



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

Oliver T. Hogg<sup>a,b,c,\*</sup>, Veerle A.I. Huvenne<sup>b</sup>, Huw J. Griffiths<sup>a</sup>, Katrin Linse<sup>a</sup>

<sup>a</sup> British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

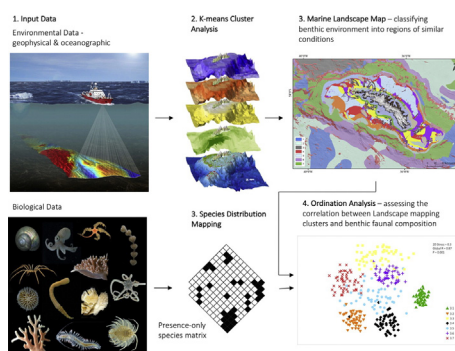
<sup>b</sup> National Oceanography Centre, University of Southampton, Waterfront Campus, European Way, Southampton SO14 3ZH, Southampton, UK

<sup>c</sup> University of Southampton, Waterfront Campus, European Way, Southampton SO14 3ZH, UK

## HIGHLIGHTS

- Broad-scale landscape maps correlate with sub-Antarctic benthic faunal composition.
- Landscape maps effective in ensuring representative protection in MPA design.
- Analysis highlights challenges associated with analysing large historical datasets.
- Functional trait analysis effective in an environment dominated by rare species.

## GRAPHICAL ABSTRACT



## ARTICLE INFO

### Article history:

Received 14 November 2017

Received in revised form 1 January 2018

Accepted 2 January 2018

Available online 19 February 2018

Editor: D. Barcelo

### Keywords:

Marine protected areas

Marine spatial planning

Habitat mapping

South Georgia

Biogeography

Benthic ecology

## ABSTRACT

In recent years very large marine protected areas (VLMAs) 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 VLMAs, 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 VLMAs remains, thus far, largely undetermined.

The aim of this study was to assess the ecological relevance of broadscale 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 cosmopolitanism, 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

\* Corresponding author.

E-mail address: [olgg@bas.ac.uk](mailto:olgg@bas.ac.uk) (O.T. Hogg).

plans. Such scientific underpinning of marine spatial planning is critical in balancing the needs of multiple stakeholders whilst maximising conservation payoff.

© 2018 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

## 1. Introduction

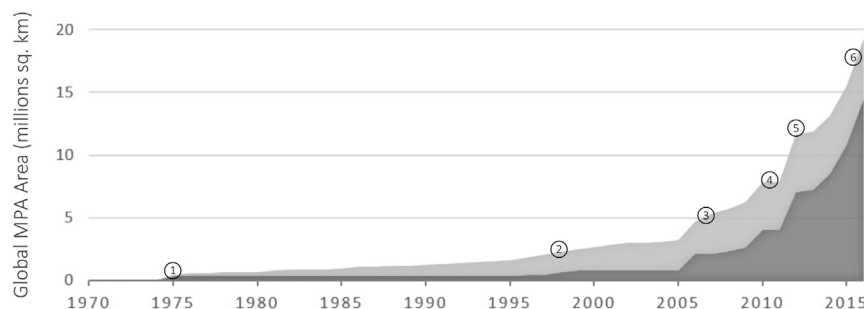
Currently, there is a disconnect between a global trend towards the establishment of very large-scale marine protected areas (VLMPAs), and the data available to underpin their establishment and inform on their zonation. Biological sampling, especially in isolated locations, is logistically difficult, 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<sup>2</sup> 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% (Boonzaijer and Pauly, 2016). This increase has overwhelmingly been met by VLMPAs (Fig. 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; Roberts et al., 2017; Toonen et al., 2013). 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 (Fox et al., 2012; Lester et al., 2009; 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 Agardy et al., 2016; Leenhardt et al., 2013; Jones and De Santo, 2016; Wilhelm et al., 2014). 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).

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; PAME, 2015), transnational co-operative 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



**Fig. 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 km<sup>2</sup>) 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).

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 (Brown et al., 2011; Harris and Baker, 2012; Pressey and Bottrill, 2009). 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 (Cox and Moore, 2005; Hawkins, 2001; Passlow et al., 2006; Sanders et al., 2007), which in turn drive changes in temperature, day length and light penetration (Chaudhary et al., 2016; Hawkins and Diniz-Filho, 2004; Rex et al., 1993; Tittensor et al., 2010), 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 (Solán et al., 2012), geomorphology (Beaman and Harris, 2007; Kostylev et al., 2003), and disturbance processes such as slope instability and turbidity currents (Paull et al., 2010) and, at higher latitudes, ice-berg 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 (Cogan et al., 2009; Ehler and Douvère, 2009; Wright and Heyman, 2008). Its use as a framework for the representative protection of habitats can be 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; Copeland et al., 2013; Ierodiaconou et al., 2011; 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 VLMPPAs (Day and Roff, 2000; Harris and Whiteway, 2009; Roff and Taylor, 2000). As such, whilst habitat mapping is demonstrably an effective tool at smaller spatial scales (often at finer spatial resolution), with conservation initiatives prioritising VLMPPAs, 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<sup>2</sup>). 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?

## 2. Methodology

### 2.1. Study area

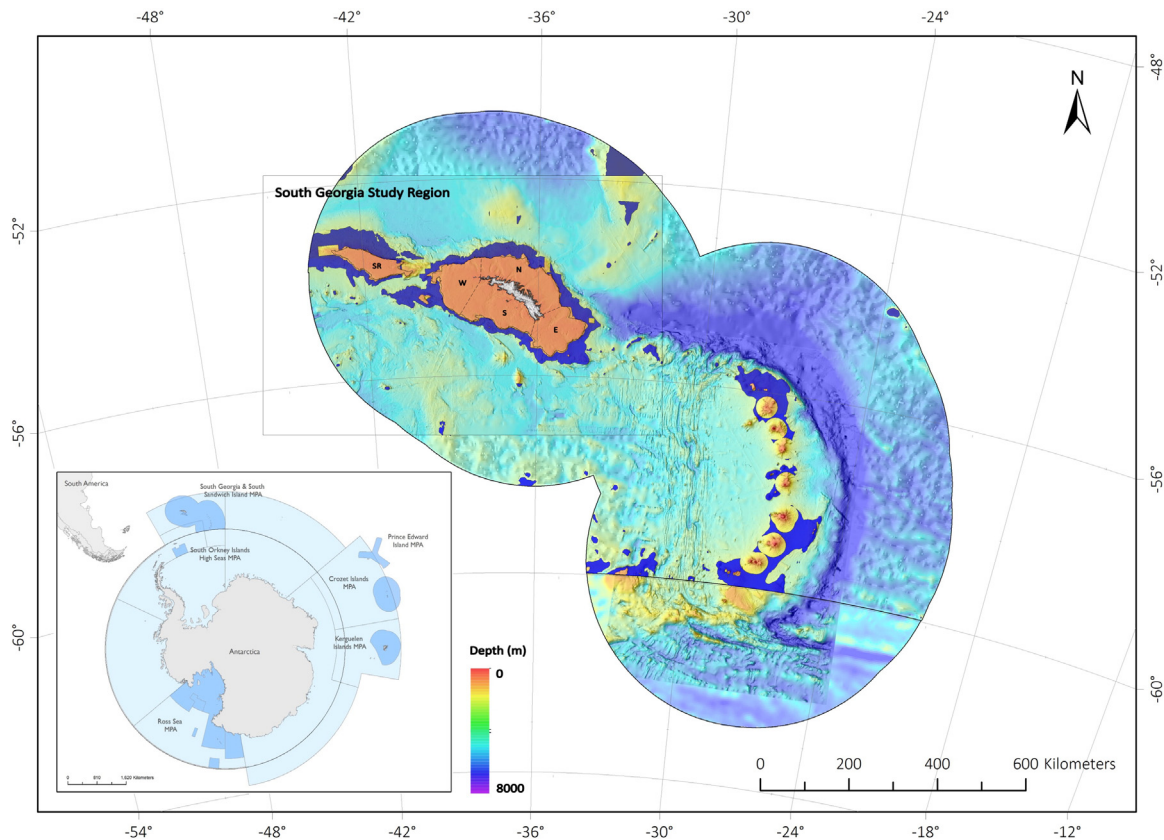
Positioned 1800 km east of the South American continental shelf, the island of South Georgia represents one of the most isolated continental shelf areas in the World (Fig. 2). The region supports high levels of biological richness across taxonomic levels (most notably at species level); a high proportion 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 VLMPPAs covering areas of over 1 million km<sup>2</sup> (Rogers et al., 2015; Trathan et al., 2014). 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 fishing), and scientific study dating back to the 19th Century.

### 2.2. Physical landscape data

Environmental data for the region includes an extensive bathymetry dataset (Hogg et al., 2016) and oceanographic data modelled at meso-scale (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 Appendix Table A1, 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





**Fig. 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.

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<sup>2</sup>, 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 (Fig. 3a), hereafter referred to as level-1 cluster (or clusters 1–7), covering an area of 530,000 km<sup>2</sup> 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 (Fig. 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 2.

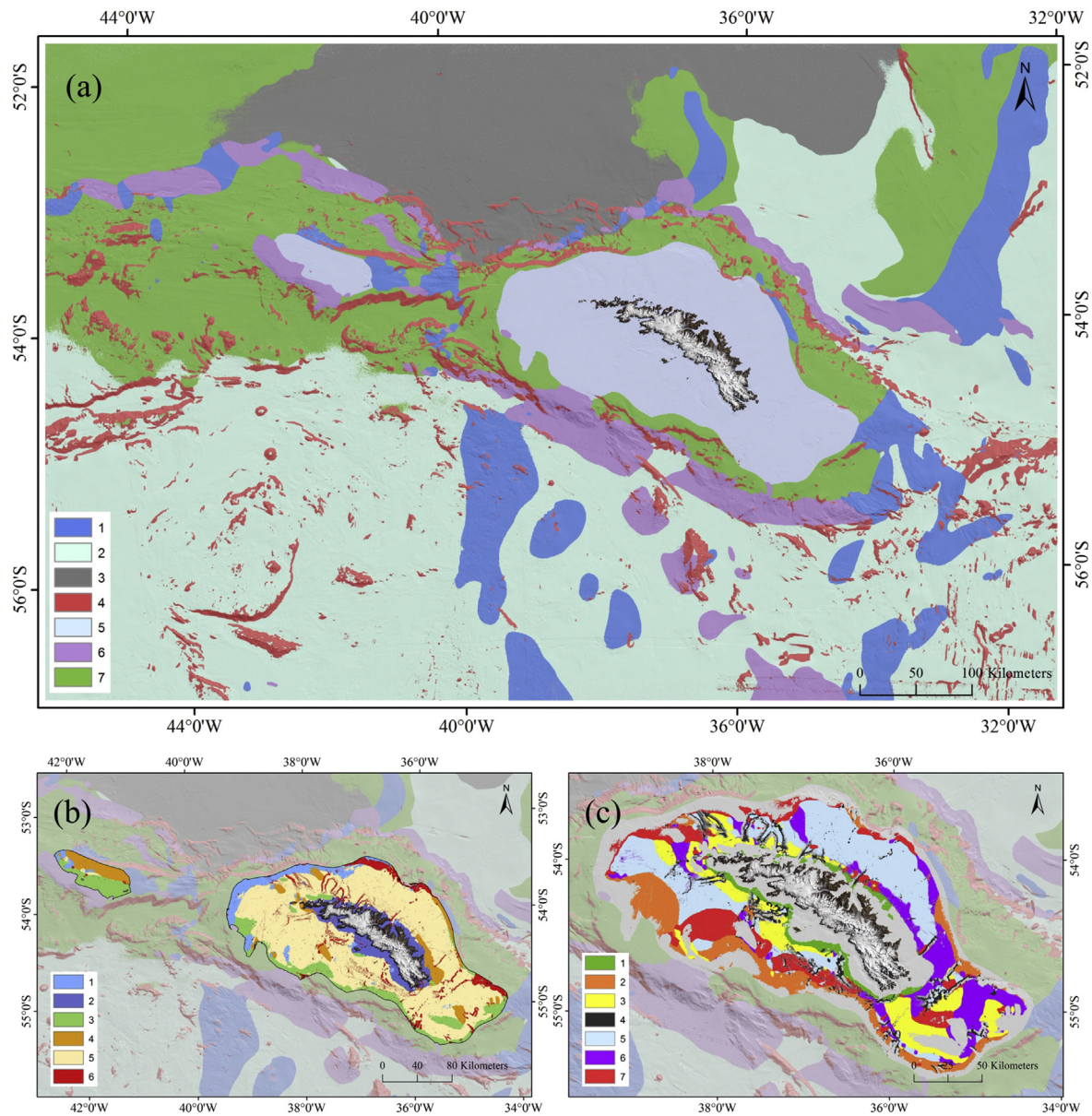
### 2.3. Biological data

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 and JR287). 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 1.



**Fig. 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/](http://www.esri.com/software/Arcgis/)]).

#### 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 (Fig. 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 or fewer records.



**Table 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
Life style	Drifter	An organism whose movement is dependent on wind or water currents
	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
Substratum affinity	Pelagic	Inhabiting the open waters of the sea or ocean, excluding the bottom layers
	Mud	Predominantly mud
	Muddy-sand	Mixture of Sand and mud with either component representing no >80% of the described sediment
	Sand	Predominantly sand
	Small	Small, unstable hard substrate
Reef building	Boulders/cobbles	
	Hard Substratum	Any stable hard substratum, not separated into small boulders or smaller sediment units.
	Yes	An organism that creates a massive biogenic physical structure raised above the surrounding seabed creating a consolidated habitat for epibenthic species
Habitat forming	No	Does not do the above
	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
Ecological succession	No	Does not do the above
	Early	Rapidly colonising & rapid growing; early successional pioneers; Tend to be R-strategists
	Mid	Members of a community at an Intermediate stage of succession
Fragility	Late	Late successional members of climax community; members of a very stable ecological community; K-strategists
	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

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 (Fig. 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 (Fig. 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).

### 3. Results

#### 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 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 3b, Fig. 4). The number of species recorded  $\leq 2$  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 (Fig. 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 (Tables 3a).

Table 3d 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.

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 Table A2). 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 3b). 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.

### 3.2. Functional traits

Classifying species based on their functional traits demonstrated further distinction between clusters (Table 3c). Cluster 4 was characterised by steep slopes ( $>10^\circ$ ), 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% ( $\sigma = 2.9\%$ ) of total species. Cluster 4 also had a higher proportion of sessile species (57.7% (124)) compared to other clusters ( $\bar{x} = 21.1\%$ ,  $\sigma = 13.5\%$ ) 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 ( $\bar{x} = 58.4\%$ ,  $\sigma = 0.5\%$ ), 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

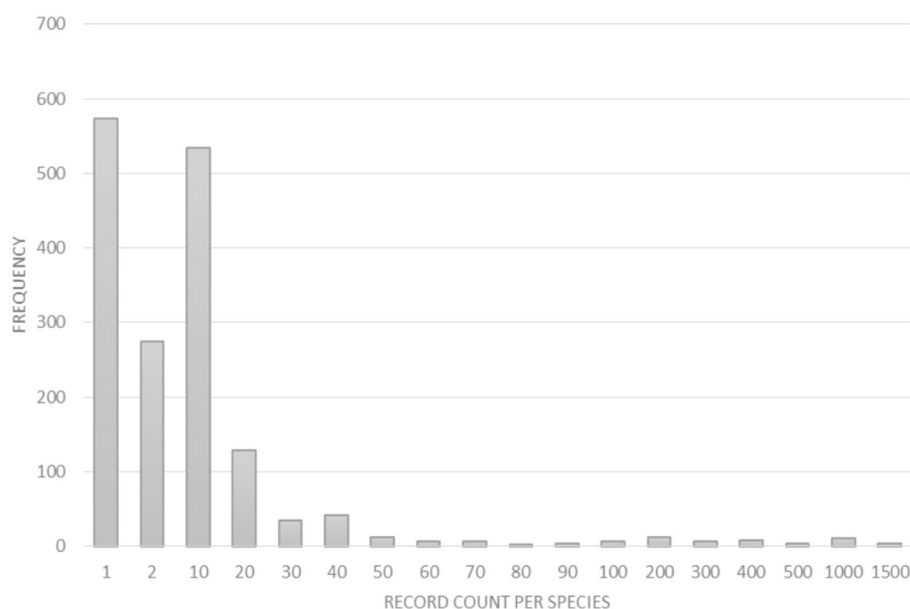
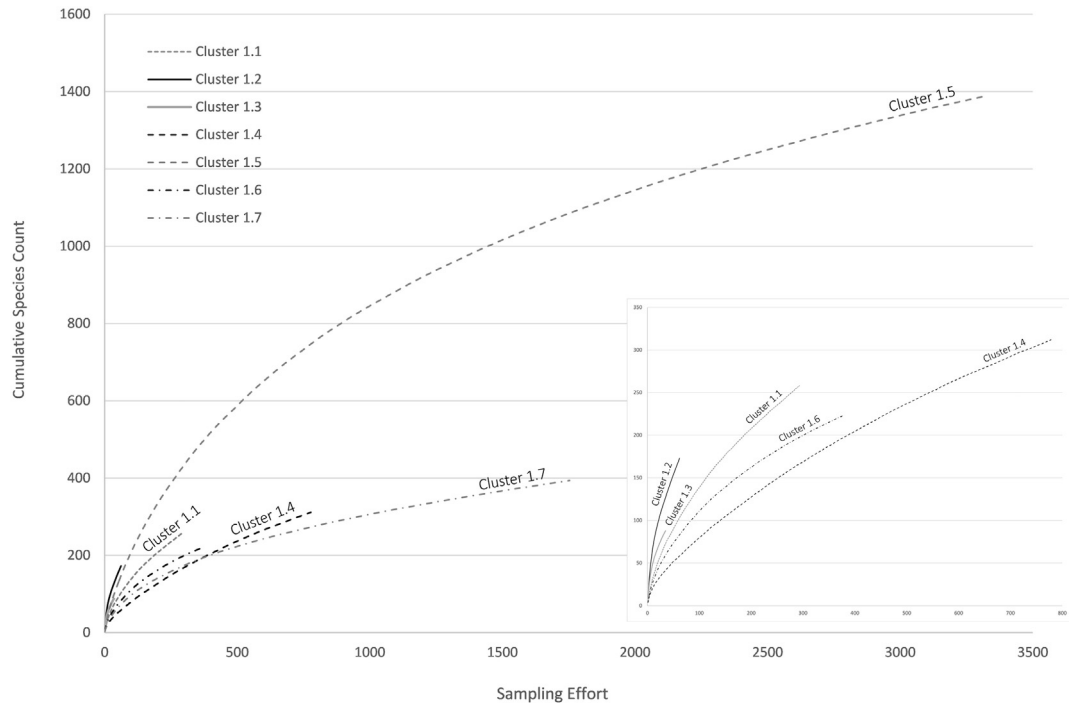


Fig. 4. Species frequency at South Georgia. Species are ranked according to the number of distinct locations at which samples were recorded. Species records at South Georgia were dominated by a large number of species recording very low record counts or by a small number of species recording very high record counts.



**Fig. 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.

strong current regimes, and those without. The strongest differentiation in functional traits was seen between cluster 4 and the other level-1 clusters.

### 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 (Fig. 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 (Fig. 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

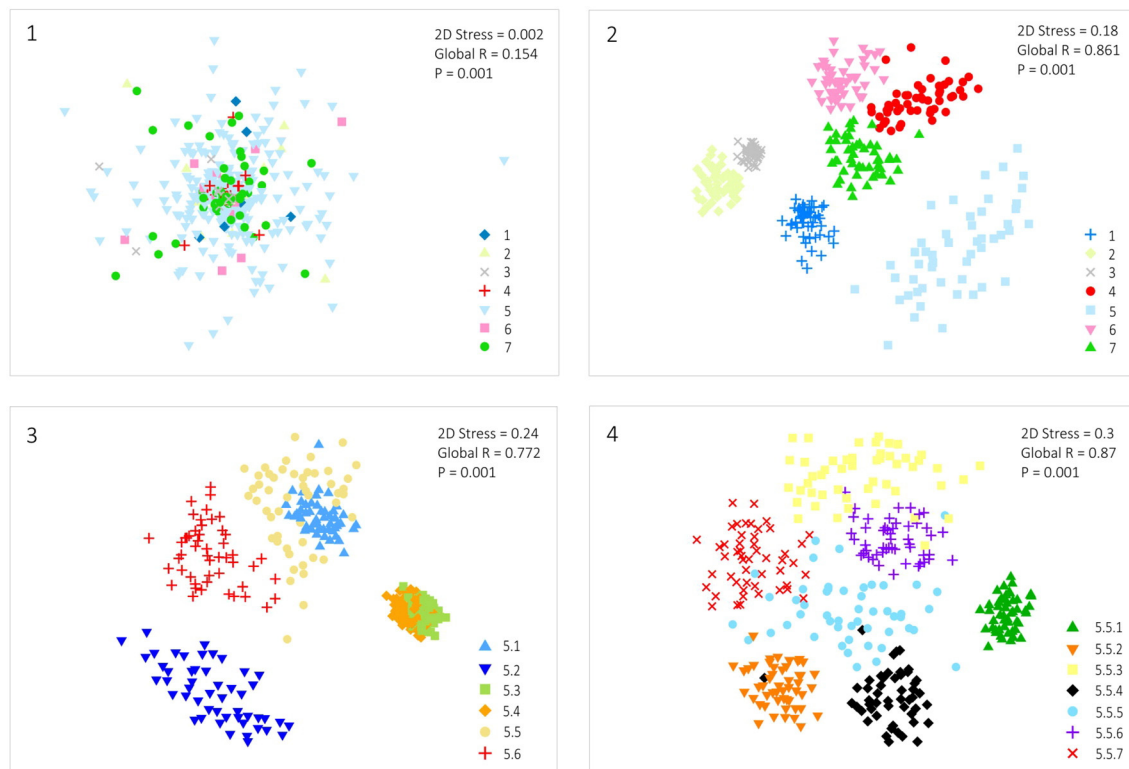
records, could be having a disproportionate effect on increasing intra-cluster variability based on a relatively small number of samples, two more NMDS iterations were run, again excluding singleton and doubleton species, but in addition excluding all stations with fewer than 10 records and 20 records 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





**Fig. 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 (Fig. 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.

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 Fig. 3) rather than between individual sampling stations. To do this, species lists for stations occurring in the same cluster were merged. They were then randomly re-sampled (with replacement) for 50 records a total of 50 times. These 'pseudo stations' were then input into the NMDS analysis to determine whether after removing station-level variability, each cluster had its own distinct biological signature. NMDS of this dataset demonstrated a strong degree of separation between clusters (Global  $R = 0.861$ ,  $P = 0.001$ ). Cluster 5 appeared most distinct from other clusters whilst deep-water clusters 2 and 3 were shown to be most similar (Fig. 6.2). 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 (Fig. 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. Fig. 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 Fig. 6.4 is not a good reflection of the true nature of the data.

### 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% ( $\sigma = 5.3\%$ ) 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 ctenophores. 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.

## 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 (Ainley et al., 2010; Davies et al., 2004; 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?

### 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 (Fig. 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 (Fig. 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 km<sup>2</sup> 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.

### 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 (Hogg et al., 2016 [Fig. 6; Supplementary materials Figs. 2 & 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 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 homogeneously 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.

#### 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 VLMAs 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 VLMAs 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 VLMAs 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 disproportionately 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

**Table 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 (2500–4500 m), low sea-bed temperature ( $\bar{x}$ = 0.75 °C), predominantly southerly distribution
3	Exclusively deep-sea (>2500 m), low seabed temperature ( $\bar{x}$ = 0.5 °C), northerly distribution, high sea-surface primary productivity ( $\bar{x}$ = 420 Mg C/m <sup>2</sup> /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 <250 m and predominantly 2000–3000 m), 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



**Table 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	17,713	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 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 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	412	1305	3268	1922	3030
Cluster 6	18	149	48	17	56	47	131	103	111
Cluster 7	21	469	98	37	134	92	431	255	353

**Table 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

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. 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<sup>2</sup>) to much smaller spatially constrained features ( $10^1$  km<sup>2</sup>).

In order to demonstrate this relationship however, required specific treatment of the data to remove biological rarity, biological cosmopolitanism, 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.

## Acknowledgements

This work was supported by the National Environmental Research Council [grant number NE/L002531/1]. VAIH was funded by the ERC Starting Grant project CODEMAP (Grant no. 258482) and the UK Natural Environment Research Council MAREMAP programme. For help cataloguing taxa specific functional traits the authors would like to thank David Barnes (BAS), Angelika Brandt (Senckenberg), Rachel Downey (Australian National University), Marc Eléaume (Muséum National d'Histoire Naturelle, Paris), Anne-Nina Lörz (NIWA), Melanie Mackenzie (Museum Victoria), Camille Moreau (Université Libre de Bruxelles), Estefania Rodriguez (American Museum of Natural History), Chester Sands (BAS) and Thomas Saucède (Université de Bourgogne). The authors would also like to thank the two anonymous reviewers for their constructive comments.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2018.01.009>.

## References

- Agardy, T., Claudet, J., Day, J.C., 2016. 'Dangerous targets' revisited: old dangers in new contexts plague marine protected areas. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* 26:7–23. <https://doi.org/10.1002/aqc.2675>.
- Ainley, D.G., Ballard, G., Weller, J., 2010. Ross Sea Bioregionalization, Part I: Validation of the 2007 CCAMLR Bioregionalization Workshop Results Towards Including the Ross Sea in a Representative Network of Marine Protected Areas in the Southern Ocean. CCAMLR Reference Number: CCAMLR WG-EMM-10/11.
- Allcock, A.L., Brierley, A.S., Thorpe, J.P., et al., 1997. Restricted gene flow and evolutionary divergence between geographically separated populations of the Antarctic octopus *Pareledone turqueti*. *Mar. Biol.* 129, 97–102.
- Allee, R.J., David, A.W., Narr, D.F., 2011. Two shelf edge marine protected areas in the eastern Gulf of Mexico. In: Harris, P.T., Baker, E.K. (Eds.), *Seafloor Geomorphology as Benthic Habitat: GeoHab Atlas of Seafloor Geomorphic Features and Benthic Habitats*. Elsevier, Amsterdam (Chapter 30).
- Andreoufouet, S., Muller-Karger, F.E., Robinson, J.A., Kranenburg, C.J., Torres-Pulliza, D., Spraggins, S.A., Murch, B., 2006. June. Global assessment of modern coral reef extent and diversity for regional science and management applications: a view from space. *Proceedings of the 10th International Coral Reef Symposium. vol. 2. Japanese Coral Reef Society Okinawa, Japan*, pp. 1732–1745.
- BALANCE, 2008. Towards Marine Spatial Planning in the Baltic Sea, BALANCE Technical Summary Report 4/4.
- Barnes, D.K., Sands, C.J., 2017. Functional group diversity is key to Southern Ocean benthic carbon pathways. *PLoS One* 12 (6), e0179735.
- Barnes, D.K.A., Collins, M.A., Brickle, P., Fretwell, P., Griffiths, H.J., et al., 2011. The need to implement the convention on biological diversity at the high latitude site, South Georgia. *Antarct. Sci.* <https://doi.org/10.1017/S0954102011000253>.
- Barnes, D.K.A., Sands, C.J., Hogg, O.T., Robinson, B.J.O., Downey, R.V., Smith, J.A., 2016. Biodiversity signature of the last glacial maximum at South Georgia, Southern Ocean. *J. Biogeogr.* 43, 2391–2399.
- Beaman, R.J., Harris, P.T., 2007. Geophysical variables as predictors of megabenthos assemblages from the northern Great Barrier Reef, Australia. In: Todd, B.J., Greene, H.G. (Eds.), *Mapping the Seafloor for Habitat Characterization*. Geological Association of Canada (Special Paper).
- Beaman, R.J., Daniell, J., Harris, P.T., 2005. Geology-benthos relationships on a temperate rocky bank, eastern Bass Strait, Australia. *Mar. Freshw. Res.* 56, 943–958.
- Beck, Michael W., Heck, Kenneth L., Able, Kenneth W., Childers, Daniel L., Eggleston, David B., Gillanders, Bronwyn M., Halpern, Benjamin, Hays, Cynthia G., Hoshino, Kaho, Minello, Thomas J., Orth, Robert J., Sheridan, Peter F., Weinstein, Michael P., 1 August 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates: a better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. *BioScience* 51 (8):633–641. [https://doi.org/10.1641/0006-3568\(2001\)051\[0633:TICAMO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2).
- Boonzaier, L., Pauly, D., 2016. Marine protection targets: an updated assessment of global progress. *Oryx* 50 (2016):27–35. <https://doi.org/10.1017/0030605315000848>.
- Brown, C.J., Smith, S.J., Lawton, P., Anderson, J.T., 2011. Benthic habitat mapping: a review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. *Estuar. Coast. Shelf Sci.* 92 (3), 502–520.
- Chaudhary, C., et al., 2016. Bimodality of latitudinal gradients in marine species richness. *Trends Ecol. Evol.* 31, 670–676.
- Clark, M.R., Watling, L., Smith, C., Rowden, A., Guinotte, J.M., 2011. A global seamount classification to aid the scientific design of marine protected area networks. *Ocean Coast. Manag.* 54 (1), 19–36.
- Cogan, C.B., Todd, B.J., Lawton, P., Noji, T.T., 2009. The role of marine habitat mapping in ecosystem-based management. *ICES J. Mar. Sci.* 66, 2033–2042.
- Copeland, A., Edinger, E., Devillers, R., Bell, T., LeBlanc, P., Wroblewski, J., 2013. Marine habitat mapping in support of marine protected area management in a subarctic fjord: Gilbert Bay, Labrador, Canada. *J. Coast. Conserv.* 17 (2), 225–237.
- Cox, C.B., Moore, P.D., 2005. *Biogeography: An Ecological and Evolutionary Approach*. Blackwell Publishing, p. 67.
- Davies, C.E., Moss, D., Hill, M.O., 2004. EUNIS Habitat Classification Revised 2004. Report to: European Environment Agency-European Topic Centre on Nature Protection and Biodiversity. pp. 127–143.
- Day, J.C., Roff, J.C., 2000. *Planning for Representative Marine Protected Areas: A Framework for Canada's Oceans*. World Wildlife Fund, Toronto, Ontario, Canada.
- Devillers, R., Pressey, R.L., Grech, A., Kittinger, J.N., Edgar, G.J., Ward, T., Watson, R., 2015. Reinventing residual reserves in the sea: are we favouring ease of establishment over need for protection? *Aquat. Conserv. Mar. Freshwat. Ecosyst.* 25:480–504. <https://doi.org/10.1002/aqc.2445>.
- Douglass, L.L., Turner, J., Grantham, H.S., Kaiser, S., Constable, A., Nicoll, R., ... Beaver, D., 2014. A hierarchical classification of benthic biodiversity and assessment of protected areas in the Southern Ocean. *PLoS One* 9 (7), e100551. <https://doi.org/10.1371/journal.pone.0100551>.
- Ehler, C., Douvère, F., 2009. *Marine Spatial Planning: A Step-by-step Approach Toward Ecosystem-based Management*. Intergovernmental Oceanographic Commission and Man and the Biosphere Programme. IOC Manual and Guides, No. 53, IOCAM Dossier No. 6. UNESCO, Paris.
- Foley, M.M., Halpern, B.S., Micheli, F., Armsby, M.H., Caldwell, M.R., Crain, C.M., ... Carr, M. H., 2010. Guiding ecological principles for marine spatial planning. *Mar. Policy* 34 (5), 955–966.
- Fox, H.E., Mascia, M.B., Basurto, X., Costa, A., Glew, L., Heinemann, D., Karrer, L.B., Lester, S. E., Lombana, A.V., Pomeroy, R.S., Recchia, C.A., Roberts, C.M., Sanchirico, J.N., Pet-Soede, L., White, A.T., 2012. Reexamining the science of marine protected areas: linking knowledge to action. *Conserv. Lett.* 5:1–10. <https://doi.org/10.1111/j.1755-263X.2011.00207>.
- Gales, J.A., Larter, R., Leat, P.T., 2016. Submarine gullies on the Southern Weddell Sea slope, Antarctica. In: Dowdeswell, J.A. (Ed.), *Atlas of Submarine Glacial Landforms: Modern, Quaternary and Ancient*. Geological Society of London, London, UK, pp. 383–384.
- Galparsoro, I., Rodríguez, J.G., Menchaca, I., Quincoces, I., Garmendia, J.M., Borja, Á., 2015. Benthic habitat mapping on the Basque continental shelf (SE Bay of Biscay) and its application to the European Marine Strategy Framework Directive. *J. Sea Res.* 100, 70–76.
- GBRMPA Zoning Plan, 2003. Great Barrier Reef Marine Park Authority, Townsville, QLD, 2004.
- Gjerde, K. (Ed.), 2003. Ten-year Strategy to Promote the Development of a Global Representative System of High Seas Marine Protected Area Networks, as Agreed by Marine Theme Participants at the 5th World Parks Conference Governance Session "Promoting Marine Biodiversity Beyond National Jurisdiction". IUCN, Durban, South Africa (September 8–17, 7 pp.).
- Gladstone, W., 2007. Requirements for marine protected areas to conserve the biodiversity of rocky reef fishes. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* 17:71–87. <https://doi.org/10.1002/aqc.759>.
- Grant, S., Constable, A., Raymond, B., Doust, S., 2006. *Bioregionalisation of the Southern Ocean*. Report of Experts Workshop, Hobart, pp. 1–48.
- Harris, P.T., 2012. Surrogacy. In: Harris, P.T., Baker, E.K. (Eds.), *GeoHAB Atlas of seafloor geomorphic features and benthic habitats*. Elsevier, London.
- Harris, P.T., Baker, E., 2012. Seafloor geomorphology as benthic habitat. In: Harris, P.T., Baker, E.K. (Eds.), *GeoHAB Atlas of Seafloor Geomorphic Features and Benthic Habitats*. Elsevier, London.
- Harris, P.T., Macmillan-Lawler, M., 2016. Global overview of continental shelf geomorphology based on the SRTM30\_PLUS 30-arc second database. In: Finkl, C.W.,

- Makowski, C. (Eds.). Seafloor Mapping Along Continental Shelves. Research and Techniques for Visualising Benthic Environments. Springer International Publishing, Switzerland <https://doi.org/10.1007/978-3-319-25121-9>.
- Harris, P.T., Whiteway, T., 2009. High seas marine protected areas: benthic environmental conservation priorities from a GIS analysis of global ocean biophysical data. *Ocean Coast. Manag.* 52, 22–38.
- Harris, P.T., Heap, A.D., Whiteway, T., Post, A., 2008. Application of biophysical information to support Australia's representative marine protected area program. *Ocean Coast. Manag.* 51 (10), 701–711.
- Hawkins, B.A., 2001. Ecology's oldest pattern? *Endeavour* 25, 133–134.
- Hawkins, B.A., Diniz-Filho, J.A.F., 2004. "Latitude" and geographic patterns in species richness. *Ecography* 27, 268–272.
- Henriques, V., Guerra, M.T., Mendes, B., Gaudêncio, M.J., Fonseca, P., 2015. Benthic habitat mapping in a Portuguese marine protected area using EUNIS: an integrated approach. *J. Sea Res.* 100, 77–90.
- Hewitt, J.E., Thrush, S.F., Dayton, P.D., 2008. Habitat variation, species diversity and ecological functioning in a marine system. *J. Exp. Mar. Biol. Ecol.* 366 (1–2), 116–122.
- Hofmann, E.E., Klinck, J.M., Locarnini, R.A., Fach, B.A., Murphy, E.J., 1998. Krill transport in the Scotia Sea and environs. *Antarct. Sci.* 10, 406–415.
- Hogg, O.T., Barnes, D.K.A., Griffiths, H.J., 2011. Highly diverse, poorly studied and uniquely threatened by climate change: an assessment of marine biodiversity on South Georgia's continental shelf. *PLoS One* 6 (16 pp.). <https://doi.org/10.1371/journal.pone.0019795>.
- 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. *Sci. Rep.* 6 <https://doi.org/10.1038/srep33163>.
- Howell, K.L., Davies, J.S., Narayanaswamy, B.E., 2010. Identifying deep-sea megafaunal epibenthic assemblages for use in habitat mapping and marine protected area network design. *J. Mar. Biol. Assoc. U. K.* 90 (1), 33–68.
- Huvenne, V.A., Tyler, P.A., Masson, D.G., Fisher, E.H., Hauton, C., Hühnerbach, V., ... Wolff, G.A., 2011. A picture on the wall: innovative mapping reveals cold-water coral refuge in submarine canyon. *PLoS One* 6 (12), e28755.
- Ierodionou, D., Monk, J., Rattray, A., Laurenson, L., Versace, V.L., 2011. Comparison of automated classification techniques for predicting benthic biological communities using hydro-acoustics and video observations. *Cont. Shelf Res.* 31:528–538. <https://doi.org/10.1016/j.csr.2010.01.012>.
- Jeftic, L., Glennie, P., Talae-McManus, L., Thornton, J.A., 2011. Methodology and Arrangements for the GEF Transboundary Water Assessment Programme. Methodology for the Assessment of Transboundary Aquifers vol. 1. Lake Basins, River Basins, Large Marine Ecosystems, and the Open Ocean, United Nations Environment Programme.
- Jones, P.J.S., De Santo, E.M., 2016. Viewpoint – is the race for remote, very large marine protected areas (VLPAs) taking us down the wrong track? *Mar. Policy* 73: 231–234 (ISSN 0308-597X). <https://doi.org/10.1016/j.marpol.2016.08.015>.
- Jutt, J., Starman, A., 2001. Quantification of iceberg impact and benthic recolonisation patterns in the Weddell Sea (Antarctica). *Polar Biol.* 24:615–619. <https://doi.org/10.1007/s003000100263>.
- Kostylev, V.E., Courtney, R.C., Robert, G., Todd, B.J., 2003. Stock evaluation of giant scallop (*Placopecten magellanicus*) using high-resolution acoustics for seabed mapping. *Fish. Res.* 60, 479–492.
- Koubbi, P., Moteki, M., Duhamel, G., Goarant, A., Hulley, P.A., O'Driscoll, R., ... Hosie, G., 2011. Ecoregionalization of myctophid fish in the Indian sector of the Southern Ocean: results from generalized dissimilarity models. *Deep-Sea Res. II Top. Stud. Oceanogr.* 58 (1), 170–180.
- Kuhn, K.L., Gaffney, P.M., 2006. Preliminary assessment of population structure in the mackerel icefish (*Champsocephalus gunnari*). *Polar Biol.* 29, 927–935.
- Last, P.R., Lyne, V.D., Williams, A., Davies, C.R., Butler, A.J., Yearsley, G.K., 2010. A hierarchical framework for classifying seabed biodiversity with application to planning and managing Australia's marine biological resources. *Biol. Conserv.* 143 (7), 1675–1686.
- Leat, P.T., Fretwell, P.T., Tate, A.J., Larter, R.D., Martin, T.J., Smellie, J.L., Joket, W., Bohrmann, G., 2016. Bathymetry and geological setting of the South Sandwich Islands volcanic arc. *Antarct. Sci.* 28 (4), 293–303.
- Lecours, V., Devillers, R., Schneider, D.C., Lucieer, V.L., Brown, C.J., Edinger, E.N., 2015. Spatial scale and geographic context in benthic habitat mapping: review and future directions. *Mar. Ecol. Prog. Ser.* 535, 259–284.
- Leenhardt, P., Cazalet, B., Salvat, B., Claudet, J., Feral, F., 2013. The rise of large-scale marine protected areas: conservation or geopolitics? *Ocean Coast. Manag.* <https://doi.org/10.1016/j.ocecoaman.2013.08.013>.
- Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., et al., 2009. Biological effects within no-take marine reserves: a global synthesis. *Mar. Ecol. Prog. Ser.* 384:33–46. <https://doi.org/10.3354/meps08029>.
- Maxwell, S.M., Morgan, L.E., 2013. Foraging of seabirds on pelagic fishes: implications for management of pelagic marine protected areas. *Mar. Ecol. Prog. Ser.* 481:289–303. <https://doi.org/10.3354/meps10255>.
- McClain, C.R., Barry, J.P., 2010. Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons. *Ecology* 91 (4), 964–976.
- McCrea-Strub, A., et al., 2011. Understanding the cost of establishing marine protected areas. *Mar. Policy* 35 (1). <https://doi.org/10.1016/j.marpol.2010.07.001>.
- McHenry, J., Steneck, R.S., Brady, D.C., 2017. Abiotic proxies for predictive mapping of nearshore benthic assemblages: implications for marine spatial planning. *Ecol. Appl.* 27:603–618. <https://doi.org/10.1002/eap.1469>.
- Meyer, K.S., 2017. Chapter One-Islands in a sea of mud: insights from terrestrial island theory for community assembly on insular marine substrata. *Adv. Mar. Biol.* 76, 1–40.
- Meyer, K., Young, C., Sweetman, A.K., Taylor, J., Soltwedel, T., Bergmann, M., 2016. Rocky islands in a sea of mud: biotic and abiotic factors structuring deep-sea dropstone communities. *Mar. Ecol. Prog. Ser.* 556, 45–57.
- Micheli, F., Saenz-Arroyo, A., Greenley, A., Vazquez, L., Espinoza Montes, J.A., et al., 2012. Evidence that marine reserves enhance resilience to climatic impacts. *PLoS One* 7 (7), e40832.
- Mumby, P.J., Broad, K., Brumbaugh, D.R., Dahlgren, C.P., Harborne, A.R., Hastings, A., et al., 2008. Coral reef habitats as surrogates of species, ecological functions, and ecosystem services. *Conserv. Biol.* 22 (4), 941–951.
- Notarbartolo di Sciara, G., Agardy, T., Hyrenbach, D., Scovazzi, T., Van Klaveren, P., 2008. The Pelagos Sanctuary for Mediterranean marine mammals. *Aquat. Conserv.* 18, 367–391.
- O'Brien, P.E., Post, A.L., Romeyn, R., 2009. Antarctic-wide Geomorphology as an Aid to Habitat Mapping and Locating Vulnerable Marine Ecosystems. Science Committee to the Commission of Antarctic Marine Living Resources (SC-CAMLR-XXVIII/10) Workshop on Vulnerable Marine Ecosystems. La Jolla, CA, USA 3–7th August 2009: GeoScience Australia. Conference paper: WS-VME-09/10.
- O'Leary, B.C., Brown, R.L., Johnson, D.E., Von Nordheim, H., Ardron, J., Packeiser, T., Roberts, C.M., 2012. The first network of marine protected areas (MPAs) in the high seas: the process, the challenges and where next. *Mar. Policy* 36 (3), 598–605.
- Passlow, V., O'Hara, T.D., Daniell, T., Beaman, R.J., Twyford, L.M., 2006. Sediments and Benthic Biota of Bass Strait: An Approach to Benthic Habitat Mapping. Geoscience Australia, Canberra, p. 96.
- Paull, C.K., Schlining, B., Ussler III, W., Lundsten, E., Barry, J.P., Caress, D.W., Johnson, J.E., McGann, M., 2010. Submarine mass transport within Monterey Canyon: benthic disturbance controls on the distribution of chemosynthetic biological communities. In: Mosher, D.C., Shipp, R.C., Moscardelli, L., Chaytor, J.D., Baxter, C.D.P., Lee, H.J., Urgeles, R. (Eds.), *Submarine Mass Movements and Their Consequences, Advances in Natural and Technological Hazard Research. 4th International Symposium on Submarine Mass Movements and Their Consequences* vol. 28. Springer, London, pp. 229–247.
- Pearce, B., Tappin, D.R., Dove, D., Pinnion, J., 2011. Benthos supported by the tunnel-valleys of the southern North Sea. In: Harris, P.T., Baker, E.K. (Eds.), *Seafloor Geomorphology as Benthic Habitat: GeoHab Atlas of Seafloor Geomorphic Features and Benthic Habitats*. Elsevier, Amsterdam (Chapter 42).
- Potthoff, P., Johst, K., Gutt, J., 2006. How to survive as a pioneer species in the Antarctic benthos: minimum dispersal distance as a function of lifetime and disturbance. *Polar Biol.* 29:543–551. <https://doi.org/10.1007/s00300-005-0086-1>.
- Pressey, R.L., Bottrill, M.C., 2009. Approaches to landscape-and seascape-scale conservation planning: convergence, contrasts and challenges. *Oryx* 43, 464–475.
- Protection of the Arctic Marine Environment (PAME), 2015. Framework for a Pan-Arctic Network of Marine Protected Areas. A Network of Places and Natural Features Specially-managed for the Conservation and Protection of the Arctic Marine Environment. SAO Meeting, 4–5 March, 2015, Whitehorse, Canada. <http://hdl.handle.net/11374/1471>.
- Rees, M.J., Jordan, A., Price, O.F., Coleman, M.A., Davis, A.R., 2014. Abiotic surrogates for temperate rocky reef biodiversity: implications for marine protected areas. *Divers. Distrib.* 20 (3), 284–296.
- Rex, M.A., et al., 1993. Global-scale latitudinal patterns of species diversity in the deep-sea benthos. *Nature* 365, 636–639.
- Roberts, C.M., Andelman, S., Branch, G., Bustamante, R.H., Castilla, J.C., Dugan, J., et al., 2003. Ecological criteria for evaluating candidate sites for marine reserves. *Ecol. Appl.* 13 (1), S199–214.
- Roberts, C.M., O'Leary, B.C., McCauley, D.J., Cury, P.M., Duarte, C.M., Lubchenco, J., et al., 2017. Marine reserves can mitigate and promote adaptation to climate change. *Proc. Natl. Acad. Sci. U. S. A.* 114:6167–6175. <https://doi.org/10.1073/pnas.1701262114>.
- Roff, J.C., Taylor, M.E., 2000. National frameworks for marine conservation – a hierarchical geophysical approach. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* 10, 209–223.
- Rogers, A.D., Yesson, C., Gravestock, P., 2015. A Biophysical and Economic Profile of South Georgia & the South Sandwich Islands as Potential Large-scale Antarctic Protected Areas. *Advances in Marine Biology*. 70. Elsevier Academic Press 978-0-12-802140-8 (298 pp.).
- Sanders, J.L., Kendall, M.A., Hawkins, A.J.S., Spicer, J.L., 2007. Can functional groups be used to indicate estuarine ecological status? *Hydrobiologia* 588, 45–58.
- Secretariat of the Convention on Biological Diversity, 2010. Strategic plan for biodiversity 2011–2020 and the Aichi targets. <https://www.cbd.int/doc/strategic-plan/2011-2020>, Accessed date: 8 October 2015.
- Shaw, P.W., Arkhipkin, A.I., Al-Khairulla, H., 2004. Genetic structuring of Patagonian toothfish populations in the Southwest Atlantic Ocean: the effect of the Antarctic Polar Front and deep-water troughs as barriers to genetic exchange. *Mol. Ecol.* 13, 3293–3303.
- Sheppard, C.R.C., Atweberhan, M., Bowen, B.W., et al., 2012. Reefs and islands of the Chagos Archipelago, Indian Ocean: why it is the world's largest no-take marine protected area. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* 22, 232–261.
- Shugart-Schmidt, K.L.P., Pike, E.P., Moffitt, R.A., Saccomanno, V.R., Magier, S.A., Morgan, L. E., 2015. SeaStates G20 2014: how much of the seas are G20 nations really protecting? *Ocean Coast. Manag.* 115:25–30. <https://doi.org/10.1016/j.ocecoaman.2015.05.020>.
- Solan, M., Germano, J.D., Rhoads, D.C., Smith, C., Michaud, E., Parry, D., Wenzhöfer, F., Kennedy, B., Henriques, C., Battle, E., Carey, D., 2003. Towards a greater understanding of pattern, scale and process in marine benthic systems: a picture is worth a thousand worms. *J. Exp. Mar. Biol. Ecol.* 285, 313–338.
- Solan, M., Aspdén, R.J., Paterson, D.M., 2012. Marine Biodiversity and Ecosystem Functioning: Frameworks, Methodologies, and Integration. (Oxford).
- Strugnell, J.M., Watts, P.C., Smith, P.J., Allcock, A.L., 2012. Persistent genetic signatures of historic climatic events in an Antarctic octopus. *Mol. Ecol.* 21 (11), 2775–2787.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277 (5330), 1300–1302.



- Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Berghe, E.V., Worm, B., 2010. Global patterns and predictors of marine biodiversity across taxa. *Nature* 466 (7310), 1098–1101.
- Toonen, R.J., Andrews, K.R., Baums, I.B., et al., 2011. Defining boundaries for ecosystem-based management: a multispecies case study of marine connectivity across the Hawaiian Archipelago. *J. Mar. Biol.* 2011, 1–13.
- Toonen, R.J., et al., 2013. (2013). One size does not fit all: the emerging frontier in large-scale marine conservation. *Mar. Pollut. Bull.* 77, 7–10.
- Trathan, P.N., Collins, M.A., et al., 2014. The South Georgia and the South Sandwich Islands MPA: protecting a biodiverse oceanic island chain situated in the flow of the Antarctic circumpolar current. *Adv. Mar. Biol.* 69, 15–78.
- Trathan, P.N., et al., 2015. The South Georgia and the South Sandwich Islands MPA: protecting a biodiverse oceanic island chain situated in the flow of the Antarctic Circumpolar Current. In: Johnson, M.L., Sandell, J. (Eds.), *Marine Managed Areas and Fisheries*. Advances in Marine Biology. 69. Elsevier, pp. 15–78.
- Wallace, A.R., 1876. *The Geographical Distribution of Animals: With a Study of the Relations of Living and Extinct Faunas as Elucidating the Past Changes of the Earth's Surface*. Macmillan, London.
- Wilhelm, T.A., Taei, S., Teroroko, T., 2011. *Big Ocean: a network of the world's large-scale marine managed areas*. 2nd International Marine Conservation Congress (Victoria, Canada).
- Wilhelm, T.A., Sheppard, C.R.C., Sheppard, A.L.S., Gaymer, C.F., Parks, J., Wagner, D., Lewis, N., 2014. Large marine protected areas – advantages and challenges of going big. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* 24:24–30. <https://doi.org/10.1002/aqc.2499>.
- Williams, C.B., 1943. Area and number of species. *Nature* 152, 264–267.
- Wright, D.J., Heyman, W.D., 2008. Introduction to the special issue: marine and coastal GIS for geomorphology, habitat mapping and marine reserves. *Mar. Geod.* 31: 223–230. <https://doi.org/10.1080/01490410802466306>.
- Young, E.F., Meredith, M.P., Murphy, E.J., Carvalho, G.R., 2011. High resolution modelling of the shelf and open ocean adjacent to South Georgia, Southern Ocean. *Deep-Sea Res. II* <https://doi.org/10.1016/j.dsr2.2009.11.003>.
- Zeppilli, D., Pusceddu, A., Trincardi, F., Danovaro, R., 2016. Seafloor heterogeneity influences the biodiversity–ecosystem functioning relationships in the deep sea. *Sci. Rep.* 6, 26352.