold green. Where a model has multiple variables driving its distribution these are also highlighted.

Bryozoa	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	**0.55**	**0.44**	**0.52**	**0.72**	**0.64**	**0.45**	**0.40**	**0.43**	**0.31**	**0.40**
PC2	0.00	0.00	0.01	0.00	0.07	0.12	0.00	0.00	0.03	0.00
PC3	0.00	0.05	0.03	0.00	0.00	0.14	0.00	0.08	0.04	0.00
PC4	0.05	0.04	0.04	0.00	0.02	0.06	0.05	0.00	0.08	0.16
PC5	0.26	**0.32**	0.16	0.19	**0.42**	0.05	**0.42**	**0.41**	0.21	**0.26**
PC6	0.01	0.01	0.02	0.00	0.00	0.10	0.00	0.00	0.03	0.06
PC7	0.13	0.12	0.11	0.21	0.13	**0.28**	0.18	0.12	0.11	0.19

Cnidaria	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	0.04	0.19	0.12	0.19	**0.40**	**0.52**	0.16	**0.21**	0.19	0.16
PC2	0.01	0.01	0.00	0.00	0.04	0.07	0.01	0.01	0.04	0.03
PC3	0.00	0.01	0.00	0.00	0.02	0.08	0.00	0.00	0.02	0.02
PC4	**0.26**	0.17	0.19	**0.25**	**0.28**	0.17	0.15	0.15	0.16	0.20
PC5	**0.56**	**0.31**	**0.42**	**0.66**	0.13	0.19	**0.31**	**0.26**	**0.30**	**0.33**
PC6	0.00	0.00	0.00	0.00	0.02	0.09	0.00	0.00	0.02	0.01
PC7	0.00	0.00	0.00	0.00	0.02	0.10	0.00	0.00	0.03	0.03

Annelida	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	0.02	0.20	0.09	0.00	**0.26**	**0.52**	0.16	**0.24**	0.17	**0.57**
PC2	0.01	0.01	0.00	0.00	0.05	0.07	0.01	0.02	0.04	0.31
PC3	0.00	0.01	0.00	0.00	0.01	0.08	0.00	0.00	0.02	0.05
PC4	0.26	0.16	0.18	**0.26**	**0.24**	0.17	0.12	0.13	0.16	**0.31**
PC5	**0.60**	**0.34**	**0.45**	**0.78**	**0.28**	0.18	**0.32**	**0.24**	**0.34**	**0.88**
PC6	0.01	0.00	0.00	0.00	0.01	0.10	0.01	0.01	0.03	0.16
PC7	0.00	0.01	0.01	0.00	0.03	0.10	0.00	0.01	0.05	0.17

Echinodermata	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	0.11	**0.27**	0.09	0.04	0.16	**0.57**	0.09	**0.24**	0.17	0.19
PC2	0.00	0.01	0.01	0.00	0.07	0.08	0.01	0.02	0.05	0.04
PC3	0.01	0.02	0.00	0.01	0.03	0.07	0.00	0.00	0.03	0.01
PC4	0.19	0.14	0.13	0.20	**0.27**	0.12	0.11	0.13	0.14	0.13
PC5	**0.61**	**0.53**	**0.55**	**0.83**	**0.62**	0.20	**0.66**	**0.51**	**0.40**	**0.41**
PC6	0.00	0.00	0.00	0.00	0.01	0.09	0.00	0.00	0.03	0.01
PC7	0.00	0.00	0.00	0.00	0.05	0.11	0.00	0.00	0.04	0.02

Porifera	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	0.18	0.19	0.10	0.12	0.15	**0.48**	0.15	**0.31**	0.13	**0.21**
PC2	0.01	0.02	0.01	0.03	0.02	0.06	0.00	0.00	0.02	0.08
PC3	0.00	0.00	0.00	0.00	0.01	0.08	0.00	0.00	0.01	0.03
PC4	**0.30**	**0.26**	**0.29**	**0.37**	**0.42**	**0.30**	**0.31**	**0.23**	**0.22**	**0.29**
PC5	**0.31**	**0.32**	**0.32**	**0.46**	**0.34**	0.17	**0.24**	0.18	**0.24**	**0.23**
PC6	0.00	0.01	0.00	0.02	0.03	0.10	0.00	0.00	0.01	0.03
PC7	0.04	0.04	0.03	0.11	0.05	0.12	0.03	0.05	0.06	0.17

VME	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	0.04	**0.25**	0.12	0.00	**0.20**	**0.53**	0.14	**0.27**	**0.21**	0.17
PC2	0.01	0.01	0.01	0.00	0.04	0.07	0.02	0.03	0.05	0.04
PC3	0.01	0.02	0.00	0.00	0.04	0.08	0.01	0.01	0.03	0.04
PC4	**0.29**	0.18	0.19	**0.22**	**0.32**	0.18	0.16	0.15	0.14	0.18
PC5	**0.57**	**0.36**	**0.41**	**0.83**	**0.36**	0.19	**0.35**	**0.24**	**0.30**	**0.37**
PC6	0.00	0.01	0.01	0.00	0.04	0.11	0.01	0.00	0.03	0.03
PC7	0.00	0.00	0.00	0.00	0.01	0.11	0.00	0.00	0.03	0.02

Reef	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	**0.86**	**0.87**	**0.92**	**1.00**	**0.96**	**0.72**	**0.83**	**0.95**	**0.71**	**0.83**
PC2	0.09	**0.41**	0.02	0.00	0.04	0.13	0.00	0.14	0.06	0.23
PC3	0.09	**0.38**	0.07	0.00	0.12	0.12	0.00	0.03	0.03	**0.31**
PC4	0.04	0.25	0.07	0.00	0.20	0.05	0.06	0.02	0.04	0.29
PC5	**0.27**	**0.48**	0.13	0.00	0.18	0.08	0.06	0.27	0.12	**0.53**
PC6	0.00	0.13	0.01	0.00	0.08	0.10	0.00	0.00	0.03	0.24
PC7	0.07	**0.40**	0.03	0.00	0.09	0.13	0.00	0.04	0.06	**0.33**

Hard	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	**0.85**	**0.90**	**0.94**	**1.00**	**0.89**	**0.67**	**0.91**	**0.95**	**0.68**	**0.89**
PC2	0.01	0.01	0.02	0.00	0.11	0.15	0.00	0.00	0.04	0.00
PC3	0.04	0.02	0.01	0.00	0.08	0.09	0.04	0.03	0.02	0.00
PC4	0.02	0.01	0.00	0.00	0.04	0.05	0.00	0.00	0.03	0.00
PC5	0.11	0.10	0.05	0.00	0.18	0.04	0.15	0.09	0.08	0.11
PC6	0.05	0.02	0.01	0.00	0.03	0.11	0.00	0.00	0.02	0.05
PC7	0.01	0.05	0.02	0.00	0.05	0.13	0.00	0.00	0.03	0.08

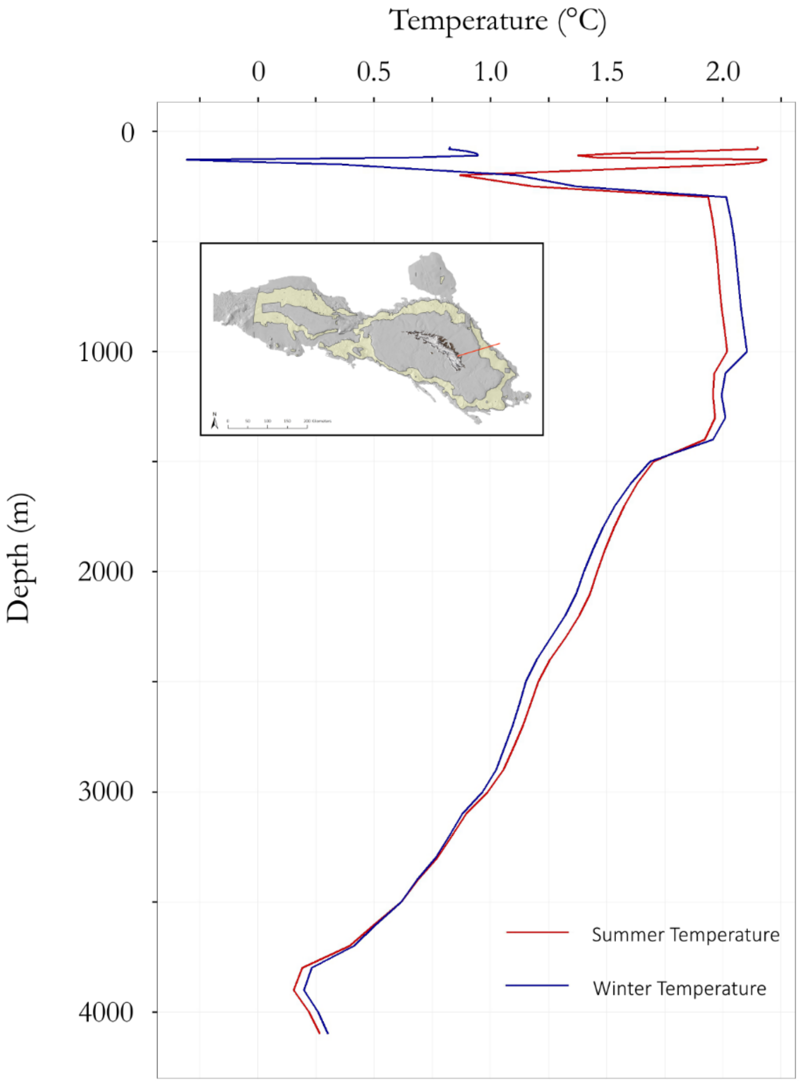
Soft	GLM	GAM	GBM	CTA	ANN	SRE	FDA	MARS	RF	MaxEnt
PC1	**0.76**	**0.53**	**0.70**	**0.95**	**0.96**	**0.53**	**0.86**	**0.46**	**0.50**	**1.00**
PC2	0.03	0.18	0.04	0.00	0.25	0.16	0.01	0.08	0.07	0.00
PC3	0.15	0.27	0.03	0.00	0.00	0.24	0.00	0.10	0.02	0.00
PC4	0.02	0.06	0.04	0.00	0.00	0.05	0.00	0.00	0.02	0.00
PC5	0.05	0.35	0.06	0.00	0.14	0.15	0.07	0.33	0.10	0.13
PC6	0.07	0.13	0.08	0.12	0.03	0.13	0.00	0.07	0.05	0.00
PC7	0.08	0.27	0.04	0.00	0.06	0.11	0.03	0.11	0.05	0.00

Supplementary materials Table 6.3. Summary of SGSSI marine protected area protection zones discussed in this study, detailing the extent of protection and conservation objective. Adapted from the Marine Protected Areas Order (2013).

AREA	PROTECTED FEATURE	CONSERVATION OBJECTIVE
WEST GULLY BENTHIC CLOSED AREA	The seabed, and associated organisms in an area of 1557 km2	The vulnerable marine fauna in this area and protect juvenile toothfish, which are abundant in this area.
NORTH GEORGIA RISE BENTHIC CLOSED AREA	The seabed, and associated organisms in an area of 4590 km2	The potentially sensitive (but largely unknown) benthic fauna; provides refugia for adult toothfish.
NE SOUTH GEORGIA BENTHIC CLOSED AREA	The seabed, and associated organisms in an area of 441 km2	The vulnerable marine fauna identified in this location; provides refugia for toothfish.
WEST SHAG ROCK BENTHIC CLOSED AREA	The seabed, and associated organisms in an area of 1039 km2	The vulnerable marine fauna identified in this location; provides refugia for toothfish.
SOUTH GEORGIA NO-TAKE ZONE	The seabed, overlying water and associated organisms in an area of 13899 km2	The shallow marine environment around South Georgia including: 1. The spawning grounds of many fish species, including mackerel icefish; 2. The inshore foraging areas of marine predators such as Gentoo penguins, cormorants, petrels and prions.
CLERKE ROCKS NO-TAKE ZONE	The seabed, overlying water and associated organisms in an area of 1923 km2	The shallow marine environment to the SE of South Georgia including: 1. The spawning grounds of many fish species, including mackerel icefish; 2. The inshore foraging areas of marine predators such as Gentoo penguins, cormorants, petrels and prions; 3. The "spirulid reef" at approximately 55o00'S, 34o31'W.
SHAG ROCKS NO-TAKE ZONE	The pelagic ecosystem in an area of 1.07 million km2 during a 5 month period.	Mammalian and avian krill dependent predators, such as penguins and fur seals during the key part of the breeding season.

Supplementary materials Table 6.4. Summary of SGSSI marine protected area protection zones not explicitly discussed in this study, detailing the extent of protection and conservation objective. Adapted from the Marine Protected Areas Order (2013).

AREA	PROTECTED FEATURE	CONSERVATION OBJECTIVE
SOUTHERN SEAMOUNTS BENTHIC CLOSED AREA A	The seabed, and Associated organisms in an area of 1557 km2	The potentially sensitive (but largely unknown) benthic fauna; provides refugia for adult toothfish.
SOUTHERN SEAMOUNTS BENTHIC CLOSED AREA B	The seabed, and associated organisms in an area of 1158 km2	The potentially sensitive (but largely unknown) benthic fauna; provides refugia for adult toothfish.
NORTH EAST GEORGIA RISE BENTHIC CLOSED AREA	The seabed, and associated organisms in an area of 9853 km2	The potentially sensitive (but largely unknown) benthic fauna of this area; provides refugia for adult toothfish.
PROTECTOR SHOALS BENTHIC CLOSED AREA	The seabed, and associated organisms in an area of 1935 km2	The potentially sensitive (but largely unknown) benthic fauna; provides refugia for adult toothfish.
KEMP SEAMOUNT & CALDERAS BENTHIC CLOSED AREA	The seabed, and associated organisms in an area of 352 km2	The potentially sensitive (largely unknown) benthic fauna of this seamount and caldera. Protects different chemosynthetic habitats, including white smoker vent fields
SEASONAL CLOSURE OF THE FISHERY FOR ANTARCTIC KRILL	The pelagic ecosystem in an area of 1.07 million km2 during a 5 month period.	Mammalian and avian krill dependent predators, such as penguins and fur seals during the key part of the breeding season.
SOUTH SANDWICH ISLANDS NO-TAKE ZONES	The seabed, overlying water and associated organisms in areas that total 2272 km2	The shallow marine environment around each of the South Sandwich Islands including: 1. The inshore foraging grounds of marine predators; 2. The spawning grounds of fish species.
SOUTH SANDWICH ISLANDS PELAGIC CLOSED AREA	The pelagic ecosystem around each of the South Sandwich Islands in an area of 18,042 km2	The pelagic ecosystem and dependent predators in the area around each of the South Sandwich Islands, particularly the highly abundant chinstrap and Adelie penguins.



Supplementary materials Figure 6.4. Modelled summer and winter temperature profiles by depth. Profile is taken between 70 and 4100m. The location of the profile transect is shown by a red line in the inset map.

Appendix E: Research papers co-authored during the course of this PhD

This appendix consists of three additional peer-reviewed papers that I have co-authored during the course of this PhD. They are included in chronological order. The citations for each, in the same order, are as follows:

Barnes, D.K., Ireland, L., **Hogg, O.T.,** Morley, S., Enderlein, P. and Sands, C.J., 2016. Why is the South Orkney Island shelf (the world's first high seas marine protected area) a carbon immobilization hotspot? Global change biology, 22(3), pp.1110-1120.

Barnes, D.K.A., Sands, C. J., **Hogg, O. T.,** Robinson, B. J., Downey, R. V., & Smith, J. A. (2016). Biodiversity signature of the last glacial maximum at South Georgia, Southern Ocean. Journal of biogeography, 43(12), 2391-2399.

Nolan, E.T., Barnes, D.K.A., Brown, J., Downes, K., Enderlein, P., Gowland, E., **Hogg, O.T.,** Laptikhovsky, V., Morley, S.A., Mrowicki, R.J. and Richardson, A., 2017. Biological and physical characterization of the seabed surrounding Ascension Island from 100–1000 m. Journal of the Marine Biological Association of the United Kingdom, 97(4), pp.647-659.

Global Change Biology

Global Change Biology (2016) **22**, 1110–1120, doi: 10.1111/gcb.13157

Why is the South Orkney Island shelf (the world's first high seas marine protected area) a carbon immobilization hotspot?

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Abstract

The Southern Ocean archipelago, the South Orkney Islands (SOI), became the world's first entirely high seas marine protected area (MPA) in 2010. The SOI continental shelf (~44 000 km^2), was less than half covered by grounded ice sheet during glaciations, is biologically rich and a key area of both sea surface warming and sea-ice losses. Little was known of the carbon cycle there, but recent work showed it was a very important site of carbon immobilization (net annual carbon accumulation) by benthos, one of the few demonstrable negative feedbacks to climate change. Carbon immobilization by SOI bryozoans was higher, per species, unit area and ice-free day, than anywhere-else polar. Here, we investigate why carbon immobilization has been so high at SOI, and whether this is due to high density, longevity or high annual production in six study species of bryozoans (benthic suspension feeders). We compared benthic carbon immobilization across major regions around West Antarctica with sea-ice and primary production, from remotely sensed and directly sampled sources. Lowest carbon immobilization was at the northernmost study regions (South Georgia) and southernmost Amundsen Sea. However, data standardized for age and density showed that only SOI was anomalous (high). High immobilization at SOI was due to very high annual production of bryozoans (rather than high densities or longevity), which were 2x, 3x and 5x higher than on the Bellingshausen, South Georgia and Amundsen shelves, respectively. We found that carbon immobilization correlated to the duration (but not peak or integrated biomass) of phytoplankton blooms, both in directly sampled, local scale data and across regions using remote-sensed data. The long bloom at SOI seems to drive considerable carbon immobilization, but sea-ice losses across West Antarctica mean that significant carbon sinks and negative feedbacks to climate change could also develop in the Bellingshausen and Amundsen seas.

Keywords: benthos, carbon sink, climate change, feedback, phytoplankton, Southern Ocean

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Introduction

West Antarctica is a global hotspot of climate-forced environment changes but it is also one of the few places where climate-forced change is increasing carbon draw down (Peck *et al*., 2010; Barnes, 2015). West Antarctic air and sea temperatures, seasonal sea-ice loss, glacier retreat, ice shelf collapse and primary productivity are patchily increasing (Cook *et al*., 2005; Meredith & King, 2005; Arrigo *et al*., 2008). However, ice shelf losses are generating a significant carbon sink and one of the few negative feedbacks on climate change (Peck *et al*., 2010); new blooms of phytoplankton (in water previously covered with ice shelves prior to their collapse) take aerial CO_2, which are eaten by benthos and this carbon is held and buried on the seabed by long-lived animals. Seasonal sea-ice losses and arctoboreal forest growth are thought to be the most significant negative feedbacks on climate change (Peck *et al*., 2010) of which sea-ice losses are potentially the most important (Barnes, 2015).

In three decades, nearly a million km^2 of sea ice has decreased by an average of about 80 days (Stammerjohn *et al*., 2008). There is a strong negative correlation between sea-ice duration and primary productivity around Antarctica; increased open water leads to longer blooms and more primary productivity (Arrigo *et al*., 2008). Duration of food may be the most limiting factor to feeding activity and growth of benthic primary consumers on the continental shelf (see Barnes & Clarke, 1994 and Barnes, 1995 respectively). This is important as the continental shelves around Antarctic are massive (>3 million square km); the Weddell Sea alone has a larger shelf than the United States.

Many representatives of the productive high latitude shelf benthos, such as some bryozoans, bivalve molluscs and brachiopods, form annual nodes or rings

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between phases of growth and growth cessation (see, e.g. Winston, 1983). Such lines demark both age and quantities of growth, which can be compared with variation in environmental characters such as sea ice and primary productivity. Although growth of individual Antarctic benthic animals is slower than in lower latitudes (Heilmayer *et al*., 2004; Clarke *et al*., 2005), their high abundance and longevity on wide continental shelves (Arntz *et al*., 1994; Brey *et al*., 1995; Smith, 2007) in a growing carbon sink means they can be of global significance in carbon sequestration (see Peck *et al*., 2010; Barnes, 2015). The term 'drawdown' is usually reserved for photosynthetic (autotrophic) uptake. Carbon held in deep benthos skeletons, which is likely to be buried on death and remain out of the carbon cycle for significant time periods, is here termed 'immobilization'.

Bryozoans are complex phytoplanktivorous animals that are mainly sessile, benthic and colonial, composed of many tiny modules called zooids. A recent comparison of carbon immobilization by bryozoans across the major West Antarctic sea continental shelves found the highest values per unit area at the South Orkney Islands (Barnes, 2015). To date, it is unknown why this should be the case and given the recent designation of SOI as the world's first high seas Marine Protected Area (MPA), and regional importance as both carbon sink and negative feedback to climate change, we suggest that understanding drivers should be a priority. Thus, this study investigates bryozoan densities, longevity and growth performance by region to ask why some shelves are much more benthos-productive per area than others. Previously identified possible environmental drivers include mortality (Winston, 1983), food supply (Barnes, 1995) and sea-ice duration (Barnes, 2015). This study tests the hypotheses that (1) high SOI benthic carbon immobilization is directly due to a combination of high benthos density, lifespan and growth performance, and this is driven by (2) low sea-ice duration and high phytoplankton production. Finally, given the remoteness of the region and paucity of direct observation and samples, we compare satellite-derived remote-sensed data (SeaWiFs) with directly observed and sampled data from research station-based, long-term time series datasets.

Materials and methods

Density, age spectra and growth data (in terms of carbon content) of specimens of six bryozoan species were considered from benthic collections around the South Atlantic and West Antarctic, from 1993 through to 2013 (data from Barnes *et al*., 2007, 2011; Griffiths *et al*., 2008; Kaiser *et al*., 2008; Barnes, 2015; and D.K.A Barnes and C.J. Sands, unpublished data from JR275 and JR287 cruises). The study species were chosen on the basis of well established, wide distributions and distinct, annual, growth check lines (Winston, 1983; Barnes, 1995). The main locations considered were South Georgia, South Orkney Islands (SOI), Bellingshausen Sea (West Antarctic Peninsula), East Amundsen Sea, East Ross Sea, and Weddell Sea (Fig 1a). In addition, data from the Falkland Trough and South Sandwich Griffiths *et al*. (2008) and Kaiser *et al*. (2008) and data from Gough Island were collected during science cruise JR287. The study focussed on the SOI region, for which the position of samples used, maximum ice extent and MPA boundaries are shown.

The study taxa, *Cellarinella nutti* Rogick, 1956; *C. rogickae* Moyano, 1965; *C. watersi* Calvet, 1909; *Melicerita obliqua* Rogick, 1956; *Stomhypselosaria watersi* Hayward & Thorpe, 1989; and *Systenopora contracta* Waters, 1904, grow as rigid erect

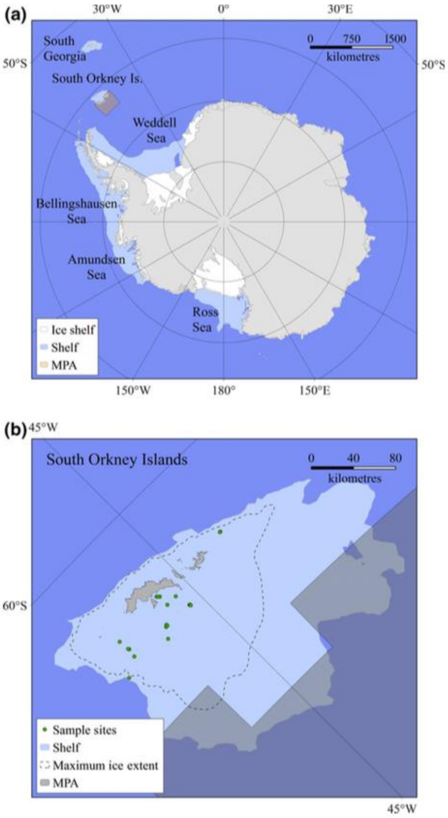

Fig. 1 Southern Ocean continental shelf study regions and detail of South Orkney Islands (b). The Marine Protected Area is shown in grey shade and the dashed line shows the maximum extent of grounded ice sheet during recent glacial maxima.

forms which are heavily calcified with strong growth check lines visible. Such lines are laid down with annual periodicity in bryozoans (Barnes, 1995; Brey *et al.*, 1998, 1999) and other Antarctic suspension feeders, such as molluscs and brachiopods (Brey *et al.*, 1995; Brey & Macksensen, 1997). Counting back these lines to the 'rooted' base shows the age of colonies such that the age, and year of formation, of each band can be calculated. Carbonate skeletal mass was calculated (following Barnes *et al.*, 2007) and carbon 'immobilization' by multiplying ash free dry (organic) mass by 0.5 (see Salonen *et al.*, 1976) and adding the value to the carbon proportion of skeletal mass which we calculated to be ~13.3% (±2.5%). Density values were estimated from cameras deployed, mainly on a dedicated camera lander (Shelf Underwater camera System – SUCS) but also from remote-operated vehicles (ROVs). The study species and total bryozoans were estimated to constitute about ~3% and ~15%, respectively, of total benthic biomass across the Southern Ocean study regions (Barnes, 2015 suppl materials). There is a wide variety of estimates of what proportion of Southern Ocean benthos is constituted by bryozoans but most of these are derived from nonquantitative samples (such a trawls and sledges), so we consider that the most accurate estimates are the 3% and 15% values.

Overlying sea-ice duration was taken from remote-sensed data in Cavalieri *et al.* (1996, updated yearly (http://dx.doi.org/10.5067/8GQ8LZQVL0VL) and Stammerjohn *et al.* (2008). Sea-ice duration is determined using daily passive microwave measurements of sea-ice concentration. We used a modification of the method defined by Stammerjohn *et al.* (2008); we calculated the interval between the date of sea-ice advance (first day after 15 February when sea-ice concentration is >90% for five consecutive days) and the date of sea-ice retreat (day when sea-ice concentration remains below 90% until 14 February). This provided us with a sea-ice duration grid for each year from 1979 to 2012. Fitting a linear least squares trend through the values for each cell in the grid provides us with a measure of annual change in days of sea-ice duration. The regional pattern of these trends is shown in Fig. 2. In addition, direction observations by observers at manned Antarctic research stations (Rothera, Adelaide Island, West Antarctic Peninsula) and by static sea-ice cameras at unmanned stations (Signy Island, South Orkney Islands) were recorded. Remote-sensed phytoplankton productivity taken from Arrigo *et al.* (2008) and http://www.science.oregonstate.edu/ocean.productivity. Directly measured (size fractionated) phytoplankton data were taken from the long-term

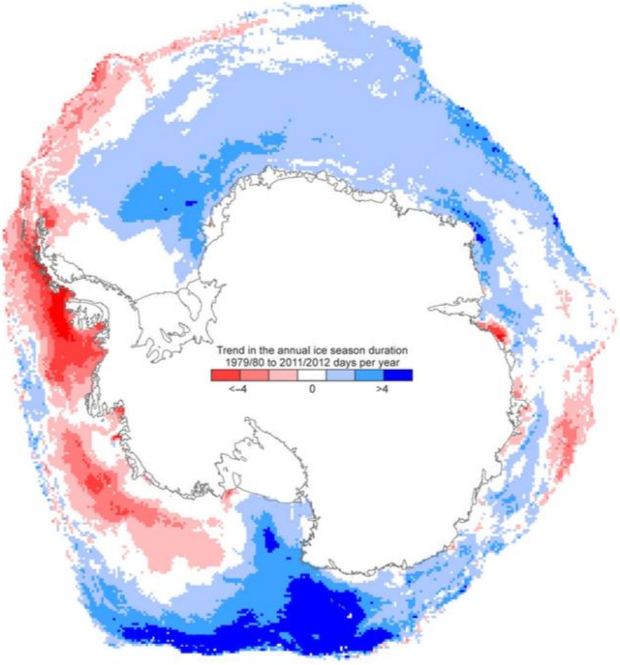

Fig. 2 Annual change in sea-ice duration around Antarctica. Sea-ice data from Cavalieri *et al.*, 1996, updated yearly (http://dx.doi.org/10.5067/8GQ8LZQVL0VL). The scale −4 to +4 relates to the average number of days lost or gained per year (respectively) of sea ice from 1979 to 2012.

time series at Signy Island (see Clarke & Leakey, 1996) and at Rothera Research Station (Rothera marine assistant reports, BAS archives). The current study focussed on nanophytoplankton (e.g. ciliates and flagellates), as the size fraction of phytoplankton utilized by bryozoans. To generate estimates of 'duration of food availability, we compared the number of days each year for which nanophytoplankton had been directly measured to exceed thresholds of 100 $\mu g\ L^{-1}$ and 200 $\mu g\ L^{-1}$ (equal to ~6 $\mu g\ L^{-1}$ of carbon [3% cell mass]). This generated a data set of duration of nanophytoplankton by year adjacent to Signy and Rothera stations, which could be compared with remote-sensed data for the same areas. Nanophytoplankton (or any other particular size fraction) cannot be estimated from remote-sensed data, which measures colour intensity. The intensity of colour is ~proportional to total near-surface chlorophyll concentrations. The biomass of phytoplankton blooms in the Southern Ocean is typically dominated by large celled types, such as diatoms (see Clarke & Leakey, 1996; Arrigo *et al*., 2008). However, as many herbivores, such as bryozoans, do not posses equipment to mechanically break the tough silicon tests (and such cells often bigger than their mouths), they are not important in their diet (although may be found undigested in stomachs), we therefore do not consider them further. We plotted the pattern of duration of directly measured nanophytoplankton by year against the remotely sensed total chlorophyll data to examine whether the trend was significantly different. By showing that remote-sensed data captured the trend (i.e. long duration years for direct measured nanophytoplankton corresponded to long duration years for total remote-sensed chlorophyll), we were then able to investigate temporal trends in bryozoan carbon immobilization data- vs remote-sensed phytoplankton (food availability).

Results

Carbon immobilization

Of the nine initial study locations, none the study species were found in Gough Island trawl samples (or seabed photographs) and were too rare to be of any impact at the Falkland Trough or South Sandwich Islands, so these localities were not considered further. Most or all of the study species occurred at the remaining six locations.

Mean annual carbon immobilization by region per unit area is shown in Fig. 3. Annual carbon accumulation (=immobilization) significantly differed between these locations (ANOVA, $F = 61.8$, $P < 0.001$). *Post hoc* Tukey tests showed that annual carbon accumulation at SOI was significantly higher than at any other study location (Fig. 3). To examine this difference in more detail, the total carbon accumulation by bryozoans was split into component study species by study location. The mean annual carbon immobilization performance of bryozoans in each region compared with those at SOI varied considerably with species identity (Table 1) from *C. nutti* in the Bellingshausen Sea accumulating 96% that of the same species at SOI to *C. rogickae* in the Amundsen Sea accumulating just 10% of the same species at SOI.

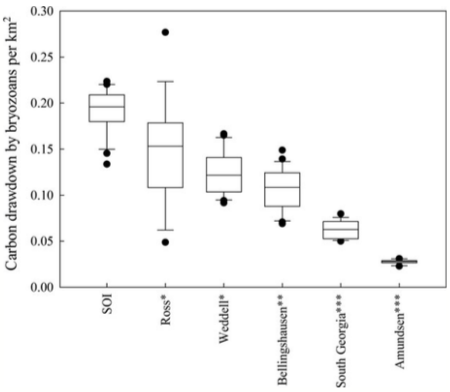

Fig. 3 Carbon accumulation immobilization (by bryozoans per km^2) by study location around West Antarctica. The boxplots are mean, standard error and 95% confidence intervals. Asterix by location indicates that carbon accumulation there was significantly less than at; (*) SOI, (**) SOI and Ross, and (***) SOI, Ross, Weddell and Bellingshausen sea shelves. Dots are data outside the 95% confidence interval.

At more detail, the deficit to SOI accumulation levels varied with age within species (shown for *C. nutti*, suppl materials Fig. S1). In the first few years of growth, there was little performance difference between study locations, except at South Georgia. With increased age, the deficit to SOI generally increased, but the reverse was true at South Georgia. So whether measured at the regional pooled species and ages level (Fig. 3) or deconstructed by species and age, the highest carbon accumulation occurred at SOI and the lowest at the Amundsen Sea and South Georgia.

Study species density and age structure

The density of study species was highest overall at the Weddell Sea, and lowest at the northernmost study site of South Georgia (Table 2). Density differences partly explained the low carbon accumulation at South Georgia, but these did not explain either the anomalously high production at SOI or the very low values associated with the Amundsen Sea.

There were significant differences between the age structure of the three *Cellarinella* species (ANOVA, $F > 6$, $P < 0.01$), with the most differences occurring in *C. nutti* (Table 3). Notably, the mean and maximum ages were depressed on the Amundsen and South Georgia shelves. Neither age structure, density (Table 2

Table 1 Growth performance by region relative to at SOI. Relative mean growth performance of species (carbon immobilization), across study regions. The values are annual carbon increment as a proportion of that at the South Orkney Islands, meaned across ages (e.g. 0.1 = 10% of value at SOI)

	Bellingshausen	Ross	Weddell	South Georgia	Amundsen
Cellarinella nutti	0.96 (0.02)	0.90 (0.05)	0.89 (0.05)	0.82 (0.51)	0.35 (0.27)
C. rogickae	–	0.20 (0.11)	0.19 (0.11)	0.44 (0.15)	0.11 (0.07)
C. watersi	0.44 (0.20)	0.35 (0.04)	0.37 (0.04)	0.19 (0.11)	0.13 (0.08)
Systenopora contracta	~0.85	~0.75	~0.8	~0.6	~0.33

Table 2 Density of species with region. Mean density of study species across shelf sea study sites (m^{-2}). Location codes are South Orkney Islands (SOI) and South Sandwich Islands (SSI). None of the study species were found in other regional locations sampled (Falkland Trough and Gough Island)

	Weddell	Ross	Bellingshausen	Amundsen	SOI	South Georgia	SSI
Cellarinella nutti	5.2	3.1	1.7	0.4	0.3	0.1	0
C. rogickae	0.4	0.1	0	0.2	0.7	0.1	0
C. watersi	1.3	0.1	0.8	1.2	0.7	0.3	0
M. obliqua	3.3	0.8	0.1	0.4	0.1	0	0
Systenopora contracta	0.2	0.3	0.1	0	0.1	0	0
S. watersi	0.1	0.1	0	0.1	0.2	0.1	0.1

Table 3 Age of species with region. Mean, standard error and maximum ages of the most heavily calcifying study species across shelf sea study regions (in years)

	Weddell	Ross	Bellings.	SOI	Amundsen	South Georgia
Cellarinella nutti	**10.3** (0.4) *23*	**9.2** (0.3) *24*	**8.0** (0.7) *15*	**7.8** (1.0) *15*	**5.6** (0.6) *10***	**6.8** (1.4) *12**
C. rogickae	**9.7** (0.4) *19*	**7.9** (1.3) *12*	–	**5.3** (0.4) *11**	**5.1** (0.9) *9**	**4.8** (0.3) *10**
C. watersi	**7.7** (0.5) *14*	**7.3** (1.0) *12*	**6.8** (1.0) *13*	**7.1** (0.6) *14†*	**7.1** (0.5) *13†*	**4.9** (0.3) *11**
Systenopora contracta	**6.6** (0.7) *10*	**6.9** (0.9) *12*	**6** (0.2) *9*	**6.2** (0.2) *9*	–	–

Post hoc Tukey tests showed (*) significantly younger than Weddell, (**) significantly younger than Weddell and Ross significantly older and (†) significantly younger than Weddell, SOI and Amundsen. The significance values do relate to the values in bold. The values in italics are absolute maximum so be definition there is only one per species so are not suitable for testing significance.

and 3) or reduced young age performance (suppl materials Fig. S1) of bryozoans at South Georgia explain the low carbon accumulation values per unit area (Fig. 3). When data were corrected for density and age differences, and carbon immobilization, both South Georgia and Amundsen values were as high as or higher than other locations – except SOI (Table 4, top row). SOI was still significantly higher than at any other location (ANOVA, $F = 286$, $P < 0.001$ and *Post Hoc* Tukey test).

Sea-ice duration

The sea did not freeze during the study period at South Georgia preventing any investigation of a potential relationship between carbon accumulation and sea-ice duration – there was open water 365 days per year. No significant relationships were found between sea-ice duration and carbon accumulation in the Ross Sea or in the Amundsen seas (ANOVA, $F < 1$, $P > 0.4$), despite the Amundsen being an important area of sea-ice loss (Fig. 2). Sea-ice duration has been linked to within-region trend in carbon immobilization on the SOI, Weddell and Bellingshausen sea shelves (Barnes, 2015), but not to between-region differences. Carbon immobilization per km^2 at SOI was about 20% higher than in the Weddell and about 50% higher than the Bellingshausen for a similar level duration of sea ice. However, there was a significant difference between the sea-ice duration at different study sites (ANOVA, $F = 15$, $P < 0.01$), with SOI and Bellingshausen having significantly less (i.e. longer open water duration) than elsewhere (except South Georgia). Within study regions, sea-ice duration was a strong predictor of carbon immobilization (all $r^2 > 48\%$ and see Fig. 4) but even the significant difference between regions did not explain the why SOI carbon immobilization was higher than other study regions, especially the Bellingshausen (which had similar sea-ice durations).

At two locations, SOI and Bellingshausen, both remotely sensed and directly observed sea-ice data, were

Table 4 Carbon immobilization values and factors driving benthic carbon immobilization by region. Regions are ranked in immobilization per unit area from left (high) to right (low). Carbon immobilization values are for all bryozoans and are standardized (corrected) for age and density (means from Fig. 5b)

	SOI	South Georgia	Bellings.	Ross	Amundsen	Weddell
Mean corrected Carbon immobilization (tonnes km^{-2})	0.289	0.148	0.102	0.071	0.071	0.022
Benthos density	mid	low	mid	mid-high	mid	high
Benthos lifespan	mid	low	mid	mid-high	low	high
Benthos production	high	low	mid	mid	low	mid
Sea-ice duration	low	none	mid-low	mid	high	mid
Phytoplankton duration	high	high	mid	mid	low	mid

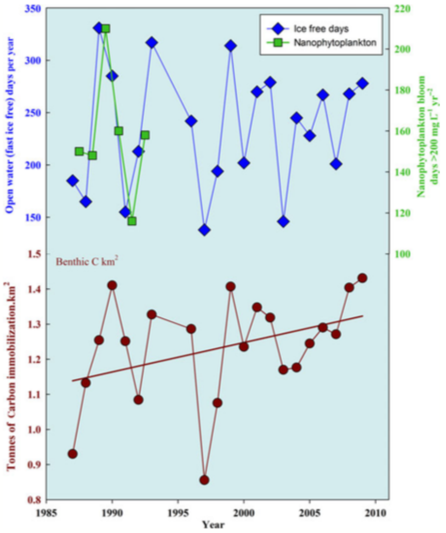

Fig. 4 Duration of open water, nanophytoplankton blooms and carbon immobilization by benthos around the South Orkney Islands, Southern Ocean over three decades. The data shown are (blue) number of days in the year that open water was recorded (i.e. not fast ice) using daily direct observations and sea-ice camera; (green) number of days in the year for which nanophytoplankton (5–20 μm size fraction) concentrations were ≥200 μg L^{-1}, and (dark red) estimated carbon immobilization by benthos per km^2 (scaled up from bryozoan values as in Barnes, 2015).

available for similar areas. Comparison of these estimation techniques showed significant regressions between remote sensed and directly observed data ($r^2 = 63\%$ ANOVA, $F = 12.9$, $P = 0.011$ at SOI and $r^2 = 15\%$ $F = 5.8$, $P = 0.024$ at Bellingshausen). Therefore, remote-sensed data detected a similar trend to directly observed data. However, remote-sensed data significantly underestimated directly observed fast-ice duration at SOI (by 57.7% at SOI, T test, $T > 3$, $P < 0.02$).

Phytoplankton (food) availability

No relationships were found between carbon accumulation in bryozoans and peak phytoplankton values, using either directly sampled phytoplankton size fractions or remotely sensed chlorophyll a. Likewise no relationship was found between benthic carbon immobilization and estimated total integrated biomass values of phytoplankton. However, there was a significant relationship between the duration of (directly sampled) nanophytoplankton abundance when the threshold was set to >200 μg L^{-1} (as in Barnes, 1995) but not at >100 μg L^{-1} (as in Clarke & Leakey, 1996) ($r^2 = 72\%$ ANOVA, $F = 13.8$, $P = 0.021$). Figure 4 shows fast-ice duration, directly sampled phytoplankton duration and carbon immobilization of bryozoans at Signy Island, SOI.

Finally, we then investigated whether such a phytoplankton duration-benthic carbon immobilization relationship could explain the high SOI (and low Amundsen) immobilization values (of Fig. 3). We found a significant difference across study regions between the remotely-sensed duration of phytoplankton blooms (ANOVA, $F = 9.6$, $P < 0.001$). *Post hoc* Tukey tests showed phytoplankton duration at SOI were significantly longer than elsewhere (a month more than Bellingshausen and 2 months longer than Amundsen). Overall there was a significant relationship between regional benthic carbon immobilization and phytoplankton duration (Fig. 5). Whilst phytoplankton duration seems to be the major driver for the SOI hotspot of carbon immobilization, the direct and indirect causes in the study species are clearly complex (Table 4).

Discussion

Sea-ice losses, both in terms of area and duration, are one of the most obvious impacts of climate change at the global scale (Parkinson, 2014). As with most climate-forced influences on the environment, there are positive feedbacks associated with sea-ice losses as the blue of open water absorbs more heat leading to more

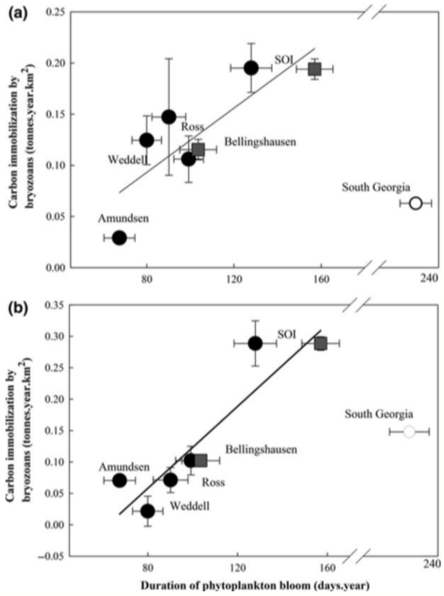

Fig. 5 Carbon immobilization by bryozoans by region with phytoplankton bloom duration. Data are a) means of total carbon immobilization by bryozoans across years, species and ages, with mean phytoplankton duration across years, and b) as [a] but carbon immobilization by bryozoans which has been age and density standardized. The symbols are remotely sensed data (circles) and directly sampled data (squares). The variation shown is standard error bars.

sea-ice losses. Even the few negative feedbacks discovered may have been overestimated, for example because of slower than expected growth of arctoboreal forests in response to warming (Houssett *et al.*, 2014). The recent discovery of increased benthic carbon capture coincident with sea-ice losses on Antarctic continental shelves, also found potential sequestration varied considerably by region (Barnes, 2015). The current study shows that the magnitude of what we term benthic carbon immobilization around the Southern Ocean (per unit area) varies by almost an order of magnitude (see Fig. 3). The term immobilization (in place of 'drawdown' see Barnes, 2015) makes assumptions that the carbon held in skeletons will typically remain on the seabed and be buried. Grounded ice advance during glaciations would invalidate this, but although such activity is unlikely occasional icebergs may be large enough to scour small areas of shelves hundreds of metres deep (Gutt, 2001). This may ground up or re-expose formerly buried carbon decreasing immobilization and representing error in our calculations.

One of the world's newest Marine Protected Areas (MPA), and the first in the high seas), the South Orkney Islands (SOI) seems to have anomalously high carbon immobilization, compared with other high latitude regions. Thus, the MPA, which was selected for other reasons (see Trathan *et al*., 2014), now could be even more important. However, it was unclear why benthic growth was so considerable in the SOI. Increased carbon immobilization with decreasing sea-ice duration was shown within SOI and two other regions (Barnes, 2015), but this did not explain between-region differences.

One of the key reasons for regional carbon immobilization differences was density and age spectra of benthos. Densities of each study species were depressed in all the most northerly of the study regions; Gough Island, Falkland Islands shelf, South Georgia and South Sandwich Islands (Table 2 – although perhaps Gough and South Sandwich islands are too little sampled to establish density). Where they were abundant enough to assess lifespan (at South Georgia), this too was depressed (Table 3). Species richness can be very high at some of these northernmost range limits for Antarctic benthos (Hogg *et al*., 2011) but with depressed densities and ages, carbon immobilization is bound to be reduced. There are taxa at South Georgia with both high density and lifespans, such as octocorals but these are thought to be extremely slow growing (Taylor, 2011). Previously, mortality and thus reduced age and density of bryozoans, and other Antarctic benthos has been associated with iceberg activity (Gutt, 2001; Barnes & Souster, 2011), but this is highly unlikely as far north as 40–58°S. Although the proportion of benthos represented by the study species, and bryozoans in general, did not significantly differ between regions, variation in benthic taxonomic composition must be regarded as a strong potential source of error. An ideal avenue of future work will be estimation of carbon accumulation and immobilization using different model taxa at the same regions for proxy comparisons. Such studies could also investigate variance in production–accumulation–immobilization. Although bryozoans are median in terms of benthic production rates, their high skeletal composition means that they are likely to convert more accumulation to immobilization than many taxa.

Other possibilities for what underlies reduced densities and lifespans at these locations include the following: the origin of individuals, sea temperatures and extreme current flow. If the origin of many individuals of species at such range limits is not local, but from transport from the northern Antarctic Peninsula and archipelagos, the densities then reflect the serial dilution over that distance. Typical sea temperatures around South Georgia are several degrees warmer than around the other study regions further south, and species close to their thermal maximum may have reduced viability of young (effecting density) and become more susceptible to disease, competitors and predators (effecting age)(Morley *et al.*, 2014). As erect rigid bryozoans grow older, they grow progressively out into currents and can be broken and toppled (see Barnes, 2015). Finally, near-bottom overshelf current velocities around South Georgia (and South Sandwich Islands) could occasionally be much higher than further south due to their position in the path of the strong Antarctic Circumpolar Current, lack of protection from nearby continent margins and sloping shelves lacking deepened basins. Although the literature data show similar ranges of current velocities across study regions (e.g. Thompson *et al.*, 2009; Young *et al.*, 2014), these are surface and mean values, whereas it is near-bottom maximum values that are of relevance.

At the southernmost limit of sample origin, 74°S in the Amundsen Sea carbon immobilization was similarly low to those northernmost. Growth rates of ectotherms (i.e. includes all benthos) are thought to be mostly very slow in the Southern Ocean (Arntz *et al.*, 1994; Heilmayer *et al.*, 2004; Clarke *et al.*, 2005). Nevertheless, the growth rates of bryozoans in the Amundsen Sea were extraordinary. With a specific growth rate of ~0.0006, the erect bryozoan *Cellarinella watersi* in the Amundsen Sea has the lowest recorded for any bryozoan species reported (suppl materials Fig. S2), although some individuals in Ross Sea *Cellarinella* species may also approach these levels (see Smith, 2007). Bryozoan ages were depressed in the Amundsen (possibly due to ice-scour frequency), but densities were not (Table 2). Density and age-corrected data showed that South Georgia values were significantly higher than Ross, Amundsen or Weddell – so reduced density and/or age of benthos was an important explanatory factor to depressed carbon immobilization at extreme regions. However, our first hypothesis concerned high SOI benthic carbon immobilization, and benthic density and lifespan did not explain this so it was not accepted (see Table 4), but clearly there was high individual growth performance at SOI (Fig. 3).

The extreme north and south regions (e.g. South Georgia and Amundsen) also had the shortest and longest durations of sea ice (data from Stammerjohn *et al.*, 2008). However, neither patterns in remotely-sensed sea-ice duration nor those that were directly observed (Fig. 4) could explain why bryozoans accumulated significantly more carbon at SOI than elsewhere. Sea-ice timing and duration is clearly crucial for pagophilic organisms (see Thomas, 2004) and has shown to be important in mediating disturbance to benthos in the shallows (Barnes *et al.*, 2014) but to date has not been shown to directly influence deeper benthos at typical polar continental shelf depths to our knowledge.

There is clear evidence of the potential for indirect influence of sea ice on benthos, primarily because of strong correlation with primary production (Arrigo *et al.*, 2008). All investigations of peak and integrated phytoplankton production (e.g. see Clarke & Leakey, 1996 for values around SOI) revealed no obvious link with carbon immobilization by bryozoans, suggesting that such suspension feeding benthos are not food limited (therefore do not have food resource competition) during the summer blooms. However, carbon immobilization increased significantly with the duration of directly sampled nanophytoplankton (>200 μg L^{-1}), as suspected decades ago (due to correlations with feeding activity, see Barnes & Clarke, 1994). Crucial to our second hypothesis, this also proved true across regions using remotely-sensed data (Fig. 5a). This showed carbon immobilization at SOI was not anomalous but driven by longer duration of food availability. Furthermore, when regional carbon immobilization values were corrected for differences in bryozoan density and age (i.e. individual performance), the relationship shown altered from r^2 = 63% (in Fig. 5a) to r^2 = 80% (in Fig. 5b). Thus, overall duration of food availability seems to be key to regional carbon immobilization – except at South Georgia. The lack of correlation between other measures of phytoplankton abundance (peak or total integrated biomass) could be related to many hydrographic variables, especially considering that shelf benthos may be hundreds of metres below the chlorophyll maximum. Considerable differences in current velocities and directions, sedimentation rates, and depth could confound potential correlations. However, the limited literature of where benthos are in close contact (in the shallows) with phytoplankton blooms showed similar feeding and growth correlation with only duration (not peak or TIB)(Barnes & Clarke, 1994).

Whilst we have demonstrated a strong potential explanation for high SOI carbon immobilization (and new value to the high seas MPA), we have also shown South Georgia to be a massively low anomaly. All the study species are at the edge of their described geographic ranges (see SCAR-MarBIN.be) and might be living in waters that are close to, or beyond their thermal optima (Fig. 5b). Environmental temperature is known to influence growth rates of ectotherms and the optimum temperature for growth can change through development, resulting in juveniles growing faster at higher temperatures but adults of the same species growing faster at lower temperatures (isopods, Anguilletta *et al*., 2004). Larger individuals of many shallow water Antarctic marine invertebrates are also generally more susceptible to acute temperature stress than smaller ones (Peck *et al*., 2009). A pattern of faster initial growth but shorter lifespan could therefore provide evidence that these bryozoans are living at the edge of their thermal range at South Georgia and can provide an explanation for the pattern of carbon draw down recorded at South Georgia.

Are the results at SOI scalable to have wider relevance?

SOI is a small region of just 44 000 square km, but the findings there may be scalable across taxa and to other, larger regions. The scalability of six species up to all bryozoans and other benthos is a reasonable leap (Barnes, 2015) for three reasons. They are suspension feeders, and this feeding type typically dominates shelf communities in the region underlying most sea-ice loss (see Mühlenhardt-Siegel, 1988; Arntz *et al*., 1994; Ramos, 1999; Griffiths *et al*., 2008). There is some local scale evidence that other suspension feeders similarly increase growth with food availability (e.g. see Peck *et al*., 2005 for evidence in brachiopods). Finally, production values of bryozoans are approximately mean amongst Antarctic benthos (P/B ratio of 1.8, see Pinkerton *et al*., 2010). Our estimates are likely to be very conservative because heavily calcified bryozoans such as the study species typically grow (and accumulate carbon) more slowly than other bryozoan species (see, e.g. Smith, 2007).

Carbon immobilization measured to date already suggests regional carbon immobilization in West Antarctica is globally significant (Barnes, 2015). The current study shows that this is mainly due to phytoplankton duration, and previous work (Arrigo *et al*., 2008) suggests regional phytoplankton blooms should continue to increase (in association with sea-ice losses – Stammerjohn *et al*., 2008). The current finding that remotely sensed trends of sea ice and phytoplankton broadly mirror those which have been directly sampled, should aid scaling in areas far from research stations and ship accessibility. SOI may already be a hotspot of carbon immobilization but we expect sustained increases in carbon immobilization there to continue assuming sustained sea-ice loss rate in both space and time.

Such estimates of carbon immobilization have been conservative – for example, nearly all sampling has been within the area covered by grounded ice during the last glaciation (Fig. 1b). The shelf beyond this is likely to have been colonized for hundreds of thousands of years longer. A 2016 research cruise by RRS James Clark Ross has plans sampling outside of the previously grounded ice region (of SOI) and in the MPA, which should reveal whether production differs across them. Although not planned to be as such, the MPA encompasses areas both covered by ice and ice-free during recent glaciations, a significant area within a global hotspot of carbon immobilization and one of the few areas with remote sensed and directly measured sea ice and phytoplankton – arguably it would be difficult to select a scientifically more interesting location. Yet successful implementation of Marine Protected Areas is often due to proposing areas which are of least interest to user groups rather than strict scientific underpinning. For example, the SOI is a comparatively well sampled region, except in the area within the MPA (see www.SCARMarBIN.be).

Could SOI levels of carbon immobilization happen elsewhere? In less than half a century, the Bellingshausen and Amundsen seas may have comparable sea-ice duration to around SOI (see Fig. 2). Being further south, the light climate will be more extreme, but phytoplankton durations are likely to considerably increase (Arrigo *et al*., 2008), which should lead to significant carbon immobilization increases. The current study links benthic carbon immobilization with phytoplankton duration at regional level but there remains considerable within regional variation that is not understood (e.g. recent Ross Sea increases, Barnes *et al*., 2011).

Complexity of biotic response and feedbacks to climate change

There is a considerable diversity of climate impacts acting and interacting in much of the Arctic and west Antarctic. These include warming air and sea temperatures, sea ice, glacier and ice shelf losses, acidification, freshening, precipitation, UV and wind strength (see Turner *et al*., 2009). The geography, magnitude and timing of many of these are hard to project or predict because of paucity of historic data. Sea-ice changes are one of the most obvious physical responses to warming and one that has had clear biological ramifications, detailed in the current study. However, carbon gains from increased phytoplankton blooms because of ice shelf (Peck *et al*., 2010; Fillinger *et al*., 2013) and sea-ice (Barnes, 2015) losses could be reversed if predicted acidification happens. Modelled data (e.g. Orr *et al*., 2005) suggest insignificant change at typical Antarctic shelf depths within 2060, although it seems likely that in the longer term acidification could negate many polar carbon immobilization increases. Biologically meaningful levels of acidification change have yet to be reported in West Antarctic seas and initial change are, like temperature and salinity, likely to be near surface (Antarctic continental shelves are typically 500 + m deep). This is important because otherwise raised acidity at the seabed could dissolve newly sequestered carbon. Significant (climate change linked-)sea temperature increases have only been detected in the top ~50 m of parts of West Antarctic seas and even these have only increased by a degree in 50 years at 50 m depth (Meredith & King, 2005). The continental shelves of the Bellingshausen and Amundsen seas (unlike other Antarctic shelves) are flooded by 'old' Circumpolar Deep Water (a modified water mass from the north Atlantic). Thus, amongst the least changing areas of the planet could underlie some of the fastest changing surface conditions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Ratio of annual Carbon accumulation (immobilization) by *C. nutti* with age at SOI compared with elsewhere.
Figure S2. Specific growth rates of 35 cheilostome bryozoan species across regions.

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ORIGINAL ARTICLE

Biodiversity signature of the Last Glacial Maximum at South Georgia, Southern Ocean

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ABSTRACT

Aim High-latitude biodiversity distributions can preserve signals of the timing and geography of past glaciations, and as such ground truth ice-sheet models. Discrete polar archipelagos offer the fewest confounding factors for testing historic ice position records in extant biodiversity. At South Georgia, two competing geological hypotheses suggest that either the Last Glacial Maximum (LGM) ice was extensive, nearly covering the continental shelf (H_1 Big ice) or restricted to the inner fjords (H_2 Little ice). We examined the past configuration of the South Georgia ice cap using seabed biodiversity.

Location South Georgia, Southern Ocean.

Methods We used a bespoke camera lander (SUCS) and Agassiz trawl deployments across 'big ice' and 'little ice' hypothesized positions of LGM grounded ice around the South Georgia continental shelf. We investigated faunal assemblage structure and richness, especially of brooders, and modelled low dispersal taxa, for example, those with limited pelagic larvae (bryozoans and sponges).

Results We found a striking 'line' of major richness discontinuity, with significantly higher richness, especially of brooders and low dispersal model taxa, mainly conforming to the 'big ice' hypothesized position. What few bryozoans and sponges occurred inside this line were a subset of those outside.

Main conclusions Benthic biodiversity is consistent with extensive LGM grounded ice advancing to near the shelf break in most, but not all locations around South Georgia's shelf, for example, the eastern shelf area. We suggest that most of the shelf is still undergoing recolonization from when grounded ice covered the shelf ~20 kyr ago. Our alternative hypothesis of LGM ice position, H_3 'Limited-Extensive ice', best fitted our data and is easily further testable, but if verified, shows that shelf recolonization following glaciation is much slower than previously thought. This contrasts with surprisingly rapid colonization of continental shelves after ice-shelf collapses, but these are not grounded, which may be crucial to polar recolonization rates.

Keywords
benthos, biodiversity, continental shelf, glaciation, Last Glacial Maximum, moraine, polar, recolonization, Southern Ocean

INTRODUCTION

An important step towards understanding the impacts of past glaciations on biological communities is in determining the extent and duration of ice in recent geological time (that we also have high resolution CO_2 and temperature records for in ice cores). The composition and location of biodiversity has made significant contributions to the reconstruction of past ice-sheet history, by showing that certain regions, previously considered covered by grounded ice during the last glaciation, must have been at least partly ice free – both on land (Convey & Stevens, 2007) and on the continental

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shelf (Barnes & Kuklinski, 2010). Furthermore, the combination of biodiversity data as a tool with information from other disciplines, such as glaciology, oceanography, sedimentology and physical geography has enabled powerful new insights into past ice-sheet stability and recent sea-ways through Antarctica (Vaughan *et al.*, 2011). One location where the extent of the Last Glacial Maximum (LGM – meaning the point at which most area was occupied by grounded ice in the last glacial period between 23–19 ka years ago; Gersonde *et al.*, 2005) is highly debated, is the Southern Ocean island of South Georgia (Bentley *et al.*, 2007; Graham *et al.*, 2008; Hodgson *et al.*, 2014a,b). This remote island shelf is a productive marine diversity hotspot, and now the site of one of the world's largest Marine Protected Areas (Hogg *et al.*, 2011; Johnson & Sandell, 2014).

A compilation of all the available bathymetric data from the South Georgia continental shelf revealed several large glacial troughs, and taken together with shelf edge moraines, and trough mouth fans on the continental slope which indicated that an expanded ice cap once extended to the shelf edge (Graham *et al.*, 2008). Early work (e.g. Clapperton, 1990) assumed that the last 'big ice' advance occurred at the LGM, although this interpretation lacked any chronological control. More recently, Hodgson *et al.* (2014a,b) used newly acquired multibeam data from coastal fjords, alongside surface-exposure dating of erratics on land (Bentley *et al.*, 2007), to argue that the 'big ice' scenario probably pre-dated the LGM and that the LGM glaciers were restricted to the inner fjords; the 'little ice' scenario. Hodgson *et al.* (2014a) attributed the more extensive glaciation to older glacial advances, most likely during Marine Isotope Stage 6 (MIS6; 185-135 ka). However, this evidence is far from conclusive and it remains possible that a larger ice cap existed on the South Georgia shelf but retreated to inner shelf positions earlier than previously thought, or that cold-based, non-erosive glaciers existed which left little or no geomorphological signature (Hodgson *et al.*, 2014b). Much of the current uncertainty is due to the absence of marine geological data and specifically sediment cores which can date the glacial to post-glacial sedimentary sequence (Graham *et al.*, 2008).

Determining which of the two ice scenarios is correct is crucial to our understanding of post-glacial sea-level rise, rates of glacial isostatic rebound of land, and the generation and maintenance of biodiversity on South Georgia's continental shelf. For example, the implication is that either the vast majority of South Georgia's shelf fauna is at least 120 kyr, or less than 20 kyr old. Thus, the present biodiversity is either ancient climax biodiversity, or impoverished fauna still in the process of reinvasion. The answer to this question is not only significant in evaluating benthic faunal vulnerability to multiple present and future climate stresses (Gutt *et al.*, 2015); but also the ecosystem services that the shelf fauna provides in terms of carbon cycling; which include being a potential carbon reservoir (accumulation of carbon by benthos); and ultimately, when organisms die and are buried, that of key carbon sequestration zone (burial of such carbon on organism death) (Barnes *et al.*, 2016).

The current project used a bespoke camera lander (Shelf Underwater Camera System – SUCS) and Agassiz trawls to collect samples of benthic fauna around the continental shelf of South Georgia in order to investigate if the benthic faunal composition can be used as a proxy for reconstructing glaciation history on South Georgia's shelf. If the 'big ice' hypothesis of extensive recent glaciation near or at the shelf break is correct, then benthic fauna around the edge of South Georgia's shelf should be richer, especially in biota with restricted mobility. If the 'little ice' hypothesis is correct (that grounded ice during the LGM was restricted to just the inner fjords) then samples beyond the coast of South Georgia should be similarly rich. A third envisaged possibility is an intermediate 'little-big ice', whereby grounded ice nearly reached the shelf break in most, but not all areas (as in Prydz Bay, Domack *et al.*, 1998). This third possibility is suggested because of the presence of moraines close to the coast of South Georgia at the head of such troughs (Graham *et al.*, 2008). Assessment, understanding and best utilization of South Georgia's substantial marine biodiversity and ecosystem services should be facilitated when its age and history are better elucidated. Our key questions are: does the current marine benthic biodiversity of South Georgia show a 'signal' of the LGM in terms of distinct differences in the richness and/or composition of the benthic fauna on shelf reconstructed as either grounded or not grounded by previous ice advances; and if so, can these findings be used as a proxy to support either H_1 'big ice', H_2 'little ice' or H_3 'little-big ice' hypotheses in determining the maximum extent of ice around the South Georgia shelf during the LGM?

MATERIALS AND METHODS

Theorized positions of the LGM, based on the latest marine glacial geomorphological investigations, (H_1 'big ice', H_2 'little ice' or H_3 'little-big' ice) are shown in Fig. 1a. Thirty deployments of the SUCS were made around the shelf of South Georgia (Fig. 1b) during the 2011 (JR262) and 2013 (JR287) cruises of the RRS James Clark Ross. The study locations were selected from innermost fjords to shelf-break, to give a range of sites inside and outside the theorized LGM grounded-ice positions and also to cover a range of habitat types, depths (85–322 m) and distance from coast. Multibeam swath seabed imaging was used to characterize the seabed at each site prior to SUCS and Agassiz trawl deployments. The SUCS has both still and video camera, together with twin variable intensity lights, all of which are controllable from a desktop computer on ship. In addition, a USBL (Ultra Short Base Line) transponder mounted on the frame corrects for the difference in position of the lander and the ship so that an accurate GPS (Global Positioning System) position is obtained. At each deployment site, approximately 20 separate high resolution images (5 MP, of area 0.5 square meters) were captured, each at least 5 m distant from their

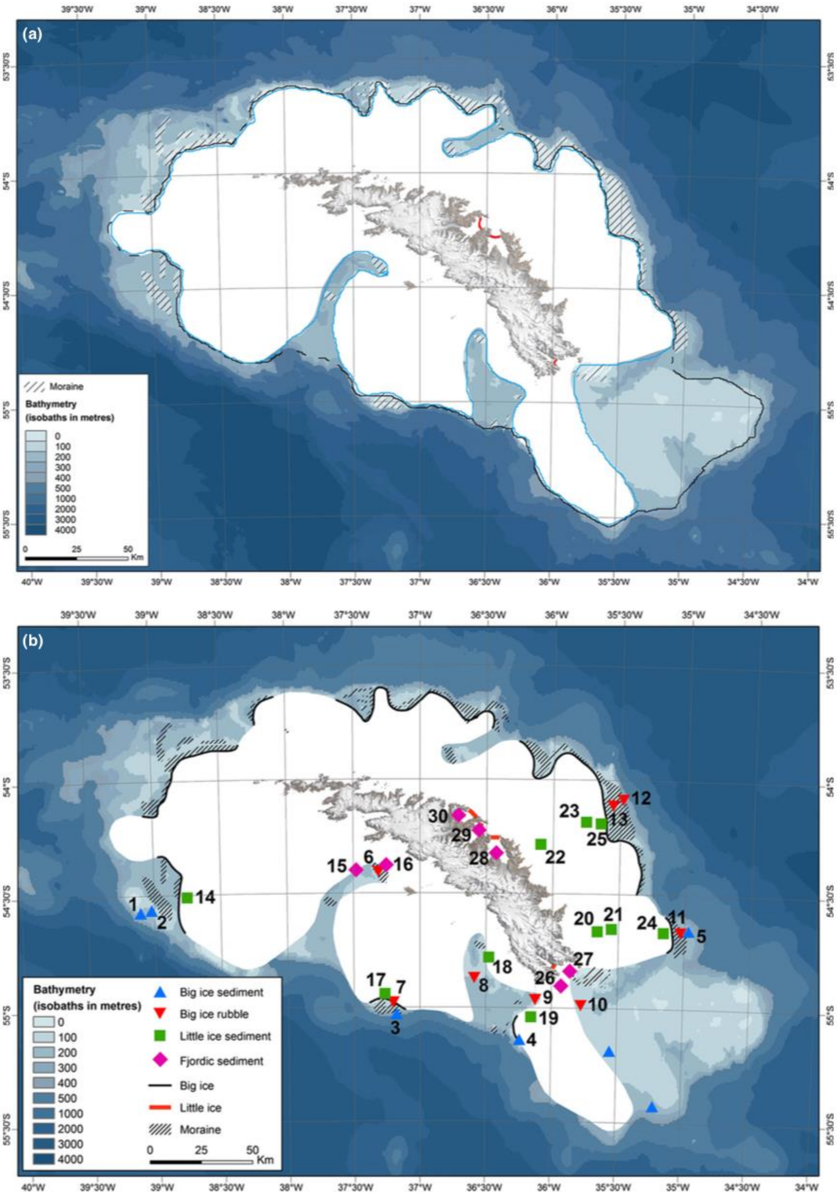

Figure 1 The continental shelf of South Georgia showing the position of moraines, sample localities and varying estimates of the maximum limit of grounded-ice sheet during the Last Glacial Maximum (LGM). (a) The suggested positions of the LGM under three competing hypotheses H_1 big ice (black line), H_2 'little ice' (red line) and H_3 'little-big ice' (blue line). (b) Shelf Underwater Camera System (SUCS) sites with associated numbers, and two additional Agassiz trawl-only samples (sites 31 and 32) are shown without associated site numbers (bottom right).

nearest neighbour image. In addition to the image collections, a 2 m wide Agassiz trawl with 1 cm mesh size was used, at a distance (length of cable out) of 1.5× depth. We used a protocol of a 5 min tow at 1 knot, which equated to a distance of 350 m (150 m actual trawl distance + 200 m while hauling in) giving an approximate area of 700 square metres. In total, 67 Agassiz trawl deployments were made across the same locations as the SUCS (see Table S1 in Appendix S1 in Supporting Information and Fig. 1b) and at an additional two locations (where technical problems prevented SUCS deployments). From the Agassiz trawl samples, two taxonomic groups, cheilostomatid bryozoans and demosponges (selected for high richness and likely low dispersal ability) were identified to the lowest possible taxonomic levels. There are cheilostomatid and demosponge species known with planktonic larvae, even in Antarctica, but these are very few (e.g. the bryozoan *Harpecia spinosissima*, Hayward, 1995 and the sponge *Mycale acerata,* Barthel & Gutt, 1992). The cheilostomatid and demosponge species found in the current study are all sessile as adults and (other than the brief planktonic phase of *M. acerata*) are known or thought to reproduce by either brooding benthic larvae or by direct development.

The SUCS images were examined using Corel Paintshop Pro. Each image was magnified to view 1/4 image full screen. Approximately 15 min was taken per image to discern all possible fauna aided by manipulation of brightness and contrast levels. All fauna was identified to the lowest taxonomic level possible (with the aid of trawl specimens from the same locations). We examined richness of study sites under three competing hypotheses; H_1 'big ice' (black line, Fig. 1a), H_2 'little ice' (red line, Fig. 1a) and H_3 'little-big ice' (white with blue line, Fig. 1a). With these hypotheses were other potential explanatory variables of benthic richness, which included substratum type, depth and distance from coast, and were treated as covariates using GLM ANOVA. The factors considered were; (1) glaciation, 2 levels. These levels were inside or outside each hypothesized limit (Fig. 1a - red for 'little ice', H_2; black for 'big ice', H_1 and blue for 'little-big ice' H_3); (2) substratum, 2 levels. These were soft or hard. (3) depth, which was the mean reading of the multibeam system during deployments at each site to the nearest meter. (4) distance from coast, recorded as distance from deployments at each site to nearest land, using great circle distance on ARCGIS software. We saw no indication from any of the SUCS images or from the multibeam swath seabed imaging that any of the study sites had been scoured by icebergs, so this was not included as a factor.

Ordination is generally considered the most powerful and visual way of comparing multidimensional data sets of this type (multiple species across multiple sites with multiple factors). We used the ordination technique, non-metric multidimensional scaling (nMDS) in the software package PRIMER 7 to compare whole assemblage composition-by-site (from SUCS images). This technique preserves the rank order distances among samples and depends on only a biologically meaningful view of the data (Clarke, 1993). Statistical analyses of such patterns were performed using the test ANOSIM (analogous to two way ANOVA), which has been developed for ecological taxa-in-samples data for comparisons of groups of samples – it replaces the classic multivariate equivalent (MANOVA) which would have problems with the formal lack of independence of samples in ordination space. Primarily MANOVA was not used because multivariate distributions were not normal nor samples equal. Primary and database literature was used to investigate the reproductive traits (as far as was known) for all sampled taxa present to assign each to brooder or non-brooder status. Overall and brooder richness is reported for the SUCS samples. The distribution of two model taxa are reported from the Agassiz trawls samples – cheilostomatid bryozoans and demosponges. These were selected on the basis of polar representatives having limited dispersal capabilities due to adults being sessile and larvae being benthic (bryozoans) and brooded (demosponges) (see respective sections in SCAR-MarBIN.be).

RESULTS

Analysis of SUCS images revealed the epifauna to comprise 13 phyla, 24 classes, 47 orders and 71 morphotypes represented across the 30 study sites (comparable with tropical and richer than temperate or polar past deployments of the same apparatus, for example, see cruise reports JR230, JR287, JR864 in British Oceanographic Database Centre). Identification of the Agassiz trawl samples revealed 52 and 48 species of the two selected study taxa, cheilostomatid bryozoans and demosponges, respectively (Tables S2 and S3). GLM ANOVA of whole assemblage data showed, unsurprisingly, that a) substrate type was a highly significant covariate, b) depth was not a significant factor and c) each of the three glaciation extent hypotheses varied in their significance. The significance increased from H_2 'little ice' ($F = 1.7$, $P = 0.2$, Table 1a) through H_1 big ice ($F = 4.9$, $P < 0.04$, Table 1b) to the best fit H_3 'little-big ice' ($F = 8.9$, $P = 0.006$, Table 1c) scenario. Notably the H_3 'little-big ice' was even more significant than the substratum covariate. Given the significant effect of substratum we re-ran the analysis just using data from sites using the reduced data set of sediment only sites as this was the only substratum types within all H_1, H_2 and H_3 limits. We found that our alternate hypothesis, H_3 'little-big ice', was overwhelmingly the most important factor of those we could measure ($F = 13.2$, $P = 0.002$, Table 1d).

An nMDS was constructed from 500 permutations, which reached a minimal stress level of 0.134, to visualize the composition of the biodiversity data. This nMDS showed that epifauna composition (from SUCS images) was not randomly distributed (Fig. 2). Coarse glacial debris from the moraines (red triangles in Fig. 2) and outer sediments (blue triangles) all occurred to the left of all other sites, with fjords being noticeably the most dispersed group (probably due to being so species-poor). Habitat suitability was clearly important in assemblage structuring; however, muddy seafloor sediments outside moraines (blue triangles in Fig. 2) were distinct from those inside moraines (green squares in Fig. 2).

Table 1 GLM ANOVA of benthic taxonomic richness of sites at South Georgia under the best fit hypothesis, H_3 'little-big ice' scenario (white in Fig. 1). The data were all fauna identified from camera lander (SUCS) images.

Source of variation	*df*	*Adj SS*	*Adj MS*	*F ratio*	*P*
(a) All richness data, H_2					
Glaciation (H_2)	1	196.7	196.7	1.7	0.2
Substratum	1	184	184	1.6	0.2
Depth	1	107.3	107.3	1.0	0.3
Distance from coast	1	168.7	168.7	1.5	0.2
Error	27	3060.1	113.3		
Total	31	3935.9			
(b) All richness data, H_1					
Glaciation (H_1)	1	502.2	502.2	4.9	0.04*
Substratum	1	444.9	444.9	4.4	0.05*
Depth	1	78.6	78.6	0.8	0.39
Distance from coast	1	0.0	0.0	0	0.99
Error	27	2754.8	102.0		
Total	31	3935.9			
(c) All richness data, H_3					
Glaciation (H_3)	1	470.7	470.7	8.9	0.006**
Substratum	1	399.9	399.9	7.6	0.01*
Depth	1	4.0	4.0	0.1	0.8
Distance from coast	1	17.2	17.2	0.3	0.6
Error	27	1423.1	52.7		
Total	31	3935.9			
(d) Just sediment sites					
Glaciation (H_3)	1	216.0	216.0	13.2	0.002**
Depth	1	3.8	3.8	0.2	0.6
Distance from coast	1	24.2	24.2	1.5	0.2
Error	19	311.3	16.4		
Total	22	883.7			

P values are shown ($*P < 0.05$ and $**P < 0.01$).

Of the factors considered (glaciation, substratum and depth) only one of these factors, glaciation, could the simplest division, that is, a single line, separate sites within and outside the factor, be constructed. This was true even of moraines well away from the shelf break (such as sites 6, 8–10, Fig. 1b). ANOSIM (*Global* $R = 0.4$, $P = 0.01$) revealed this outer and inner fauna significantly differed – coinciding with the approximate position of the 'big ice' LGM hypothesis of Graham *et al.* (2008). The most important taxonomic group driving these differences was the cheilostomatid bryozoans (the richest group present, with six recognizable morphotypes in SUCS images). The ophiuroid echinoderms were the most ubiquitous group present – the only group that was observed at every study site, Figs S1 and S2 in Appendix S1).

The richest class and order (within SUCS images), with 14 and 6 recognizable morphotypes, were the two model groups of the demosponges and cheilostomatids, respectively. Reflecting a division demonstrated in the nMDS plot and confirmed with group CLUSTER analysis (SIMPROF test), richness was highly unevenly distributed; moraines and sediment outside these were significantly richer than the shelf sediments and fjords inside them (ANOVA, $F = 22.4$, $P < 0.001$). Of the taxa reported in literature as the lowest potential dispersers, that is, those that have sessile or sedentary adults and brood or have benthic larvae, richness differences were even stronger (3–6×) (Table 2, ANOVA, $F = 30.4$, $P < 0.001$). Plotted by distance (i.e. towards the coast) from the approximate position of the 'big ice' LGM hypothesis of Graham *et al.* (2008), the richness gradient of both epifauna and especially brooders was very steep (Fig. 3). This implies that some, but very little, dispersal onto the inner shelf has taken place.

Analysis of Agassiz trawl samples yielded 67 cheilsotomatid bryozoan species of which 64 were identifiable to known species (Table S2 in Appendix S1). In terms of richness (Table 2), the bryozoans occurring on moraines and

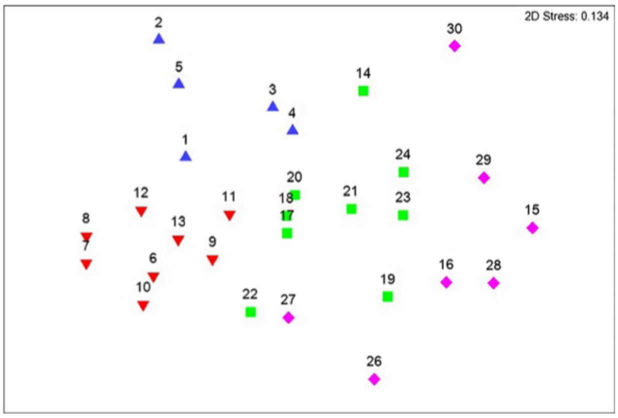

Figure 2 Biological similarity of SUCS sample data by site at South Georgia, using non-metric multidimensional scaling (nMDS), using square-root transformation and a Bray–Curtis similarity index. Site numbers (see Fig. 1) are shown, and the colours represent sediments (blue) and moraines (red) suggested as older than LGM vs. sediments (green) and fjords (purple) suggested as younger than LGM. Significant test statistic *Global R* 0.488, $P = 0.001$. Site 25 is not shown as samples were not considered comparable (lighting malfunction).

Table 2 Mean richness (with standard error) for four major continental shelf habitat types at South Georgia, Southern Ocean. The data are richness of genera per m^2 (from camera lander images) and per trawl (from Agassiz trawl deployments).

Richness per m^2 or trawl	'Outer' sediment	'Outer' moraine	Shelf sediment	Fjordic
Mean epifauna richness (camera lander)	12.2 (2.6)	25 (3.2)	8.7 (3.2)	7.0 (1.7)
Mean brooder richness (camera lander)	6.4 (1.5)	15.1 (2.6)	1.9 (0.6)	2.2 (0.8)
Bryozoan species (trawl)	9.2 (1.7)	11.0 (1.2)	3.42 (0.8)	2.25 (0.9)
Porifera species (trawl)	5.6 (0.5)	7.3 (1.7)	1.7 (0.7)	0.8 (0.6)

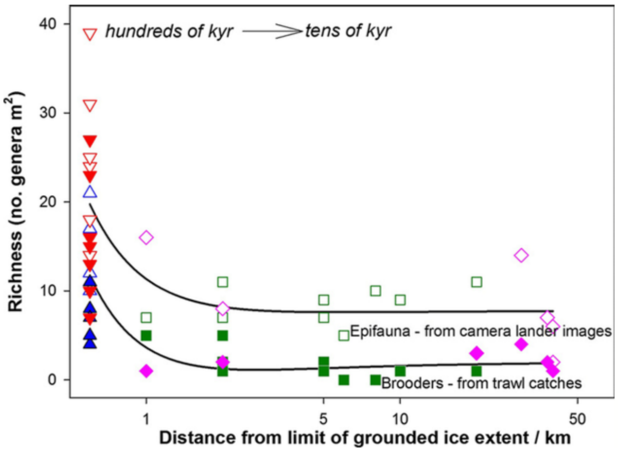

Figure 3 Richness of epifauna and epifaunal brooders from the estimated position of Last Glacial Maximum (LGM) grounded ice at South Georgia. Approximate inferred ages of assemblages are also shown below the *x* axis. Data are richness calculated from (SUCS) camera lander imagery. Lines of best fit are significant inverse second order regressions ($r^2 = 0.42$ and 0.5, both $F > 9.8$, $P < 0.001$).

sediment outside these were significantly (3×) richer than the shelf sediments and fjords inside them (ANOVA, $F = 51.9$, $P < 0.001$). There were also two striking points about the bryozoan species distributions, both pertinent to the likelihood of grounded ice (and thus recent shelf reinvasion). The species found on sediments and fjords within the moraines were entirely a subset of those found on moraines and shelf-break sediments. Secondly, all species found on mid-shelf sediments and fjords were either erect-frondose morphologies or species that were found as epibiota of such morphologies. This is important because erect species are easily uprooted or fragmented by benthic disturbance (e.g. ice scour or storms – dkab pers. obs.) but remain alive and thus may drift and recolonize wherever they are deposited.

In the same samples, 48 sponge morphotypes were recorded of which 15 could be assigned to known species (Table S3 in Appendix S1). Sponges showed similar patterns to those of the bryozoans. Those on outer moraine and sediment sites were four times richer than those of the inner shelf, and like the bryozoans, were entirely a subset of the species beyond the approximate 'big ice' line of LGM hypothesis of Graham *et al.* (2008). A search of databases and literature for South Georgia shelf depths (< 500 m) at the time of the fieldwork showed existing biodiversity records also supported these findings. In the small area not considered covered by H_1 'big ice', 16 of the 152 species only recorded there (10.5%) were South Georgia endemics compared to just 4 of 559 (<1%) of species only recorded inside (databases accessed were SCAR-MarBIN, WoRMS, OBIS and EOL). The 16 South Georgia endemics found beyond the H_1 (and H_3) ice scenarios included gymnolaemate bryozoans, such as *Hippomonavella ramosae*, anthozoan and hydrozoan cnidarians, for example, *Mirostenella articulata* and *Lepidopora acrolophos*, respectively, bivalve and gastropod molluscs, for example, *Ennucula georgiana* and *Amauropsis powelli*, and the sponge *Hymeniacidon rubiginosa*.

DISCUSSION

Once under considerable pressure from fishing, the rich seabed biodiversity (Hogg *et al.*, 2011) around South Georgia is now in one of the world's largest Marine Protected Areas yet remains under threat at local (Whitehouse *et al.*, 2008) and regional (Gutt *et al.*, 2015) scales from multiple climate-forced changes. The current study, using similar apparatus, deployments and identification effort, found considerable differences in richness across sites. Modern factors such as substratum type, and (not measurable here) recovery from iceberg disturbance, are likely to be important factors when attempting to explain richness patterns anywhere within polar-regions. Of our three hypotheses we found no GLM ANOVA support for H_2 'little ice', some for H_1 'big ice' but

H_3 'little-big ice' emerged more important than even substratum (Table 1a–c) for explaining current marine benthic richness. Thus, the high overall richness of the region may largely be due to the small margins of the shelf not reached by grounded ice for hundreds of thousands of years. However, broad-scale analysis (0.25 × 0.25° grid squares, each ~ 600 km^2, Hogg *et al.*, 2011) reported high benthic richness within the shelf sediments even when corrected for sampling effort. We think this was because the previous analysis did not account for collection methods or collector identity (for example it seems that many samples historically collected over moraines by fisheries, with little interest or ability to make species level identifications beyond commercial species). It is difficult to meaningfully assess the impact of commercial fishing on benthic biodiversity at South Georgia, as currently it is only by long line and in water deeper than study depths, and there is little comparative data from historic bottom trawling.

Overall as a region, South Georgia's shelf is biologically rich; however, our sampling indicates that the sediment plateau part of the shelf is anomalously and surprisingly impoverished in fauna (Table 2, Fig. 3). Terrestrial life on the island occurs around the margins of the central ice cap and it seems this is mirrored on the seabed, as most richness is found around-the-margins, beyond the limits of the last glaciation. These marginal environments, with moraines left from previous glacial activity, are key areas for benthic productivity, fishing and are considered to be ancient vulnerable marine ecosystems (e.g. Taylor *et al.*, 2013). As we sampled similar habitats on the inner and outer shelf, the simplest explanation for the striking pattern of faunal discontinuity, is that the inner shelf was highly disturbed by the presence and duration of grounded ice, and is still recolonizing, whereas the outer shelf was undisturbed by grounded ice. The perceived impoverishment of Arctic shelves was considered to be due to ongoing recovery from prior grounded-ice disturbance; however, new research indicates that biological richness are far higher, and therefore, these hypotheses are undergoing revision (Piepenburg, 2005). However, our data suggest that the South Georgia shelf comprises a rich margin (undisturbed by the recent glaciation) and a large impoverished inner shelf still in recovery from recent glacial disturbance. The mainly 'round-the-margins' biodiversity distribution shows a strong fit to the geographical extent of Graham *et al.*'s (2008) LGM 'big ice' theory.

Biological data have often been used to test geological hypotheses in the Antarctic, but in most cases these have been on land or using marine fossils (e.g. Convey & Stevens, 2007). When patterns in extant marine biodiversity have been used to test geological and glaciological ideas (e.g. Vaughan *et al.*, 2011) such data have not been used to generate new specific, testable hypotheses. This study shows that on the South Georgia continental shelf marine biodiversity data is largely consistent with the 'big ice' hypothesis of an extensive, grounded-ice sheet during the LGM (Graham *et al.*, 2008), and not with 'little ice' hypothesis, which was believed to be mainly restricted to the inner shelf fjords (Hodgson *et al.*, 2014a). However, our biodiversity patterns indicate that several areas of the shelf, including some cross-shelf troughs, may have remained ice free (high brooder, bryozoan and sponge richness at sites 6, 8, 9 & 10) as well as the far eastern edge of the shelf (high richness in brooders and bryozoans in Agassiz trawls – unlabelled blue triangles in Fig. 1b). This has major implications for understanding the glacial history of the region and the contribution of South Georgia shelf in harbouring refugia for marine biodiversity. Our alternative hypothesis of an ice extent reaching the near shelf-break moraines in some places but not covering all of the troughs (H_3 'little-big ice' in Fig. 1a,b), is best supported given the results from this study. There are considerable areas of uncertainty in our schematic, particularly as there is little geological or biological evidence for where grounded ice reached its maximum extent in the south-west sector of the shelf. Crucially though, the proposed ice extent in this study (Fig. 1b) generates an easily testable hypothesis of LGM ice extent, so that future studies can collect sediment cores from both side of this proposed boundary and date the transition from glacial to post-glacial sedimentation. High shelf-break sediment richness (Table 2) suggests that habitat (glacial debris vs. sediment) did not confound our findings, but could be further tested by sampling the biodiversity of moraines well inside our hypothesized LGM position (e.g. those at the mouths of and inside the major fjords (Hodgson *et al.*, 2014a). To the best of our knowledge, this is the first time that marine biodiversity patterns have been used to suggest the presence and maximum extent of grounded ice, rather than where it was not (e.g. refugia from glacial maxima; Barnes & Kuklinski, 2010).

Gutt *et al.* (2011) and Fillinger *et al.* (2013) reported surprisingly fast colonization of the East Antarctic Peninsula regions, after the Larsen A and B ice shelves collapsed. Their results suggested that maximum growth rates and dispersal ability of some elements of marine biodiversity had been underestimated. However, ice shelves [by definition] are not grounded and the extent of previous biological colonization of the underlying continental shelf was not completely clear. We interpret the strong discontinuity of sampled benthic richness, as well as database and literature endemism, inside and outside the glacial moraines as evidence of geological youth (recently grounded ice) inside the moraines. Furthermore, the literature values potentially underestimate endemism and overestimate sampling on the moraines because many of the records there are from fishery by-catch, recorded by observers. Such observers would not have the expertise to identify most endemic species and many samples may have been pelagic only. This interpretation is particularly supported by the pattern being stronger in the least dispersing of taxa (brooders and sessile model groups, Table 2, Fig. 3). Even within such taxa, it is notable that bryozoan species found inside the moraine areas are entirely a subset of those outside. Furthermore, those bryozoan species found inside the moraines are all erect species (which can be fragmented and carried by currents) or were found to be epibionts of these. Thus, the bryozoans known from inside the moraines are all those most easily dispersed and which have a source on or outside moraines. There is an exception in the literature; the species *Harpecia spinosissima* has been found coastally in the shallows (Barnes *et al.*, 2006) – but this is one of the few polar bryozoans with pelagic larvae (Hayward, 1995).

Potential causes of benthic impoverishment on the inner shelf of South Georgia, other than benthic recolonization of the South Georgia shelf taking tens of thousands of years, are discussed. The most obvious explanation of benthic richness differences is due to either habitat type or recent massive iceberg activity. Habitat has been discussed and remains a possible cause, as regions inside the moraines are mainly composed of mud. Some support for this explanation occurs at the coarse-grained site 22 which is much richer than the muddy sediments nearby, but this remains only a less impoverished subset of the biodiversity of outer moraines. Thus, habitat seems unlikely to be seriously confounding our results because of high richness on sediments outside moraines and there are some patches of coarse glacial debris on the inner shelf (e.g. site 22) and in the inner fjords (Hodgson *et al.*, 2014a).

Massive recent iceberg activity, another potential explanation for our results, could denude sites on continental shelves (see Gutt, 2001) but we have not found evidence to support this. However, multibeam data is relatively sparse may not be of high enough spatial resolution to measure the density of iceberg scours. Furthermore, the glacier termini of South Georgia are not large enough to generate massive-scale iceberg generation – but if icebergs came from elsewhere, then larger ones would impact the outer shelf sediments and moraines first.

The hypothesis which best explains our data is H_3, that the LGM grounded-ice covering most of the shelf, (as hypothesized by Graham *et al.*, 2008), but potentially several key regions indicated no grounded-ice disturbance (white in Fig. 1). Evidence for ice covering most but not all of a regional shelf has also been found on the Antarctic continental margin, for example, in Prydz Bay (Domack *et al.*, 1998). Current data on faunal survival and diversity on Antarctic marine shelves (Barnes & Kuklinski, 2010) and ice free land (Convey & Stevens, 2007) indicates similar findings to this study; with extensive ice cover reconstructed for the LGM, but with several regions indicating little evidence of glaciation. Therefore, the 'little-big ice' scenario found at South Georgia, could with future research, be established as mirroring the pattern of glaciation found around Antarctica as a whole. The rich fauna of South Georgia (Hogg *et al.*, 2011), could have survived the glaciation in refugia, close to the shelf break, and this fauna appears to be in a process of re-invasion of the nearby grounded-ice region (Fig. 3). This process of recolonization is potentially hindered by habitat discontinuity at South Georgia, as no continuous areas of hard substrata has yet been found from the shelf break to the coast, so only the most mobile species have so far been successful in re-invading the ice-disturbed zone. If this is the case, then recovery time from grounded-ice disturbance in polar waters can be measured in thousands or tens of thousands of years.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Biodiversity indicates extent of glaciation.

BIOSKETCH

This multi-institute team all have complementary interests in Antarctic benthic biodiversity. The general focus of the research team is how polar biodiversity is structured, what drives this and how it is changing with climate-forcing. In particular, we are interested in how this influences benthic carbon accumulation, immobilization and sequestration (www.asccc.co.uk). The team spans a wide range of experience, with Barnes, Sands & Smith as senior scientists, Downey and Hogg are midway through their PhDs, and Robinson undertaking a post-undergraduate project, wintering in Antarctica.

Author contributions: D.B. and C.S. conceived the idea. D.B., C.S. and R.D. worked on the images and specific study taxa; bryozoans, ophiuroids and sponges respectively. O.H. worked on seabed physical characteristics and endemicity. B.R. undertook the ANOSIM and nMDS analyses. J.S. is a marine geologist who provided the geological context to our work.

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Biological and physical characterization of the seabed surrounding Ascension Island from 100–1000 m

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*Recent studies have improved our understanding of nearshore marine ecosystems surrounding Ascension Island (central Atlantic Ocean), but little is known about Ascension's benthic environment beyond its shallow coastal waters. Here, we report the first detailed physical and biological examination of the seabed surrounding Ascension Island at 100–1000 m depth. Multibeam swath data were used to map fine scale bathymetry and derive seabed slope and rugosity indices for the entire area. Water temperature and salinity profiles were obtained from five Conductivity, Temperature, Depth (CTD) deployments, revealing a spatially consistent thermocline at 80 m depth. A camera lander (Shelf Underwater Camera System; SUCS) provided nearly 400 images from 21 sites (100 m transects) at depths of 110–1020 m, showing high variability in the structure of benthic habitats and biological communities. These surveys revealed a total of 95 faunal morphotypes (mean richness >14 per site), complemented by 213 voucher specimens constituting 60 morphotypes collected from seven targeted Agassiz trawl (AGT) deployments. While total faunal density (maximum >300 m^{-2} at 480 m depth) increased with rugosity, characteristic shifts in multivariate assemblage structure were driven by depth and substratum type. Shallow assemblages (~100 m) were dominated by black coral (*Antipatharia *sp.) on rocky substrata, cup corals (*Caryophyllia *sp.) and sea urchins (*Cidaris *sp.) were abundant on fine sediment at intermediate depths (250–500 m), and shrimps (*Nematocarcinus *spp.) were common at greater depths (>500 m). Other ubiquitous taxa included serpulid and sabellid polychaetes and brittle stars (*Ophiocantha *sp.). Cold-water corals (*Lophelia cf. *pertusa*), indicative of Vulnerable Marine Ecosystems (VMEs) and representing substantial benthic carbon accumulation, occurred in particularly dense aggregations at <350 m but were encountered as deep as 1020 m. In addition to enhancing marine biodiversity records at this locality, this study provides critical baseline data to support the future management of Ascension's marine environment.*

Keywords: Ascension Island, benthic shelf, marine biodiversity, tropical South Atlantic, Vulnerable Marine Ecosystems

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INTRODUCTION

Ascension Island is a relatively young (~1 my; Jicha *et al.*, 2013), South Atlantic Ocean island (07°57′S 14°22′W) ~80 km west of the mid-Atlantic ridge. It is extremely remote with its nearest neighbour St. Helena 1300 km to the south (Figure 1, inset). To date, most studies on the marine biodiversity surrounding the island have focussed on turtles (Weber *et al.*, 2014), seabirds (Bourne & Simmons, 2001) and shallow water coastal assemblages, typically located within depths less than 30 m (e.g. Price & John, 1980; Brewin *et al.*, 2016). The island's shallow marine biodiversity represents a unique assemblage of western and eastern Atlantic biota (Floeter *et al.*, 2007; De Grave *et al.*, in press; Tsiamis *et al.*, 2017; Wirtz *et al.*, 2017). The inshore fish community is characterized as extremely abundant with low species richness and relatively high levels of endemism when compared with other Atlantic oceanic islands (Floeter *et al.*, 2007), probably due to its young age and isolation. In comparison, invertebrate richness and diversity still needs to be quantified but is inconspicuous owing to the abundance of fish (Brewin *et al.*, 2016).

Habitat diversity in the shallow sub-littoral is comparatively limited. Being a small oceanic island (97 km^2) with no enclosed bays or sheltered lagoons, the entire coastline of Ascension is subject to large Atlantic swells. Many typical tropical coastal habitats often associated with high biological diversity such as mangroves, seagrass beds and coral reefs are absent, and the coast is dominated by volcanic rock, rhodolith (maerl) pebble and sand substrates. Coralline algal rhodolith beds, which form the only substantial biogenic

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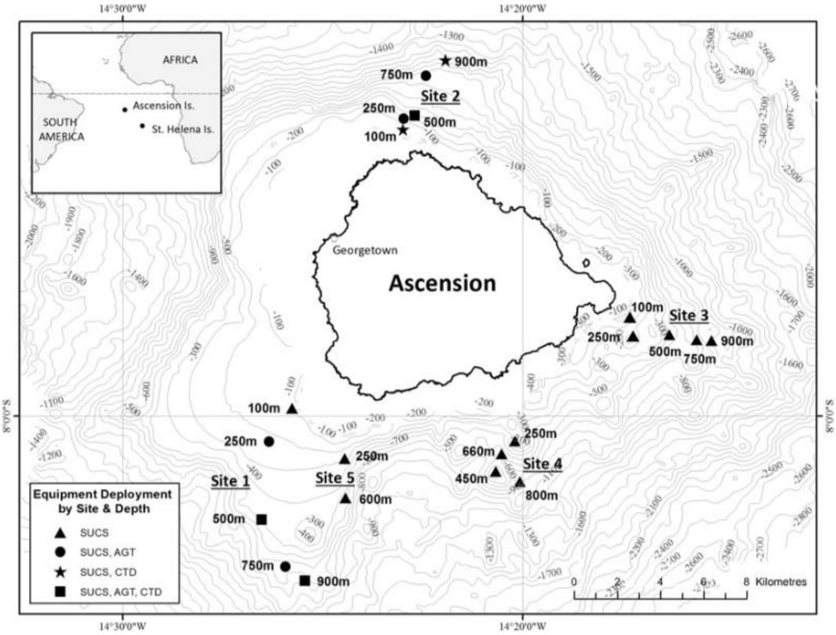

Fig. 1. Site locations showing equipment and depth. Inset: position of Ascension and St Helena Islands in the Atlantic Ocean.

three-dimensional habitat in shallow waters, are known to support a diverse infaunal community (Macaya *et al.*, 2015; Neill *et al.*, 2015; Torrano-Silva *et al.*, 2015) as well as being important in carbon cycling (Nelson, 2009; Cavalcanti *et al.*, 2014).

Although recent work has substantially advanced our understanding of Ascension's coastal marine environment (Darwin Initiative projects EIDCF012 and DPLUS021), data on benthic communities and habitats below a depth of 30 m are still remarkably rare. The marine biota of Ascension has been of interest to scientists since the 19th century, with famous expeditions such as 'Challenger' and 'Discovery' visiting the island in 1876 and 1925 respectively (Manning & Chace, 1990). These early scientific expeditions were among the only previously known attempts to systematically sample Ascension's deep-water benthos and although they contributed much to the identification of certain taxa, did little to improve our understanding of the ecology of the benthic marine environment. Given the narrow fringe of shallow, coastal water that is accessible to divers, much of Ascension's shelf ecosystem therefore remains largely undiscovered.

Knowledge of seafloor topography and habitats is similarly sparse. The UK Hydrographic Office navigational chart of the area is constructed from data collected between 1826 and 1984 and is focussed on areas surrounding the main anchorages. More complete coverage is provided by the General Bathymetric Chart of the Ocean (GEBCO), but resolution is coarse at 30 arc-seconds (~2 km) and not sufficiently detailed for mapping variation in seabed topography at the scale typically of interest for ecological studies.

This study was developed as an objective of the Darwin Initiative-funded Ascension Island Marine Sustainability project (DPLUS021) aimed at addressing some of the key knowledge gaps relating to Ascension Island's deeper water ecosystem and was conducted aboard the Natural Environment Research Council research vessel the Royal Research Ship 'James Clark Ross' (hereafter JCR) during 14–18 October 2015. The study's main objectives were: (1) to map Ascension Island's shelf seabed bathymetry and characterize spatial variation in seafloor structure and topography; (2) to identify, quantify and compare benthic assemblages to fine scale seabed characteristics between 100 and 1000 m; and (3) to collect benthic specimens for identification from previously unsampled areas.

MATERIALS AND METHODS

The sampling protocol utilized during the Ascension Island cruise (cruise identifier JR864) was adapted from previous continental shelf biodiversity survey expeditions conducted aboard the JCR (e.g. JR262 and JR287; Barnes *et al.*, 2011, 2013) and incorporated four key aspects: (1) fine scale bathymetry (multibeam echosounder); (2) temperature and salinity profiles (Conductivity-Temperature-Depth [CTD]), (3) benthic habitats and faunal assemblages (Shelf

Underwater Camera System [SUCS]) and (4) biological specimen collection (Agassiz trawl [AGT]).

Fine scale bathymetry

A Kongsberg EM122 multibeam system was used, run through the Kongsberg SIS software. The system was run in external trigger mode with the ping rate calculated by the Kongsberg Synchronization Unit (K-Sync). The number of cells in the processing grid was set to 128 × 128 and the grid cell size was set to 50 m. Angular coverage mode was set to manual and beam spacing to high density equidistant. The maximum beam angle was varied from 50° to 75° depending on the sea state, water depth and bathymetry, often on the slope the uphill beam was extended much further than the downhill beam to try and maximize data capture.

In addition to water depth, several derived bathymetric datasets were also extracted from multibeam data to describe spatial variation in aspects of seabed structure and topography that may influence biological assemblages and species distributions. Derived datasets included slope, terrain ruggedness index (TRI) and topographic position index (TPI). Slope was calculated as a measure in degrees (°) of the inclination of the seabed using Landserf (version 2.3) multi-scale analysis. TRI is a measure of seabed rugosity calculated using SAGA GIS (version 2.0) and is derived by comparing the 2-dimensional footprint area of the seabed versus the 3-dimensional area of the bathymetry dataset. A data point that differs in depth most from the mean depth of the surrounding cells will have the highest TRI. Topographic position index (TPI) is a local elevation index which measures the relative topographic position of each bathymetric point in relation to its neighbours. TPI is a useful tool in identifying landscape features and topographic boundaries at different spatial resolutions and provides an indication as to whether a site is located on a peak, in a valley or in a region of constant gradient. TPI was calculated using the Land Facet Corridor Tools extension for ArcGIS.

Data from derived bathymetric datasets were used to select five broad sampling site locations (Figure 1), representing as wide a range of bottom topography (or habitats) as possible over depths of 100 to 1000 m to deploy CTD, SUCS and AGT apparatus (Table 1).

Temperature and salinity profiles

A CTD unit was used to vertically profile the water column. The SBE9Plus unit held dual SBE3Plus temperature and SBE4 conductivity sensors and a Paroscientific pressure sensor. The CTD was raised as close to the surface as sea conditions allowed and then lowered to within 10 m of the seabed.

Table 1. Site locations, depths and unique identifiers for all deployments.

Event name	Latitude	Longitude	Depth (m)	SUCS photos
SUCS 1	S 08°4′7.068″	W 14°25′26.904″	880	20
SUCS 2	S 08°3′46.440″	W 14°25′56.208″	770	20
SUCS 3	S 08°2′35.232″	W 14°26′31.740″	500	20
SUCS 4	S 08°0′38.592″	W 14°26′21.012″	220	20
SUCS 5	S 07°59′47.832″	W 14°25′46.236″	110	20
AGT 1	S 08°0′31.104″	W 14°26′32.352″	210	
AGT 2	S 08°2′33.288″	W 14°26′34.368″	500	
AGT 3	S 08°3′47.520″	W 14°26′0.960″	770	
AGT 4	S 08°3′59.796″	W 14°25′34.680″	840	
CTD 1	S 08°4′13.512″	W 14°25′20.352″	880	
CTD 2	S 08°2′27.744″	W 14°26′40.596″	500	
CTD 3	S 07°51′5.400″	W 14°21′56.592″	960	
CTD 4	S 07°52′29.748″	W 14°22′41.448″	340	
CTD 5	S 07°52′49.620″	W 14°23′0.240″	120	
SUCS 6	S 07°52′49.476″	W 14°23′0.096″	120	20
SUCS 7	S 07°52′33.024″	W 14°22′59.088″	260	20
SUCS 8	S 07°52′28.704″	W 14°22′42.780″	340	20
SUCS 9	S 07°51′29.016″	W 14°22′25.464″	750	20
SUCS 10	S 07°51′8.784″	W 14°22′0.156″	890	20
AGT 5	S 07°51′29.880″	W 14°22′31.764″	750	
AGT 6	S 07°52′29.388″	W 14°22′48.108″	330	
AGT 7	S 07°52′33.600″	W 14°22′53.940″	230	
SUCS 11	S 07°57′31.032″	W 14°17′19.248″	110	20
SUCS 12	S 07°57′59.112″	W 14°17′15.000″	210	20
SUCS 13	S 07°57′57.744″	W 14°16′20.496″	500	20
SUCS 14	S 07°58′4.944″	W 14°15′39.420″	800	20
SUCS 15	S 07°58′6.060″	W 14°15′17.172″	1020	11
SUCS 16	S 08°0′37.404″	W 14°20′12.228″	280	20
SUCS 17	S 08°0′56.664″	W 14°20′31.776″	670	20
SUCS 18	S 08°1′22.944″	W 14°20′40.920″	480	20
SUCS 19	S 08°1′38.172″	W 14°20′4.452″	850	20
SUCS 20	S 08°1′3.828″	W 14°24′27.540″	280	20
SUCS 21[a]	S 08°2′2.400″	W 14°24′25.884″	500	7

[a] Excluded from analyses owing to small sample size.

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CTD data was collected using software Seasave Win32 (Sea-Bird Electronics, Inc). A total of five CTD deployments were undertaken (Table 1), two from the south-west of Ascension at depths of 900 and 500 m, and three to the north of the island at depths of 900, 300 and 100 m (Figure 1). CTD deployments did not take place at other locations due to time constraints.

Benthic habitats and faunal assemblages

The SUCS was used as a tool allowing insight into the conditions of the underwater landscape and investigation of the micro-scale topography of the benthic environment. SUCS imagery can also be used to estimate faunal richness and density of the benthos.

The SUCS consists of three units: (1) the laboratory-based imaging control; PC with monitor (for camera and lighting control), a cable-metering sheave indicator and deck box; (2) the deck-based deployment control; winch, underwater cable, deck monitor and metering sheave on the mid-ships gantry; and (3) the underwater camera lander unit; tripod frame with underwater housed video and stills camera, booster and power distribution board and the underwater lights.

The SUCS was deployed from the mid-ships gantry on a fibre-optic cable connected to a motorized winch system, dropping at a rate of 30 m min^{-1} until it sat and stabilized on the seabed, video and photo stills were taken using the SUCS software. The system allows high-resolution photo stills (2448 × 2050 pixels), with a field of view fixed to 0.25 m^{-2} on a flat surface, and video footage (2448 × 2050 pixels) to be taken simultaneously that produces a live feed in full colour and in HD (2448 × 2050 pixels). A photo was taken as soon as the system was settled on the seabed, the system was then lifted clear of the bed and moved ~5 m in one direction, this was repeated to achieve 20 photos (i.e. 5 m^{-2}) taken over an approximate horizontal distance of 100 m. The SUCS was deployed a total of 21 times at approximate depths of 100, 250, 500, 750 and 900 m (Table 1).

Sessile and mobile benthic fauna observed in SUCS photos were distinguished according to morphotype, as a proxy for taxonomic group (species, genus or class), and enumerated. To allow faunal assemblage structure to be related to benthic habitat characteristics, SUCS photos were categorized according to (1) roughness, on a scale from 0 (smooth mud or fine sand) to 5 (complex 3-dimensional cover), and (2) dominant substratum type, on a scale from 0 (silt) to 8 (boulders or bedrock; Table 2).

Data analyses

For each transect, faunal counts were summed and divided by accumulated photo area to obtain densities of individual morphotypes, which were used to calculate morphotype richness (S) and evenness (Simpson's $1 - \lambda$) (Table 3). Owing to an exceptionally low sample size ($N = 7$), the 500 m-depth transect at site 5 (SUCS21) was excluded from further analyses.

Transects were ranked according to average roughness, determined from the mean of the ordinal roughness categories (Table 2) assigned to individual photos. Additionally, the relative proportions of photos within the nine substratum categories (Table 2) were used to estimate the per cent cover of different substrata (i.e. silt, fine sand, coarse sand, small pebbles, large pebbles, cobbles, small rocks, large rocks and boulders/bedrock) along each transect. Thus, nine separate variables, each representing the per cent cover of a different substratum type, were assigned to individual transects.

Table 2. Classifications used for roughness and substratum identification across SUCS imagery.

Roughness	Description
0	Completely smooth (mud/fine sand)
1	Sand waves/ripples/small pebbles
2	Scattered rocks
3	Scattered larger rocks/bedrock
4	Scattered larger rocks/bedrock covering >50% of image
5	Complex 3-D cover

Substratum	Description
0	Silt
1	Fine sand
2	Coarse sand
3	Fine pebbles
4	Coarse pebbles
5	Cobbles
6	Rocks
7	Large rocks
8	Boulder/bedrock

Subsequent analyses focussed on the relationships of environmental variables (transect depth, average roughness and percent cover of substrata) with (1) univariate faunal abundance and diversity indices (average density [i.e. the sum of the densities of individual morphotypes], richness and evenness of morphotypes, each represented by a single value per transect) and (2) multivariate faunal assemblage structure.

Table 3. SUCS transect depths, average faunal densities and univariate diversity indices (morphotype richness and evenness). Density, richness and evenness are overall values calculated for each transect as a whole; richness is not standardized by transect area.

Transect	Depth (m)	Density (m^{-2})	Richness (S)	Evenness ($1 - \lambda$)
SUCS1	880	1.2	4	0.72
SUCS2	770	3.6	8	0.82
SUCS3	500	3.6	10	0.86
SUCS4	220	7.8	12	0.77
SUCS5	110	24.6	9	0.48
SUCS6	120	6.4	13	0.81
SUCS7	260	23.8	23	0.89
SUCS8	340	17.2	20	0.87
SUCS9	750	1.4	6	0.82
SUCS10	890	4.6	14	0.91
SUCS11	110	21.2	16	0.55
SUCS12	210	41.4	24	0.65
SUCS13	500	154.8	19	0.11
SUCS14	800	43.2	19	0.41
SUCS15	1020	6.5	11	0.88
SUCS16	280	46.4	24	0.63
SUCS17	670	2.6	10	0.88
SUCS18	480	313.8	18	0.08
SUCS19	850	22.8	16	0.72
SUCS20	280	19	15	0.82
SUCS21	500	34.3	13	0.72

Spearman rank correlations were used to determine whether average density, richness and evenness varied with transect depth and average roughness. For the purpose of these analyses, richness was standardized by transect area to account for differences in the number of photos among transects (i.e. between SUCS15 and the others). To test for relationships between the same three univariate indices and substratum characteristics, Mantel tests were performed on Euclidean distance matrices derived from both response data and multivariate substratum per cent cover data (i.e. nine variables), with 9999 permutations of the response matrix to evaluate significance (Legendre & Legendre, 2012).

Prior to multivariate analyses, pairwise Spearman rank correlations were used to assess the extent of collinearity among environmental variables (i.e. average roughness and nine substratum variables). Average roughness showed strong ($|\rho| \geq |0.70$) positive correlations with per cent cover of small rocks ($r = 0.85$) and large rocks ($r = 0.79$); therefore, roughness was excluded from further analyses. Subsequently, the biota-environment (BIOENV; Clarke & Ainsworth, 1993) routine was used to identify the optimal subset of environmental variables accounting for variability in faunal assemblage structure, via maximization of the rank correlation between environmental and biological distance matrices. The variables identified by the BIOENV analysis were then used in a canonical analysis of principal coordinates (CAP; Anderson & Willis, 2003) to enable dissimilarities in faunal assemblages among transects to be visualized in the context of key environmental variables. The resulting ordination plot incorporated vectors representing Spearman rank correlations between environmental variables and the first two CAP axes. The significance of the overall model (based on the sum of all eigenvalues) and of constraining variables (marginal terms) were assessed via ANOVA-like permutation tests involving 9999 permutations. Spearman rank correlation coefficients between individual morphotype densities and CAP axes (Anderson & Willis, 2003) were calculated to identify the most important morphotypes (i.e. $|\rho| \geq 0.5$) contributing to variability in assemblage structure. Additionally, non-metric multidimensional scaling (nMDS) plots, unconstrained by environmental variables, were produced to show the overall pattern of faunal dissimilarities and variation in morphotype densities among transects.

Multivariate analyses were performed using Euclidean distances calculated from environmental data, which were *z*-standardized to account for scaling differences between depth and substratum variables, and Bray–Curtis dissimilarities calculated from individual morphotype densities, which were $\log_{10}(x + 1)$-transformed to downweight the influence of numerically dominant species. Exclusion of rare morphotypes (i.e. overall mean density ≤ 0.01 m^{-2}) did not alter results substantially; therefore, analyses incorporated all morphotypes.

All analyses were conducted in *R* (version 3.2.0; R Core Team, 2015), in particular, using the functions *mantel()*, *bioenv()* and *capscale()* in the *vegan* package (version 2.3–5; Oksanen *et al*., 2016).

Benthic specimen collection

An Agassiz trawl (AGT) was used to sample the larger macro- and mega-fauna from the benthic environment. The AGT had a mesh size of 1 cm and a mouth width of 2 m. The cable length used was 1.5 times the water depth and was towed at 1 knot for 5 min from the ship's stern. The AGT was deployed seven times across depths of ~250, 500, 750 and 900 m (Table 1), where practicable, given the steep and abrasive topography. Samples were brought on-board and identified according to lowest possible taxonomic unit. Subsequent analysis of samples and photography records were undertaken back at the Ascension Island Government Fisheries Laboratory in the days following the cruise. Specimens that could not be identified were sent to taxonomic specialists.

RESULTS

Fine scale bathymetry

Near-complete bathymetric coverage for ocean depths from 100 to 1000 m around Ascension Island resulted from the survey (data available on request from the Polar Data Centre). Typically, the seabed is a narrow extension radiating from the island to a depth of ~450 m (Figure 2A). On the north-west and especially the south-west of the island, the seabed extends out to 450 m in a plateau which at its widest point is 7 km offshore, beyond 450 m depth the angle of the slope of the seabed increases considerably reaching 1000 m depth within 1 km (Figure 2B). This drop-off is most pronounced along the north-west coast of the island (and to the east of the large south-eastern plateau) where the seabed inclination reaches a near-vertical 78°. The slope around the island is punctuated by large topographic features rising from depths over 1000 m to, in places on the south coast, as shallow as 250 m. This complexity in the topography creates regions of high rugosity (roughness) over broad spatial scales (50 m) (Figure 2C) and large variation in TPI (Figure 2D), which may equate to greater habitat variability.

Temperature and salinity profiles

Temperature profiles around Ascension were characterized by warm surface waters (24 °C), with the top 80 m of the water column falling in a narrow temperature range of 22–24 °C. A sharp thermocline at ~80 m was identified at all deployments, with temperatures rapidly dropping to 17 °C and then continuing to drop to ~12 °C by 200 m. Below 200 m water temperature decreased to 10 °C at 300 m, 8 °C at 500 m and 5 °C at 900 m. At all deployments temperatures were seen to stabilize at ~5 °C below 800 m (Figure 3).

Salinity was recorded at 36.2 psu from 0–40 m water depth at all sites. Salinity increased between 50 and 60 m, peaking at ~36.5 psu, before decreasing with depth to ~35.0 psu at 200 m. Salinity stabilized at 34.5 psu deeper than 600 m (Figure 3).

Benthic habitats and faunal assemblages

A total of 95 morphotypes were distinguished using SUCS footage obtained from depths of 110–1020 m, of which 57 could be assigned preliminarily to genus, representing 21 identifiable classes within 12 Phyla (Supplementary Material, Table S1). Images revealed a series of characteristic faunal assemblages associated with particular substratum types that varied across the range of depths sampled (Figure 4A–F). Across all 21 transects, mean (±SE) average faunal density

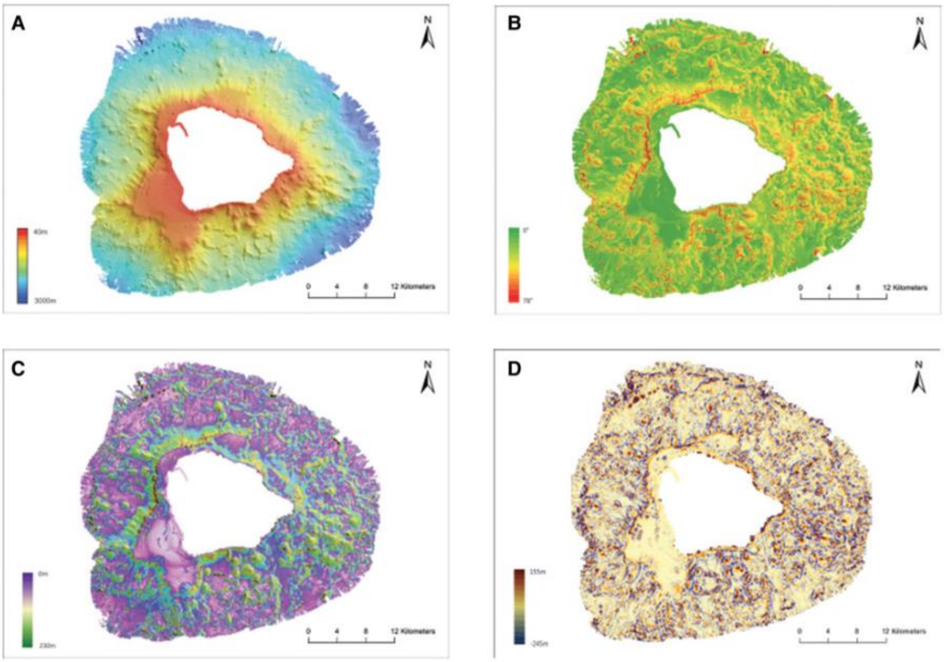

Fig. 2. (A) Bathymetry dataset gridded to 50 m resolution; (B) the measure in degrees (°) of the inclination of the seabed; (C) Terrain Ruggedness Index (TRI); (D) Topographic position index (TPI).

was 38.1 ± 15.6 m^{-2} (range 1.2–313.8), while mean morphotype richness and evenness were 14.5 ± 1.3 (4–24) and 0.7 ± 0.1 (0.1–0.9), respectively (Table 3).

The most abundant morphotype was the brittle star *Ophiacantha* sp., observed on 10 transects, with an overall mean (±SE) density of 22.2 ± 15.6 m^{-2} (maximum 300.6 m^{-2}, transect SUCS18; Figure 4C). Other relatively abundant morphotypes were sabellid polychaetes (2.6 ± 1.7 m^{-2}; Figure 4E), black corals (*Antipatharia* sp.; 1.5 ± 1.0 m^{-2}; Figure 4A) and, on particular transects, squat lobsters identified as *Munida microphthalma* (2.8 m^{-2}, SUCS18) and a shrimp-like giant mysid, likely *Gnathophausia zoea* (1.8 m^{-2}, SUCS7 and SUCS16).

Polychaetes identified as *Serpula* sp. (mean density 1.3 ± 1.1 m^{-2}) represented the most widespread morphotype, observed on 12 transects. Other commonly encountered morphotypes (≥ 10 transects) included the shrimp *Nematocarcinus* sp. (0.4 ± 0.1 m^{-2}; Figure 4D) and scleractinian corals belonging to the genera *Caryophyllia* (1.6 ± 1.3 m^{-2}; Figure 4B) and *Lophelia* cf. *pertusa* (1.1 ± 0.4 m^{-2}; Figure 4F).

The only significant relationship found with respect to average faunal density was that it correlated positively with average roughness ($\rho = 0.51$, $P = 0.021$). There was no correlation between average density and either substratum characteristics (Mantel test; $\rho = -0.03$, $P = 0.578$) or depth ($\rho = -0.38$, $P = 0.097$), but there was an apparent peak in density at 480–500 m, driven by elevated densities of *Ophiacantha* sp. within transects SUCS13 and SUCS18 (Table 3; Figure 4C). Neither morphotype richness nor evenness correlated significantly with either depth (richness: $\rho = -0.17$, $P = 0.461$; evenness: $\rho = 0.32$, $P = 0.176$) or substratum (richness: $\rho = 0.06$, $P = 0.225$; evenness: $\rho = -0.05$, $P = 0.654$). Further, while evenness was not related to roughness ($\rho = -0.27$, $P = 0.258$), there was only a marginally significant positive correlation between richness and roughness ($\rho = 0.41$, $P = 0.075$).

Transect depth and per cent cover of coarse sand and large pebbles were identified as the most important environmental variables underlying variability in faunal assemblages (BIOENV; $\rho = 0.65$). All three constraints in the CAP were significant (depth: pseudo-$F_{1,16} = 3.35$, $P < 0.001$; coarse sand: pseudo-$F_{1,16} = 2.90$, $P < 0.001$; large pebbles: pseudo-$F_{1,16} = 1.87$, $P = 0.012$). Depth showed a strong negative correlation with CAP axis 1 ($\rho = -0.90$), the converse of which was true for per cent cover of pebbles (Figure 5A). The importance of depth in explaining overall dissimilarities among faunal communities was also emphasized by the unconstrained MDS plot (Figure 6A). Per cent cover of sand correlated positively with CAP axis 2 ($\rho = 0.65$), which separated transects with the lowest average roughness (i.e. SUCS1, 3, 4, 7, 9 and 17) from the rest of the samples (Figure 5A).

A total of nine morphotypes showed strong relationships ($|\rho| \geq 0.5$) with CAP axes 1 and 2 (Figure 5B). Deeper transects were associated with greater densities of *Nematocarcinus* sp., which was not found shallower than 500 m (Figure 6B),

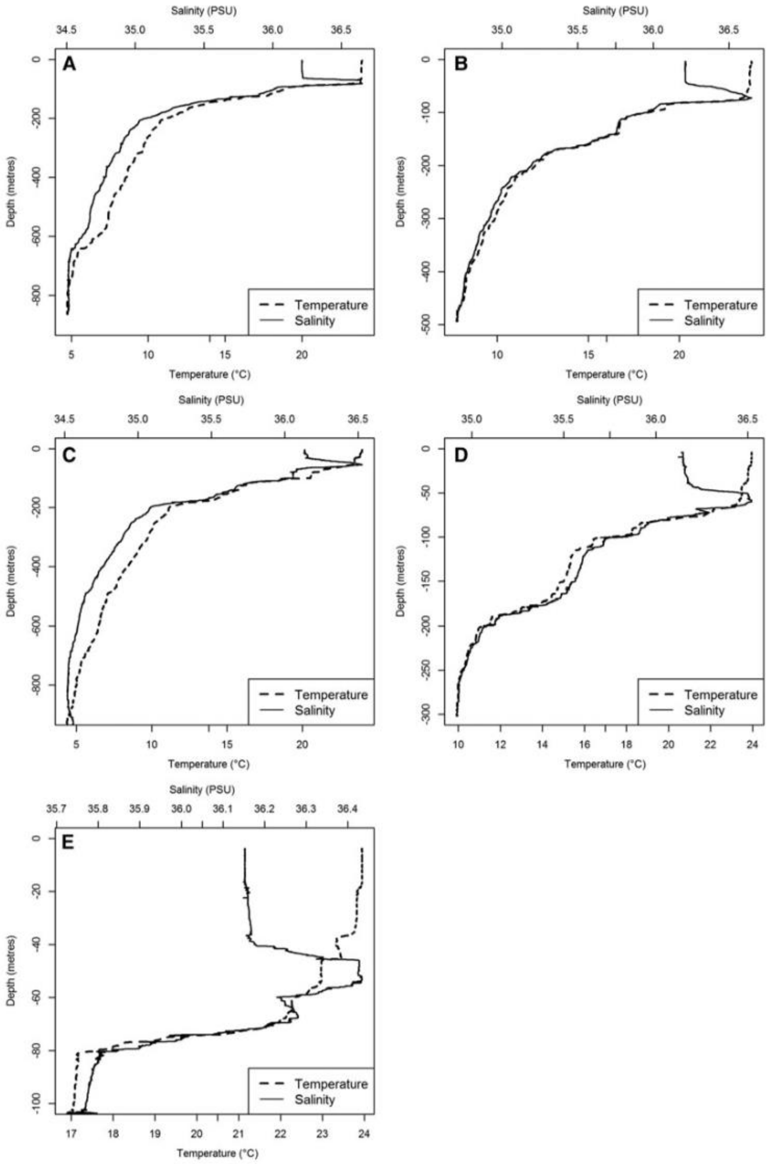

Fig. 3. CTD derived temperature and salinity profiles for each of the five deployments: (A) CTD 1; (B) CTD 2; (C) CTD 3; (D) CTD 4; (E) CTD 5.

and, to a lesser extent, sabellid polychaete and crinoid morphotypes (Figures 4E & 6C, D). While sabellid polychaetes reached relatively high densities at 800–850 m depth (SUCS14 and SUCS19; Figure 6C), they were also found on shallower transects with lower per cent cover of sand (Figure 5A). *Antipatharia* sp. and orange encrusting sponge (*Demospongiae* sp. indet.; Figure 6E) were more characteristic of shallower transects (Figure 4A) with greater per cent cover of pebbles. Although the density of *Serpula* sp. was partly related to depth (Figure 6B), this morphotype was abundant on shallower, less sandy transects (e.g. SUCS12; Figure 6F). Where present, the sea pen *Virgularia* sp. was more abundant

Fig. 4. Representative SUCS images of benthic habitats across a range of depths: (A) rocky substrata covered with black coral (*Antipatharia* sp.), encrusting algae and orange sponge (Demospongiae) at 100 m (transect SUCS5); (B) fine sediment with abundant sea urchins (*Cidaris* sp.) and scleractinian corals (*Caryophyllia* sp.) at 250 m (SUCS16); (C) large rocks with high densities of brittle stars (*Ophiacantha* sp.) at 450 m (SUCS18); (D) coarse sediment and fine pebbles inhabited by sea pens (*Virgularia* sp.), shrimps (*Nematocarcinus* sp.) and gastropod molluscs at 500 m (SUCS3); (E) large rocks associated with sabellid polychaetes and feather stars (Crinoidea) at 700 m (SUCS14); (F) boulders and bedrock supporting reefs of the scleractinian coral *Lophelia* sp. at 800 m (SUCS19). Scale bar represents 20 cm.

on transects with a higher per cent cover of sand (Figures 4D & 6B).

Benthic specimen collection

In all, the 213 specimens collected were identified into 60 morphotypes (Supplementary Material, Table S2). Samples were separated by class as follows (including the number of specimens collected in each case): Alcyonaria (4), Anthozoa (3), Bivalvia (3), Brachiopoda (2), Cirripedia (4), Crinoidea (11), Crustacea (21), Demospongia (11), Echinoidea (7), Gastropoda (5), Hexactinalida (8), Hydrozoa (2), Malacostraca (57), Ophiuridae (20), Pisces (9), Polychaetes (18), Scyphozoa (6), Sipunculida (2), Thaliacea (2),

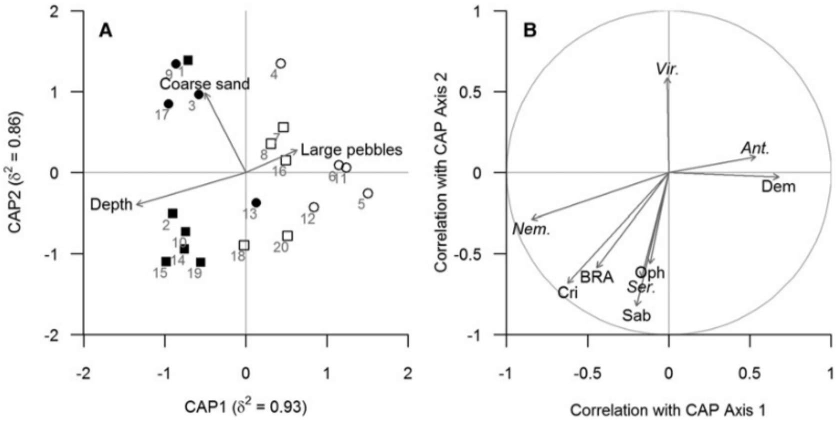

Fig. 5. (A) CAP ordination plot of faunal assemblage structure according to environmental variables (vectors represent Spearman rank correlation coefficients with axes). Point labels correspond to SUCS transect number and symbols depth category (○, 100–249 m; □, 250–499 m; ●, 500–750 m; ■, >750 m). (B) Spearman rank correlation coefficients between CAP axes and individual morphotypes for which |ρ| ≥ 0.5 (Ant., *Antipatharia* sp.; BRA, *Brachipoda* sp. indet.; Cri, *Crinoidea* sp. indet.; Dem, *Demospongiae* sp. indet.; Nem., *Nematocarcinus* sp.; Oph, *Ophiuroidea* sp. indet; Sab, *Sabellidae* sp. indet.; Ser., *Serpula* sp.; Vir., *Virgularia* sp.).

Zoantharia (18). All individuals were identified to class or lower, sorted, photographed and sent to taxonomic experts for formal identifications where necessary. Two specimens of Grenadier fish preliminarily identified as *Malacocephalus laevis* (Lowe, 1843) and *Ventrifossa* sp. (Macrouridae) are likely new records for Ascension Island.

One of the most commonly encountered species found in trawls around Ascension Island were shrimps of the genus *Nematocarcinus*, identified as *N. gracilipes* (Filhol, 1884), found between depths of 500 and 1000 m and representing 15–40% of invertebrates larger than 0.5 cm collected in samples. At a depth of 700–1000 m, most of the specimens were adults, whereas at 500 m most were juveniles. Also identified at 500 m and shallower were *N. tenuipes* (Spence Bate, 1888) and *N. faxoni* (Burukovsky, 2001). Other crustaceans also identified included a galateid *Munida* sp. (likely *Munida microphthalma*). Shrimps including *Stylopandalus richardi* (Coutière, 1905) (Pandalidae) and *Sergia* spp. (Sergestidae) and crabs *Chaceon* sp. (Geryonidae) also occurred regularly, mostly on rocky habitats between 100 and 500 m.

DISCUSSION

While our understanding of shallow marine ecosystems surrounding Ascension Island has only recently begun to improve (e.g. Weber *et al.*, 2014; Brewin *et al.*, 2016; Wirtz *et al.*, 2017), the current study represents the first detailed examination of physical and biological characteristics of Ascension's marine environment at substantially greater depths. In addition to providing extensive fine scale bathymetric data to 1000 m depth, this study generates new insight into how benthic habitats and faunal community structure vary throughout Ascension's shelf area at depths of 100–1000 m. Further, the collection of biological specimens addresses the critical lack of knowledge regarding deeper-water marine biodiversity associated with this unique and isolated oceanic island.

The detailed map of seafloor topography resulting from this study enables the quantification of benthic habitat variability at a greater scale and resolution than was previously possible for Ascension Island. These data potentially provide a basis for inferring wider distribution patterns of substratum types and faunal assemblages, and for directing future oceanographic and benthic ecological research within Ascension's marine zone. Additionally, while the number of CTD deployments was limited by logistical constraints, temperature and salinity profiles spanned the range of depths sampled for benthic habitat types and faunal assemblages, representing sites lying both north and south of Ascension Island. There is still, however, much scope for the collection of additional data to characterize variation in physical oceanographic parameters in Ascension's waters in greater detail.

Our results from the SUCS image analysis showed that the average density of benthic fauna increased with substratum roughness (rugosity), perhaps not unexpected considering that the structure of marine benthic communities and habitat heterogeneity are recognized as being inextricably linked (McClain & Barry, 2010). Further, increased habitat complexity, including roughness, is often associated with greater diversity in benthic systems (e.g. Beck, 2000; Downes *et al.*, 2000; Thrush *et al.*, 2001). However, we found no relationship between substratum roughness and measures of faunal diversity (richness and evenness) at the level of individual transects in the current study. Despite this result, benthic species diversity may be influenced by other habitat characteristics, such as sediment particle size diversity (Etter & Grassle, 1992), measured at much finer scales. It should also be noted that diversity was probably underestimated in most habitats, as many cryptic or infaunal taxa are likely to have remained undetected in SUCS imagery. This bias towards more conspicuous morphotypes could in turn mask biological patterns and their relationships with environmental variables.

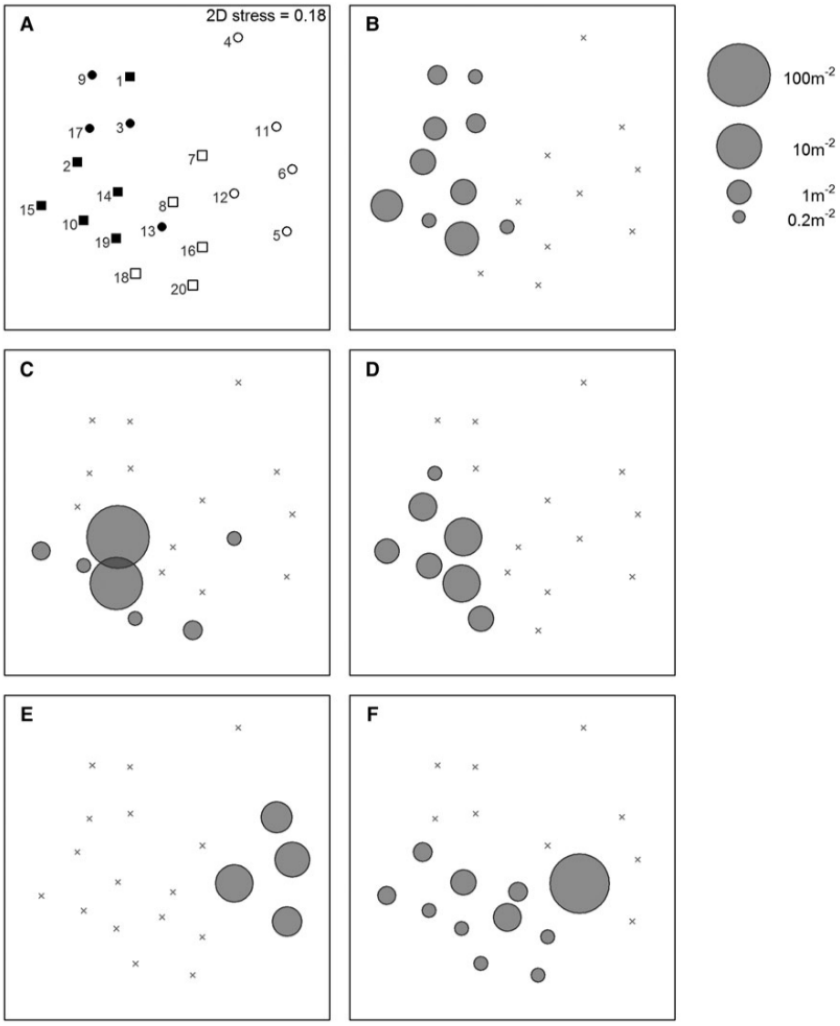

Fig. 6. (A) Non-metric MDS plot of faunal assemblage structure, based on $\log_{10}(x + 1)$-transformed morphotype densities. Point labels correspond to transect number and symbols designate depth category (○, 100–249 m; □, 250–499 m; •, 500–750 m; ■, >750 m). (B–F) The same MDS plot with superimposed circles representing densities of morphotypes exhibiting the strongest correlations ($|\rho| > 0.75$) with CAP axes: (B) *Nematocarcinus* sp.; (C) *Sabellidae* sp. indet.; (D) *Crinoidea* sp. indet.; (E) *Demospongiae* sp. indet.; (F) *Serpula* sp.

While neither roughness *per se* nor depth were related to univariate measures of diversity, the structure of benthic faunal assemblages inhabiting Ascension Island's shelf varied according to depth and substratum type. Previous studies conducted in offshore benthic habitats at comparable depths have demonstrated the importance of depth and proportional covers of different substratum types in explaining spatial variation in faunal community structure (e.g. Buhl-Mortensen *et al.*, 2009; Robert *et al.*, 2014). In addition to depth, the cover of coarse sand and large pebbles appeared to be important determinants of community structure, and we identified nine faunal morphotypes driving changes in assemblage structure across benthic habitats. Black corals (*Antipatharia* sp.) characterized the shallowest sites, a common feature of which was a relatively high cover of complex rocky substratum, with the potential to support a diverse array of epilithic and epizootic species (Warner, 1981) such as the encrusting sponges (Demospongiae) that were also recorded in abundance.

Surveys at intermediate depths revealed diverse habitats characterized by a range of sessile and mobile species. The sea pen *Virgularia* sp. was only encountered on five transects (SUCS 3, 4, 7, 8 and 9), all of which consisted predominantly of coarse sediment – thus, there was a clear association between this species and this particular substratum type. The analysis also identified an association between sabellid polychaetes and hard substrata, as this morphotype was found at particularly high densities on SUCS transects 14 and 19, for which the majority of photos were characterized by rocks, large rocks and boulders/bedrock. These transects, however, showed considerable heterogeneity in terms of substratum type, including a number of photos characterized by sediment, in which large numbers of sabellid polychaetes were also counted. This illustrates how species–substratum associations can depend on the spatial resolution of data (in this case, at the level of transect as opposed to individual photographs) and care should be taken when using such relationships to extrapolate across different scales (Williams *et al.*, 2010).

The cold-water coral *Lophelia* cf. *pertusa*, encountered on around half of all transects, was recorded as deep as 1020 m, exhibiting particularly high densities on transects shallower than 350 m. In addition to occurring in the Pacific and Indian Oceans, *L. pertusa* is distributed widely throughout the Atlantic, with relatively high abundances on the continental shelves of Europe and south-eastern North America (Roberts *et al.*, 2009). However, deep-water coral communities (including *L. pertusa*) are less well known from the South Atlantic (e.g. Arantes *et al.*, 2009; Carranza *et al.*, 2012). The current study provides the first record of substantial aggregations of reef-building scleractinian corals from Ascension Island's shelf. Currently regarded as one of the most structurally complex habitats in the deep ocean, cold-water coral reefs support high levels of biodiversity and act as potential speciation centres, while providing trophic links between the surface and seafloor and enhancing benthic carbon accumulation (Roberts *et al.*, 2006). Owing to the ecological importance of cold-water corals and associated taxa, deep sea coral reefs are regularly categorized as Vulnerable Marine Ecosystems (VMEs; e.g. Auster *et al.*, 2010; Jones & Lockhart, 2011) requiring protection from destructive fishing practices and seabed extractive operations, in addition to agents of global environmental change. Our findings indicate the importance of Ascension Island in terms of supporting cold-water coral reefs, enhancing our understanding of the distribution of these ecosystems within the South Atlantic. Additional species identified during this study can also be considered as indicator taxa for VMEs, such as cup corals (*Caryophyllia* sp.), sea whips (*Stichopathes* sp.) and erect sponges.

Nematocarcinid shrimps (mostly *Nematocarcinus gracilipes*, with lower abundances of *N. tenuipes* and *N. faxoni*) were observed frequently on transects at greater depths, particularly those deeper than 500 m, although one juvenile specimen was obtained from ~250 m. Members of this genus are widespread across the Atlantic and tend to inhabit soft muddy substrata, where they feed on detritus (Cardoso & Burukovsky, 2014). Owing to their observed abundance at Ascension Island, *Nematocarcinus* spp. may provide a staple food source for deep-sea fishes and other predators. While the distribution of *N. gracilipes* is largely within the Atlantic, *N. tenuipes* can also be found in the Indian and Pacific Oceans (Burukovsky, 2003). Thus, in this case, Ascension Island represents a zone of contact among species with different, yet overlapping, regional distributions, whose coexistence may be supported by high local productivity.

Island biodiversity is expected to increase with island size, age and proximity to continents (MacArthur & Wilson, 1963). Although Atlantic island biogeographic patterns have been evaluated for shallow marine taxa (Hachich *et al.*, 2015), fewer generalizations can be made regarding species inhabiting deeper waters. For the relatively small, young and isolated island of Ascension, we might expect comparatively low benthic biodiversity, particularly in the context of the Atlantic Ocean and of tropical regions in general. However, with morphotype (cf. species) richness averaging $14.5\ \mathrm{m}^{-2}$ across all samples (maximum $24\ \mathrm{m}^{-2}$), this may not be the case, perhaps reflecting an overall latitudinal gradient of increasing benthic diversity towards the equator (Rex *et al.*, 2000). Additionally, species inhabiting the shallow waters surrounding Ascension Island represent a unique mixture of western and eastern Atlantic taxa (De Grave *et al.*, in press; Tsiamis *et al.*, 2017; Wirtz *et al.*, 2017), but in the case of deeper marine ecosystems, different processes may govern species ranges and connectivity among regions (McClain & Hardy, 2010). The description of benthic communities and new species records arising from this study will provide valuable clues as to the biogeographic origins of deep-water taxa inhabiting the central Atlantic. On a smaller scale, while this study revealed a number of distinct benthic habitats characterized by particular faunal communities, taxonomic abundance and diversity were found to be very patchy within transects, emphasizing the importance of local variability in environmental variables in driving biological patterns. For example, we found high faunal densities ($>300\ \mathrm{m}^{-2}$) in certain areas, which may coincide with high productivity and/or substratum stability. Overall, the relative importance of environmental variables in structuring benthic marine communities varies according to scale (Williams *et al.*, 2010); although the main aim of our primarily descriptive study was to characterize the physical and biological features of Ascension's shelf environment, the results will also contribute to a more general understanding of the processes structuring deep-water ecosystems.

This study has greatly enhanced our knowledge of Ascension Island's marine environment beyond 30 m depth. The detailed physical and biological data collected here will enable the identification of ecologically important and/or vulnerable benthic habitats, which in turn will assist in the delimitation of zones for protection. These data also constitute a critical baseline against which to assess potential future ecological responses to local- and large-scale environmental change. Deep-sea ecosystems are vital to ocean biogeochemical and ecological processes, and the loss of benthic biodiversity is a serious threat to marine ecosystem functioning (Danovaro *et al.*, 2008). Additionally, confirmation of the identities of species collected in deep-water samples will increase biodiversity estimates and contribute to our understanding of biogeographic processes structuring Ascension's marine communities. While there is scope for further analysis of data from the current study to investigate relationships between environmental and biological variables in more detail, future surveys should aim to incorporate larger scales and greater depths to assess the generality of our findings. Overall, our understanding of the biogeography and functioning of deep-sea ecosystems remains limited, largely as a result of the technical and logistical challenges involved in collecting data from such large-scale, inaccessible environments. In addition to addressing this critical lack of understanding, scientific researchers must work closely with conservation bodies, industry and policymakers to ensure the successful management of these important marine ecosystems (Ramirez-Llodra *et al.*, 2010).

SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at https://doi.org/10.1017/S0025315417000820

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