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Broad-scale benthic habitat classification of the South Atlantic

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Abstract

Marine Spatial Planning (MSP) has become a priority for many states wanting to develop national blue economy plans and meet international obligations in response to the increasing cumulative impacts of human activities and climate change. In areas beyond national jurisdiction (ABNJ), MSP is proposed as part of a package of solutions for multi-sectoral management at the ocean basin scale. To facilitate planning, maps showing the spatial distribution of marine biological diversity are required. In areas lacking data, like the South Atlantic, environmental proxies can be used to predict these distributions. We undertook broad-scale benthic habitat classification of the South Atlantic, employing two top-down approaches spanning from national waters to ABNJ. The first was non-hierarchical and clustered groups of environmental variables prior to combination; the second was hierarchical and clustered Principal Components of environmental variables. Areas of agreement between the two approaches were identified and results compared with existing national and global classifications and published biodiversity patterns. We highlight several habitat classes we can be cautiously confident represent variation in biological diversity, such as topographic features, frontal systems and some abyssal basins. We also identify critical gaps in our knowledge of regional biogeography and advocate for collaborative effort to compile benthic species records and promote further exploration of the region to address these gaps. These insights into the distribution of habitats have the potential to support sustainable use and conservation of biodiversity beyond national jurisdiction, enable transboundary and ocean basin scale management, and empower nations to make progress towards achieving Sustainable Development Goals.

1 Introduction

The marine environment is under increasing pressure from human activities (Halpern et al., 2019) and the effects of climate change (Levin & Le Bris, 2015). In oceanic bottom waters particularly, where climate velocities are faster than at the surface (Brito-Morales et al., 2020), activities such as demersal fishing and oil and gas extraction are expanding (Ramirez-Llodra et al., 2011), and the commencement of seabed mining appears increasingly imminent (ISA, 2021). In the South Atlantic, cumulative impacts are increasing at some of the highest rates globally (Halpern et al., 2019). Over the last two decades, Marine Spatial Planning (MSP) has gained traction as a solution for managing multiple uses of the ocean and thus supporting integrated, multi-sector management (Ehler & Douvère, 2009). The international agenda for MSP has seen increased attention related to the concepts of blue growth and development of sustainable blue economies (Schultz-Zehden et al., 2019). This has been brought to prominence through the launch of the United Nations (UN) 2030 Sustainable Development Agenda, of which Sustainable Development Goal (SDG) 14 “Life Below Water” calls for ecosystem-based management and area-based conservation strategies (UNGA, 2015). This is supported by the UN Decade of Ocean Science for Sustainable Development, which establishes a framework to support nations in generating improved ocean science to achieve the SDGs (UN, 2021). MSP has thus become a priority for many nations due to international obligations (Simcock et al. 2021). While varying levels of political will, technical capacity and date of commencement have affected progress in MSP, numerous national policies and development plans (e.g., Angola, Brazil) have identified this process as a key tool for managing increasing human activities and achieving economic as well as conservation objectives (Finke et al., 2020; Gerhardinger et al., 2019). Some nations have already adopted specific MSP legislation (e.g., South Africa), while others are in the development phase (e.g., Namibia and the Falkland Islands¹), or the need to implement it is recognised (e.g., Uruguay) (Brickle et al., 2019; RSA, 2019a; Finke et al., 2020; MVOTMA, 2019; Marín et al., 2021).

¹ A dispute exists between the Governments of Argentina and the United Kingdom of Great Britain and Northern Ireland concerning sovereignty over the Falkland Islands. Statements are made without prejudice to the authors’ governments’ views on sovereignty in the region. Contents of this manuscript are of scientific nature and do not imply any opinion or position with respect to sovereignty issues.

In national waters, MSP brings together all sectors operating in a targeted area, and thus also the relevant management authorities and governing institutions (Ehler & Douvère, 2009). In areas beyond national jurisdiction (ABNJ), where no single nation or organisation has sole responsibility for governance and management, the situation is more complex and there is not yet a legal framework to support this (Altvater et al., 2019; Blythe et al., 2021). Currently, the various sectors in ABNJ operate under sector-specific frameworks and employ their own spatial or area-based management policies. For example, Regional Fisheries Management Organisations (RFMOs), responsible for fisheries management, designate bottom trawl closures for the protection of vulnerable marine ecosystems (VMEs) (e.g., CM 06/06, 2006; CM 30/15, 2015), and the International Seabed Authority (ISA), responsible for overseeing seabed mining, develops Regional Environmental Management Plans (e.g., ISA, 2011). There is thus no coordinated MSP for all sectors in ABNJ, and this is problematic for a number of reasons, not least because biodiversity in ABNJ tends to be poorly mapped and understood (Glover et al., 2018), but also vulnerable to disturbance and the cumulative impacts of human activities and global climate change (Ramirez-Llodra et al., 2011).

Ongoing work on a new global agreement on the conservation and sustainable use of marine biological diversity of ABNJ (called the Biodiversity Beyond National Jurisdiction (BBNJ) agreement) provides an opportunity and foundation for the development of MSP in ABNJ (Wright et al., 2021). It is hoped that the new agreement could allow for MSP at various scales, including whole ocean basins (Wright et al., 2021). Many deep-sea organisms show widespread distributions and are transboundary, both between Exclusive Economic Zones (EEZs) and between EEZs and ABNJ (McClain & Hardy, 2010). Although there are large gaps in our understanding of how populations are connected (Hilário et al., 2015; Baco et al., 2016) and how species distributions are predicted to shift under climate change (Pecl et al., 2017; Sweetman et al., 2017; Gianelli et al., submitted), for many species, MSP at the ocean basin scale would represent a key transition in management approach to an ecologically relevant scale (Bell et al., 2021; Combes et al., 2021).

MSP is underpinned by information on the spatial distribution of human activities and marine species, features, or habitats. Accordingly, nations undertaking MSP require ecological maps at varying spatial and temporal scales. Here and throughout we use the term habitat to refer to a set of environmental conditions that support a distinct benthic faunal community, and habitat maps thus convey information on the (generally predicted) distribution of different species or faunal assemblages. These maps can be derived from bottom-up predictions of species distributions, based on the modelled relationship between biological and environmental data (i.e., species distribution modelling, e.g., Howell et al., 2016; Howell et al., 2022; Ross & Howell 2013), or, where there is insufficient biological data, top-down classification of environmental surrogates to represent biological diversity (e.g., Roff & Taylor, 2000; Harris & Whiteway, 2009; Howell, 2010; Clark et al., 2011; Evans et al., 2015; McQuaid et al., 2020). Other investigations, notably in Europe, applied top-down classification schemes of environmental variables and used available biological data to fine-tune significant thresholds for likely changes in habitats for each abiotic layer (Vasquez et al., 2015; Vasquez et al., 2021).

In the South Atlantic, a number of nations have undertaken benthic and pelagic habitat mapping and/or classification to varying degrees using different approaches. Only a few have carried out continuous habitat mapping of the entire EEZ. These include South Africa (Sink et al., 2019), Namibia and Angola (Holness et al., 2014), and Brazil (Magris et al., 2020). Some have classified and mapped specific areas of the maritime zone, including parts of Namibia and Angola (Harris et al., 2013), Uruguay (Defeo et al., 2009; Hernández-Molina, 2016), Brazil (Gandra, 2020; Gandra et al., 2020), Saint Helena (Pike et al., 2018), the Falkland Islands (Golding & Black, 2020; Pearman, 2021) and South Georgia and the South Sandwich Islands (Hogg et al., 2016a; Hogg et al., 2018; Hogg et al., 2021). In some areas, fine-scale mapping and species distribution modelling have been undertaken of benthic habitats and assemblages (Nolan et al., 2017; Bridges et al., 2021), cold-water corals (Carranza et al., 2012; Taylor et al., 2013; Buhl-Mortensen et al., 2017; Carranza et al., 2021; Bridges et al. in prep), VME taxa

(MVOTMA, 2016; Brewin et al., 2020; Bridges et al., 2021; Downie et al., 2021) and targeted endangered species (Magris et al., 2020). In others, ecologically important areas like seabird foraging and breeding grounds (St. Helena Government, 2016; Carneiro et al., 2020; Requena et al., 2020), kelp forests (Pike & Medcalf, 2019; Bayley et al., 2021), and important nursery and spawning areas (Defeo et al., 2009) have been mapped, as well as specific features like hydrothermal vents, seamounts (SGSSI Government, 2013) and submarine canyons (Hernández-Molina, 2016). A number of global habitat classifications have also been produced and are relevant to the South Atlantic (e.g., UNESCO, 2009; Harris & Whiteway, 2009; Harris et al., 2014; Watling et al., 2013; Sayre et al., 2007; Clark et al., 2011; Spalding et al., 2007; Keith et al., 2020; Costello et al., 2017, see Table S1), as is a recent Atlantic-scale landscape mapping of the near seafloor (Schumacher et al., 2022).

These mapping efforts have used a range of methods and input variables. Of relevance to habitat classifications in the South Atlantic, most have adopted hierarchical approaches, supported by statistical and spatial analyses (Table S1). These classifications have focused mostly on the benthic environment and have used a range of environmental variables, the most common being depth, topography, oceanography, productivity and substrate or sediments. In several cases, these mapping efforts have been used to support spatial management within EEZs, for example the identification of Elements of Ecological Relevance and Marine Protected Areas (MPAs) in Uruguay (Brazeiro & Defeo 2006; Defeo et al., 2009), Ecologically or Biologically Significant Areas (EBSAs) in the Benguela Current Large Marine Ecosystem (Harris et al., 2022), Brazil (Brazil, 2007) and Ghana (Peace Gbeckor-Kove, pers. comm.), and MPAs in South Africa (RSA 2019b).

To facilitate MSP and an integrated approach to management that supports the achievement of national and international obligations at various spatial scales, continuous ocean basin scale habitat maps are required (Ehler & Douvère, 2009). Such mapping efforts have not been undertaken with a focus on the South Atlantic. This study brought together habitat mappers, biodiversity experts and ocean managers of several South Atlantic bordering nations with the aim of producing a broad-scale benthic habitat classification for this area. Owing to the large geographic area and scarcity of biological data across the region (OBIS, 2021; Bridges et al., in press), broad-scale, top-down approaches were used to classify environmental surrogates and identify distinct physical habitats, which we assume support distinct biological communities (Roff et al., 2003; Verfaillie et al., 2009; Galparsoro et al., 2014). Two statistical approaches were explored and their results contrasted with existing ecosystem maps and expert knowledge of biodiversity in the region.

2 Methods

2.1 Study region

This study focuses on the South Atlantic, which here is defined as approximately 7° 0' N to 60° 0' S and 36° 33' E to 67° 15' W (Figure 1). This boundary comes from the International Hydrographic Organization's definition of the South Atlantic (Flanders Marine Institute, 2020), but is extended north, south, and east to include the entire EEZs of Brazil, South Georgia and the South Sandwich Islands, and South Africa, respectively.

The South Atlantic consists of five principal basins, the Argentine, Brazil, Guinea, Angola, and Cape Basins. Major topographic features of the region include the Mid-Atlantic Ridge (MAR) and associated transverse ridges, the Rio Grande Rise, and the Walvis Ridge, and the large Patagonian shelf (Figure 1). There are also three major fracture zones, the Agulhas-Falkland Fracture Zone (AFFZ), the Rio Grande Fracture Zone (RGFZ) and the Romanche Fracture Zone (RFZ). Several inhabited and uninhabited oceanic islands are found across the region, including Saint Helena, Ascension Island, Tristan da Cunha, the Falkland Islands, and South Georgia and the South Sandwich Islands. The oceanography of the South Atlantic is dominated by the presence of an oligotrophic subtropical gyre running anticlockwise in surface and intermediate waters (McDonagh & King, 2005), with more

productive subtropical and subantarctic front systems to the south (Peterson & Stramma, 1991). In addition, there are sites of upwelling and associated increased primary productivity off the coast of southern Africa (South Africa, Namibia and Angola) (Lutjeharms & Meeuwis, 1987) and South America (Brazil, Uruguay and Argentina) (Gonzalez-Silvera et al., 2004).

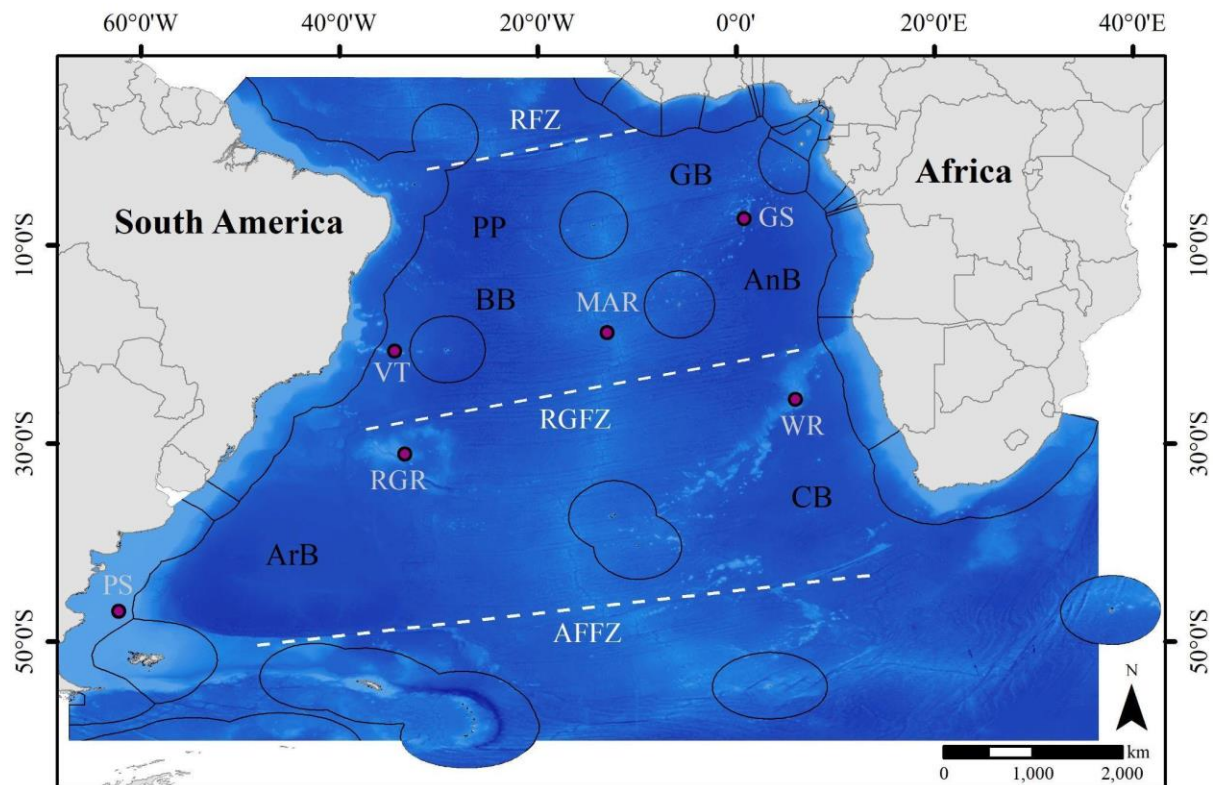


Figure 1. The South Atlantic study area showing basins and topographic features of the region. The limits for the study area are the International Hydrographic Organization’s South Atlantic boundaries (Flanders Marine Institute, 2020), extended north, south, and east to include the entire EEZs of Brazil, South Georgia and the South Sandwich Islands, and South Africa, respectively. AFFZ = Agulhas Falkland Fracture Zone, AnB = Angola Basin, ArB = Argentine Basin, BB = Brazil Basin, CB = Cape Basin, GB = Guinea Basin, GS = Guinea seamount chain, MAR = Mid-Atlantic Ridge, PS= Patagonian Shelf, PP = Pernambuco Plain, RFZ = Romanche Fracture Zone, RGFZ = Rio Grande Fracture Zone, RGR = Rio Grande Rise, VT = Vitória-Trindade seamounts, WR = Walvis Ridge. Bathymetry layer from the General Bathymetric Chart of the Oceans (GEBCO) 2020 gridded bathymetry data (https://www.gebco.net/data_and_products/gridded_bathymetry_data/gebco_2020/). [Colour, 1.5 column]

2.2 Benthic environmental data

In this study we have adopted the definition of “habitat” originally proposed in the scope of the project MESH (“Development of a framework for Mapping European Seabed Habitats”²),) to refer to “both the physical and environmental conditions that support a particular biological community together with the community itself” (MESH, 2008). The environmental data used in this study are thus those variables thought to be important drivers of faunal distribution. Importantly, these are broad-scale habitats and communities rather than biotopes. Justification for the inclusion of each variable is provided below. Input data come from freely available global datasets (Table 1). Prior to their combination in analyses, all environmental variables were resampled to 5 arcmin resolution using a bilinear interpolation method (NCAR, 2014) in ArcGIS v10.7 and reprojected to WGS84 if they had been in a different projection.

² <https://www.emodnet-seabedhabitats.eu/resources/mesh-archive/>

2.2.1 Topography

Although species show preference for certain depth ranges, this varies with geographic location and reflects correlations between depth and the variables actually driving species distributions, such as temperature and food supply (Evans et al., 2015; Bridges et al., 2022). Some variables have a relatively constant relationship with depth across latitudes (such as pressure and, to a lesser extent, light), while others do not. Given the scale of the study area, spanning a wide geographic area, we therefore excluded depth from our analyses, and instead used those variables thought to actually drive patterns in species distributions.

Topographic variation influences species distributions through factors such as current speed, sedimentation and food flux to depth (Hecker, 1990; Rice et al., 1990; Durden et al., 2015; Stefanoudis et al., 2016; Simon-Lledó et al., 2019; Perez et al., 2020). Slope acts as a surrogate for local hydrodynamics (Guinan et al., 2009), with steep slopes enhancing current velocity (Genin et al., 1986) and affecting parameters such as local sediment composition and productivity. Highly simplified, topography can act as a surrogate for substrate type, with plains and shallow slopes generally representing soft sediment habitats, while seamounts and complex features are more likely to provide areas of hard substrate.

Bathymetry data were obtained from the General Bathymetric Chart of the Oceans (GEBCO, 2020) gridded bathymetry data at approximately 450 m resolution. GEBCO data were resampled to 10 km resolution in an equal area projection, Mollweide, and bathymetric derivatives were then generated in ArcMap 10.7 using the Benthic Terrain Modeler extension (Wright et al., 2005). Slope was determined as the largest change in elevation between a cell and its three nearest neighbours. Bathymetric Position Index was derived at both broad and fine scales (called BBPI and FBPI, respectively). BBPI was derived with an inner radius of 1 and an outer radius of 10, giving a scale factor of ~100 km and thus identifying large geomorphological features, such as abyssal plains. FBPI was derived with an inner radius of 1 and an outer radius of 2, with a scale factor of ~20 km. This finer scale layer identified features in the scale of tens of kilometres, such as seamounts, abyssal hills and canyons.

2.2.2 Oceanography

Temperature controls the fundamental metabolic processes of organisms, and changes in temperature therefore alter species abundance and diversity (e.g., Rowe & Menzies, 1969). Together with salinity, temperature data also provide insight into the distribution of different water masses (Bryan & Lewis, 1979; Emery & Meincke, 1986), which affect species connectivity through transport and mixing and thus influence species distributions (Tyler & Zibrowius, 1992; Howell et al., 2002; Miller et al., 2011).

Oxygen is a key driver of benthic diversity, particularly where oxygen levels are low (Levin & Gage, 1998; Levin et al., 2001), with communities showing reduced species richness and density in oxygen minimum zones (Wishner et al., 1990; Levin & Gage, 1998). In deep waters, the concentrations of major nutrients differ with water masses (Levitus et al., 1993) and although biogeochemistry is more important in surface waters and pelagic environments where it affects productivity, differing nutrient concentrations can drive responses in benthic communities, through seafloor food webs and benthic-pelagic coupling (Henley et al., 2020). Finally, benthic currents affect sediment particle size distribution, which influences species distributions (e.g., Rowe & Menzies, 1969). Current velocity also drives near-seabed dispersal of organic matter, influencing patterns of abundance and community structure of benthic assemblages, particularly suspension feeders (Gage & Tyler, 1996; Durden et al., 2015).

Thus, benthic temperature, salinity, dissolved oxygen, nitrate, silicate, phosphate and current velocity were included in the study. Oceanographic data at the seafloor were obtained from Bio-ORACLE v2, a set of global-scale surface and benthic geophysical, biotic and environmental data (Assis et al., 2017; Tyberghein et al., 2012) and manipulated as described in Table 1.

2.2.3 Productivity

Productivity is one of the key determinants of community structure, function and diversity in both shallow (Künitzer et al., 1992) and deep (Levin et al., 2001; Smith et al., 2008) ecosystems. In the South Atlantic, chlorophyll-*a* concentration has been shown to drive benthic megafauna abundance and biomass (Kröncke & Türkay, 2003; Kröncke et al., 2013). Data on particulate organic carbon (POC) flux to the seafloor were obtained from the MEDUSA-2.0 model, an intermediate-complexity biogeochemical model of the marine carbon cycle (Yool et al., 2013). The MEDUSA-2.0 model estimates seafloor organic carbon flux using variable C:N ratios for slow- and fast-sinking detrital matter. A subset of the model was prepared for this study, as described in Table 1 (Yool, 2022).

2.2.4 Biogeography

A biogeography layer was produced to allow for differentiation between habitat classes that were environmentally similar, but geographically distant, and therefore unlikely to support the same or similar biological communities (for example habitat classes identified in the Arctic and the Antarctic). Biogeography provides information on how and when species may have evolved, and therefore sheds light on species distributions from an evolutionary standpoint (Vinogradova, 1997).

Although there are a number of existing benthic biogeographic classifications (e.g., Spalding et al., 2007; Watling et al., 2013), few span both national waters and ABNJ. Therefore, a new biogeography that covers the entire study region was created. This new biogeography was developed using the outputs of a water mass structure analysis (described below) in the knowledge that water mass structure is a driver of biological community structure (Howell et al., 2002; Miller et al., 2011; Tyler & Zibrowius, 1992) and is therefore a key determinant of biogeography (e.g., Watling et al., 2013). Discrimination between different basins was achieved by following large offshore water mass structure boundaries (classes 1-7, see Figure 2) within each basin and followed published biogeographic classifications where possible (Costello et al., 2017; Sink et al., 2019; Vinogradova, 1997; Watling et al., 2013; Zezina, 1997). The boundaries of these offshore water masses were extended to intercept with land to produce a full coverage biogeography layer. The split between the Atlantic and Indian Oceans was informed by South Africa's 2018 national ecosystem type classification (Sink et al., 2019) at the ecoregion level, where the division between the "Benguela" and "Agulhas" ecoregions was extended southwards to intercept with an Antarctic water mass. Importantly, the aim was to create a simple biogeographic model to separate unconnected water masses, and not to produce a new biogeography for use beyond this study.

Variable	Description	Units	Original cell size	Manipulation	Source	Classification Approach
Bathymetric position index – broad scale (BBPI)	Measure of where a referenced location is relative to the locations surrounding it	NA	450 x 450 m	Created in ArcGIS from GEBCO bathymetric model using Benthic Terrain Modeler extension. Inner radius 1, outer radius 10, scale factor is ~100 km	GEBCO 2020	Hierarchical & non-hierarchical
Bathymetric position index – fine scale (FBPI)	Measure of where a referenced location is relative to the locations surrounding it	NA	450 x 450 m	Created in ArcGIS from GEBCO bathymetric model using Benthic Terrain Modeler extension. Inner radius 1, outer radius 2, scale factor is ~20 km	GEBCO 2020	Hierarchical & non-hierarchical
Slope	Gradient, or rate of maximum change in z-value	°	450 x 450 m	Created in ArcGIS from GEBCO bathymetric model using Benthic Terrain Modeler extension	GEBCO 2020	Hierarchical & non-hierarchical
Salinity	Mean benthic salinity at mean depth for the period 2000-2014	PSS	5 x 5 arcmin	NA	Bio-ORACLE v2	Hierarchical & non-hierarchical
Temperature	Mean benthic temperature at mean depth for the period 2000-2014	°C	5 x 5 arcmin	NA	Bio-ORACLE v2	Hierarchical & non-hierarchical
Productivity	Mean particulate organic carbon flux to seafloor for the period 2006-2015	mmol. C m ⁻² d ⁻¹	5 x 5 arcmin	Output from the MEDUSA model (Yool et al., 2013) regrided from ORCA0083 to NEMO 5 arcmin	Yool (2022)	Hierarchical & non-hierarchical
Dissolved oxygen	Mean benthic dissolved oxygen concentration at mean depth for the period 2000-2014	mmol. m ⁻³	5 x 5 arcmin	NA	Bio-ORACLE v2	Hierarchical
Nitrate	Mean benthic nitrate concentration at mean depth for the period 2000-2014	mmol. m ⁻³	5 x 5 arcmin	NA	Bio-ORACLE v2	Hierarchical
Phosphate	Mean benthic phosphate concentration at mean depth for the period 2000-2014	mmol. m ⁻³	5 x 5 arcmin	NA	Bio-ORACLE v2	Hierarchical
Silicate	Mean benthic silicate concentration at mean depth for the period 2000-2014	mmol. m ⁻³	5 x 5 arcmin	NA	Bio-ORACLE v2	Hierarchical
Current velocity	Mean benthic current velocity at mean depth for the period 2000-2014	m.s ⁻¹	5 x 5 arcmin	NA	Bio-ORACLE v2	Hierarchical
Biogeography	Biogeographic provinces	NA	NA	Developed using the outputs of water mass structure analysis (see non-hierarchical)	Multiple (see text)	Non-hierarchical

				approach) and published biogeographic classifications where possible (e.g. Vinogradova, 1997; Watling et al., 2013; Zezina, 1997)		
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GEBCO: https://www.gebco.net/data_and_products/gridded_bathymetry_data/gebco_2020/

Bio-ORACLE v2: <https://www.bio-oracle.org/>

Yool (2022): <https://doi.org/10.5281/zenodo.6513616>

Biogeography layer: <https://github.com/DeepSeaCRU/South-Atlantic-Benthic-Habitat-Classification>

Table 1. Summary table of benthic environmental input data. “Classification Approach” indicates the approach each variable was used in.

2.3 Classification approaches

This study used two different methods to classify benthic environmental variables and produce two separate habitat classifications. The first approach, termed the ‘non-hierarchical approach’, combined pre-clustered environmental variables to produce a non-hierarchical classification. The second approach, termed the ‘hierarchical approach’, clustered principal components derived through Principal Component Analysis (PCA) of input environmental variables to produce a nested, hierarchical classification. Both approaches used slightly different variables, as outlined in Table 1 and explained in the respective sections below. The classifications were carried out at a global scale, to avoid issues that arise with retrospectively changing model extent, and then cropped to the study area extent (Figure 1). Reproducible code for these analyses is available at: <https://github.com/DeepSeaCRU/South-Atlantic-Benthic-Habitat-Classification>.

2.3.1 Non-hierarchical Approach

This method uses a two-step approach to classify environmental variables, based on McQuaid et al. (2020).

Input variables were selected based on Howell (2010) who proposed a four-tier hierarchical classification system for the deep sea structured by biogeography, depth, substratum and biology. Although other factors may drive species distributions in the deep sea (e.g. see description of environmental data above), those identified by Howell et al. (2010) are proposed to be the most important. Owing to the nature of the non-hierarchical classification methods used, inclusion of additional variables or groups of variables greatly increases the number of output habitat classes. A very high number of classes can impede the effectiveness or usefulness of a classification (Hancock et al., 2013) and thus we chose to include only those variables thought to be the most important. Based on this, the approach used data on biogeography, water mass structure (a more globally relevant variable than depth, based on temperature and salinity), topography (acting as a surrogate for sediment composition/substrate, based on FBPI, BBPI and slope) and productivity (a strong driver of biology).

Environmental variables (or classes of variables) were clustered using a *k*-medoids, non-hierarchical clustering algorithm called Clustering Large Applications (CLARA; Kaufman & Rousseeuw, 1990) in the ‘fpc’ package (Hennig, 2020) in R (R Core Team, 2019). CLARA clusters data points around the medoids (similar in concept to centroids, but taken as the median from within the dataset rather than its geometric ‘centre’) and is appropriate for use with large datasets. Prior to clustering, all variables were rescaled to have equal variance and a common scale of 0–1. Clustering was carried out on:

- (1) FBPI, BBPI and slope to produce a topography layer;
- (2) Salinity and temperature at the seafloor to produce a benthic water mass structure layer;
- (3) POC flux to the seafloor to produce a benthic productivity layer.

Clustering was carried out on each variable or class of variables (e.g., topography) separately to support equal weighting of each variable class in the classification through the inclusion of a single layer representing each class. This was deemed appropriate as there is currently insufficient evidence to support weighting the importance of variables in driving species distributions in the South Atlantic. CLARA requires a user-defined number of clusters for the output. Clustering was therefore run iteratively for each analysis, testing 2 to 40 clusters to identify the most parsimonious number of clusters. Clustering performance was evaluated using average silhouette width (ASW) (Kaufman & Rousseeuw, 1990) and the Calinski-Harabasz index (CH) (both built into the CLARA function), with the best-performing cluster solution identified as the iteration that scored highest across both indices. The decision on the number of clusters was further refined through expert judgement based on literature. This approach of using expert judgement is seen in other classifications (e.g., Sherman, 1986; Spalding et al., 2007; UNESCO, 2009; Watling et al., 2013; Harris et al., 2014; Sutton et al., 2017) and ensured

that the final variable layers depicted features known to be important in the distribution of deep-sea habitats. Where literature was used to support decision-making this is indicated, and meant that in some cases, the number of clusters chosen was not the highest scoring. Boxplots were produced of the original input variables against the clustering solutions to characterise each cluster.

The ‘Combine’ tool in ArcGIS v10.7 was used to combine the outputs of the clustering steps with the biogeography layer to produce the final habitat classification. This tool combines multiple rasters into a new raster with each output cell assigned a class that represents a unique combination of input values. The final classification was therefore a raster layer, with each cell assigned a habitat class representing a different set of environmental conditions and reflecting habitat heterogeneity across the region.

2.3.2 Hierarchical Approach

The hierarchical approach identified and then clustered principal components (PCs) of input environmental data. A number of benthic classifications in the region have included data on nutrient concentrations and current velocity (e.g., UNESCO, 2009; Hogg et al., 2016a; Karenyi et al., 2016; Sayre et al., 2017; Gandra, 2020; Table S1), and unlike the non-hierarchical approach, inclusion of additional variables as potential drivers of distribution does not influence the number of output habitat classes in the hierarchical approach. Thus, the following benthic environmental input data were selected: salinity, temperature, slope, FBPI, BBPI, silicate, nitrate, phosphate, dissolved oxygen, current velocity and particulate organic carbon flux to seafloor.

PCA was used to compute new, linearly independent variables (PCs) that captured most of the variation in the original data (Legendre & Legendre, 1998). This step acted to reduce the number of variables in the analysis without the need to manually assess the input of each variable. Prior to PCA, all environmental variables were standardised to have zero means and equal variance, and only those PCs with eigenvalues greater than 1.0 were retained in the analyses, in-line with the Kaiser-Guttman criterion (Legendre & Legendre, 1998).

The new PCs were then clustered using the same *k*-medoids algorithm as above, CLARA (Kaufman & Rousseeuw, 1990), to produce the final habitat classification. It is important to note here that the use of the term “hierarchical” to describe this approach refers to the nested nature of the classification whereby upper levels of the classification were further subdivided, and not to the clustering algorithm, which was non-hierarchical. The determination of the number of clusters in the output and further refinement followed the same methods as the non-hierarchical approach.

The PCA and clustering process was repeated for each output cluster in isolation, to give a second level of clustering nested within the first. This was carried out on the original input data, to capture environmental variation within each cluster in question. This process was then repeated to give a third level of clustering, thus identifying habitat classes at increasing detail across the region. The outputs of each level of clustering were raster layers, with each cell assigned a habitat class representing a different set of environmental conditions. Nested clustering was only carried out on those habitat classes occurring within the South Atlantic, and not at a global scale (see previous section on Biogeography). For the first level of the classification (level 1), boxplots were produced of the original input variables against the clustering solutions to characterise each cluster and decision-trees were constructed to understand which environmental variables were driving the splits in classes.

All analyses were run in R 4.1.1 using the *rasterPCA* function of the *RStoolbox* package (Leutner et al., 2019) to carry out PCA analysis, the *CLARA* function of the *fpc* package (Hennig, 2015) for clustering, and the *rpart* function of the *rpart* package (Therneau et al., 2019) to produce decision trees.

2.4 Confidence maps

Confidence layers showing cluster stability were produced to accompany (1) initial clustering of input variables for the non-hierarchical approach, and (2) output classification maps for the hierarchical approach. This involved calculating cluster membership values and a confusion index for each clustering, as per Hogg et al. (2016a). Cluster membership calculates the relative inverse distance squared between each data point and the centroids of all of the clusters. High membership values indicate that a data point is well characterised by membership to one cluster. The confusion index is then calculated using the two highest membership values for each data point, to quantify the uncertainty associated with the clustering of each point. Confusion index values range from 0 to 1, with values approaching 1 indicating greater uncertainty in the clustering solution between two or more clusters.

Analyses were run in R 4.1.1 using a custom script (see Supplementary Material).

3 Results

3.1 Non-hierarchical approach

3.1.1 Initial clustering and biogeography

For all initial clustering, ASW and CH scores were highest for two clusters. However, this did not capture the complexity of biologically relevant variation in each variable at the ocean basin scale and so decisions on the number of clusters were supported by expert opinion and literature. For topography, the second highest score for both ASW and CH was three clusters. This iteration was selected based on its high scores and ability to better capture broad patterns in topography across the region; reflecting substrate hardness, a driver of diversity in the South Atlantic (Bridges et al., 2021). When assessed against GEBCO bathymetry, these clusters were described as ‘hills and ridges’, ‘plains and shallow slopes’ and ‘seamounts and complex features’ (Figure 2a). The latter included features like seamount complexes, guyots and trenches. For water mass structure, the second highest ASW scoring iteration of 12 clusters was selected. Although this was not matched with high CH scores, the resultant clusters showed similarities to some biogeographies and water mass distributions in the literature (Menzies et al., 1973; Vinogradova, 1997). This clustering also recognised different water masses above and below the 1000m contour, a boundary supported by biological data (Pequegnat, 1983). The water mass structure clusters showed clear tendencies as being either ‘inshore’ or ‘offshore’ (Table 2, Figures 2-3), and thus discriminated between coastal water bodies resulting from tidal and wind-driven currents, and larger oceanic water bodies driven by thermohaline circulation. Finally, for POC flux to the seafloor, the second highest scoring iteration for both ASW and CH was three clusters. However, these groups only differentiated between POC flux to the seafloor between inshore/coastal waters and offshore/deep waters. Five clusters had the next highest score for ASW and CH, and this was selected as they reflected known variation in POC in ABNJ, for example the separation of offshore areas in temperate latitudes that are known to receive higher POC flux to depth than adjacent areas (e.g. around Tristan da Cunha, see Lutz et al., 2007). Most of the region (and particularly ABNJ) was covered by a ‘very low’ productivity class, with inshore waters dominated by higher productivity (Figure 2c). This was expected as POC flux to the seafloor is known to decrease with depth (Lutz et al., 2007).

Three biogeographic regions were identified for the South Atlantic (Figure 2d). Major splits were identified between the Atlantic and Antarctic, driven by water mass structure, and between the Atlantic and Indian Oceans by the southward extension of a split in the South African ecosystem classification between the “Agulhas” and “Benguela” ecoregions (Sink et al., 2019).

No. clusters	Topography		WMS		POC flux	
	ASW	CH x10 ⁶	ASW	CH x10 ⁶	ASW	CH x10 ⁶

1	0	0	0	0	0	0
2	0.57	4.17	0.92	1.53*	0.93	1.18*
3	0.52	4.02	0.57	8.75	0.89	1.14*
4	0.27	2.68	0.56	1.07*	0.62	7.77
5	0.29	3.37	0.54	8.92	0.71	1.07*
6	0.31	2.66	0.49	1.01*	0.60	9.44
7	0.36	2.40	0.50	1.04*	0.54	8.35
8	0.29	2.77	0.48	9.43	0.55	7.60
9	0.39	2.68	0.41	8.55	0.58	7.56
10	0.35	2.39	0.43	8.44	0.50	7.77
11	0.38	2.42	0.54	9.00	0.52	7.22
12	0.34	2.43	0.61	7.50	0.54	6.59

Table 2. Average silhouette width (ASW) and Calinski-Harabasz (CH) index scores for clustering on 2-40 iterations, showing the first 12. Bold indicates clustering solution selected. WMS = water mass structure, POC = particulate organic carbon. * = CH values $\times 10^7$.

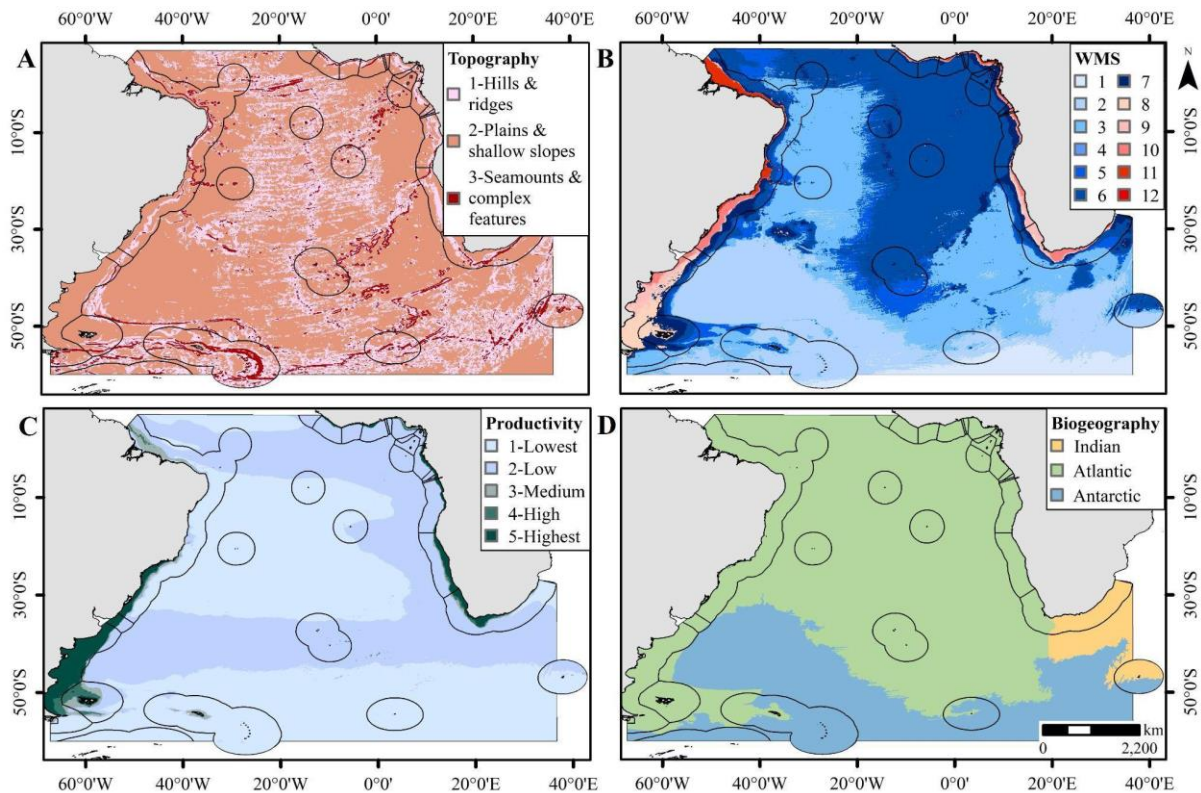


Figure 2. Outputs of initial clustering for the non-hierarchical approach on variable classes to represent (a) topography, (b) water mass structure (WMS), and (c) seafloor productivity, as well as (d) outputs of the biogeography layer for the South Atlantic. Clusters 1-7 for WMS are indicative of offshore water masses, while clusters 8-12 are considered inshore water masses. [Colour, double column]

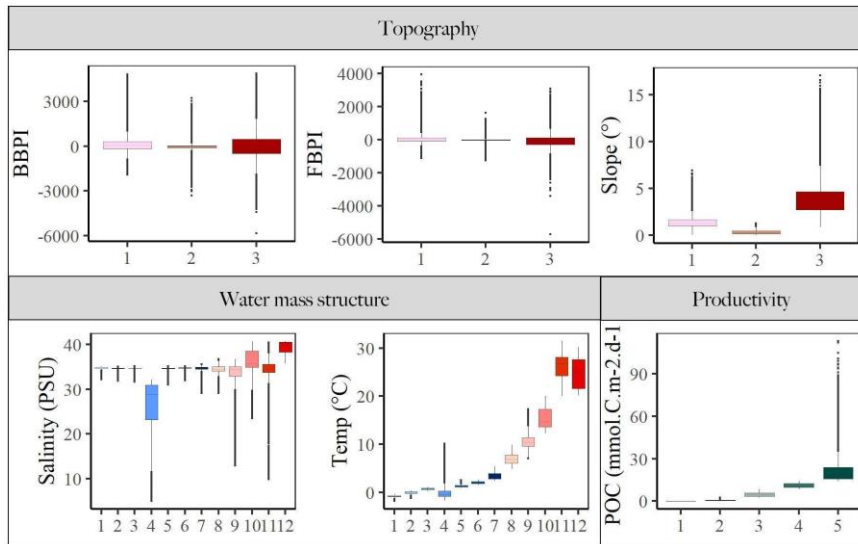


Figure 3. Environmental characteristics of initial output clusters of the non-hierarchical approach. Boxplots show the median, first and third quartiles as well as the maximum and minimum observed values. The x axis gives cluster numbers. [Colour, 1.5 column]

3.1.2 Final non-hierarchical classification

The final broad-scale habitat classification produced with the non-hierarchical approach proposed 204 benthic habitat classes in the South Atlantic (Figure 4). These classes reflected variation in environmental conditions (at 10 km resolution, Table S2) and are assumed to support distinct groups of faunal communities at this scale. The boundaries between classes will include transition zones that are not captured by the classification.

There were clear distinctions between inshore and offshore habitat classes, with higher variability in habitat classes concentrated inshore of the continental rise. Inshore habitat classes (based on clusters 8-12 of the water mass structure layer, Figure 2b) formed 43% of the total number of habitat classes, but only 0.5% of the total extent of the study area. This was also reflected in the geographic size of habitat classes, with a small number of classes covering large areas (> 200 000 km², mostly seen in abyssal plain areas), and a large number of classes covering smaller areas in the region.

The classification identified several large abyssal plain areas (Figure 4), reflecting the Argentine Basin (bounded to the south by the Patagonian Shelf and to the north by the Rio Grande Rise), the Brazil Basin (split by the Vitória-Trindade seamount chain), the Pernambuco Plain and the Romanche Fracture Zone, the Guinea Basin and seamount chain, and the Angola Basin separated from the Cape Basin to the south by the Walvis Ridge. Differentiation in habitat classes on either side of the MAR was observed northwards of 38°S, as well as between temperate and tropical areas.

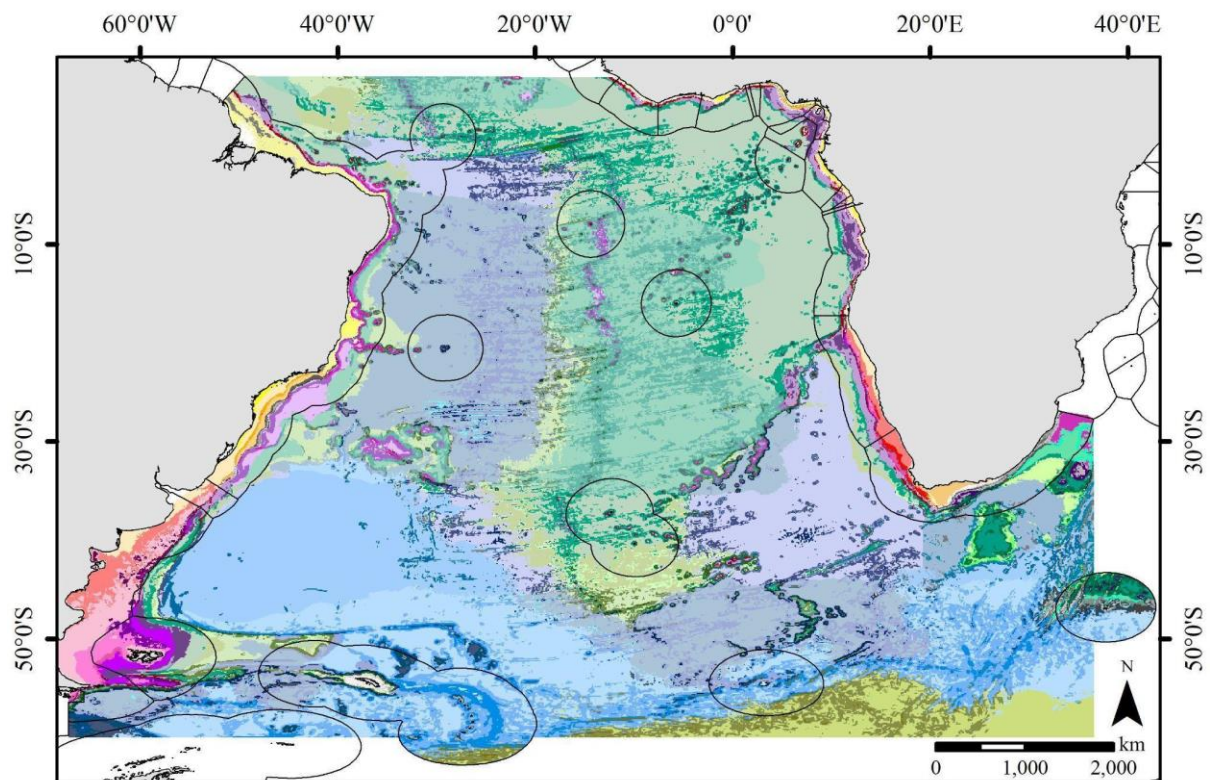


Figure 4. Final habitat classification for the South Atlantic produced through the non-hierarchical approach of combining layers of clustered environmental variables. The habitat map shows 204 habitat classes within the study area, denoted by different colours. [Colour, 1.5 column]

3.2 Hierarchical approach

3.2.1 PCA and clustering: Level 1

The PCA on environmental variables across the study area revealed four PCs with eigenvalues greater than one, which together explained 74% of total variance (Table 3). Concentrations of nutrients and oxygen explained most of this variance and were strongly correlated with PC 1. Nitrate, phosphate and silicate were highly correlated and thus loaded on the same PC. PC 2 was correlated with FBPI and BBPI, showing an influence of topography, while PC 3 was correlated with temperature and PC 4 with salinity.

The cluster selection indices (ASW & CH) suggested that the four PCs were best clustered into two groups (Table 4). However, this was not expected to sufficiently represent biologically relevant variation across the region and thus the second highest scoring iteration of four clusters was selected. Similar to the non-hierarchical approach, this clustering broadly captured patterns from existing biogeographies based on biological data (Menzies et al., 1973; Vinogradova, 1997; Figure 5a). Two of these clusters were large and covered the majority of the region, including most of ABNJ: a north-eastern and “offshore” South Atlantic cluster (Class 1); and a southern and north-western South Atlantic cluster (Class 3). The boundary between these extends along the Walvis Ridge to the MAR at around 40°S. The boundary follows the MAR northwards to the equator, where it broadly follows the Romanche Fracture Zone towards South America. Class 1 was characterised by high dissolved oxygen and mid-range nutrient concentrations, while Class 3 was characterised by low dissolved oxygen and high nutrient concentrations, with little variability at low temperatures (Figure 6). The two remaining cluster groups were much smaller in extent, and included a shelf cluster (Class 2), and one around deep-water trenches in the Antarctic Polar Front region between approximately 45°S and 60°S, belonging to

a larger global cluster (not presented here) (Class 4). Class 2 was characterised by high POC flux to the seafloor when compared to all other classes, high current velocity and temperature, and low nutrient concentrations, with high variability in salinity and temperature. This reflects cases where major river systems meet the Atlantic, such as the Amazon River in northern Brazil. Class 4 had the lowest nutrient concentrations and lowest dissolved oxygen, with sloped topography relatively lower than surrounding areas. The splits between habitat classes as seen in the decision-tree analysis were driven by nutrient concentration (specifically nitrate), temperature, and POC flux to seafloor (Figure 7).

Environmental variable	PC1	PC2	PC3	PC4
FBPI		0.756	-0.391	
BBPI		0.829	-0.326	
Slope			-0.395	-0.517
Salinity				-0.790
Temperature	0.387	0.434	0.646	
POC	0.511		0.454	
Dissolved oxygen	0.756	-0.340	-0.394	
Nitrate	-0.983			
Phosphate	-0.975			
Silicate	-0.940			
Current velocity		0.341	0.427	
Variance explained (%)	34.93	16.43	12.67	10.04
Cumulative variance (%)	34.93	51.36	64.02	74.06
Eigenvalue	1.96	1.34	1.18	1.05

Table 3. Correlations between environmental input data and PCs for level 1, with variance explained and eigenvalues. Strong correlations (<-0.6 or > 0.6) are shown in bold; weak correlations (<-0.3 or > 0.3) removed for clarity.

No. clusters	ASW	CH (x10 ⁶)
2	0.63	1.52
3	0.38	1.41
4	0.48	1.79
5	0.40	1.62
6	0.41	1.79
7	0.35	1.65
8	0.46	1.58
9	0.46	1.49
10		0. 1.
	47	66
11	0.47	1.
		24
12	0.46	1.
		64

Table 4. Average silhouette width (ASW) and Calinski-Harabasz (CH) index scores for clustering on 2-40 iterations at level 1, showing the first 12. Bold indicates clustering solution selected.

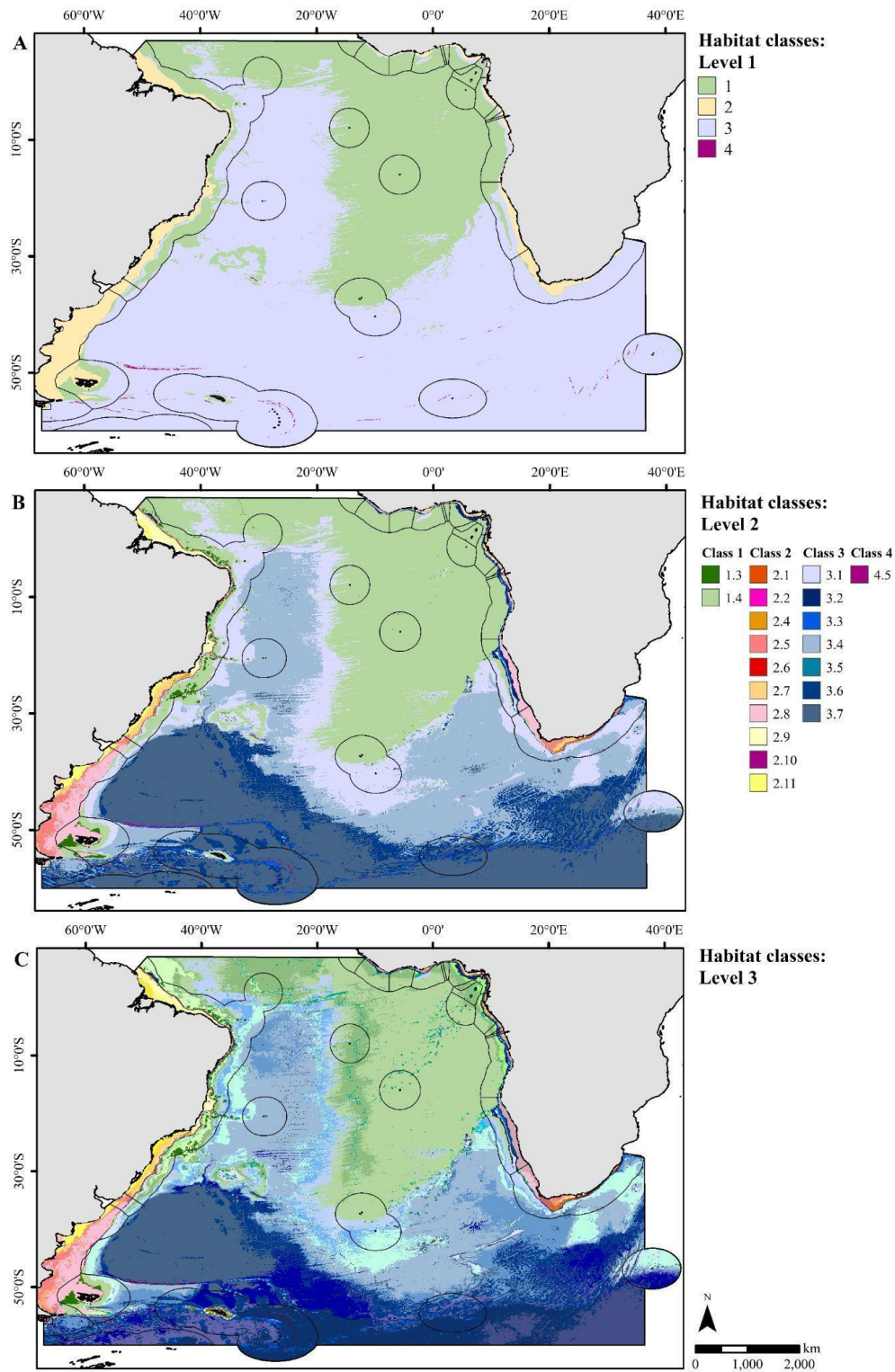


Figure 5. Outputs of clustering Principal Components of environmental input data to produce a nested hierarchical habitat classification. (a) Highest level of classification showing Classes 1 to 4 (level 1); (b) second level of classification showing subclasses of habitat Classes 1 to 4 (level 2); and (c) third level of classification showing further subdivision of level 2 (level 3). [Colour, 1.5 column]

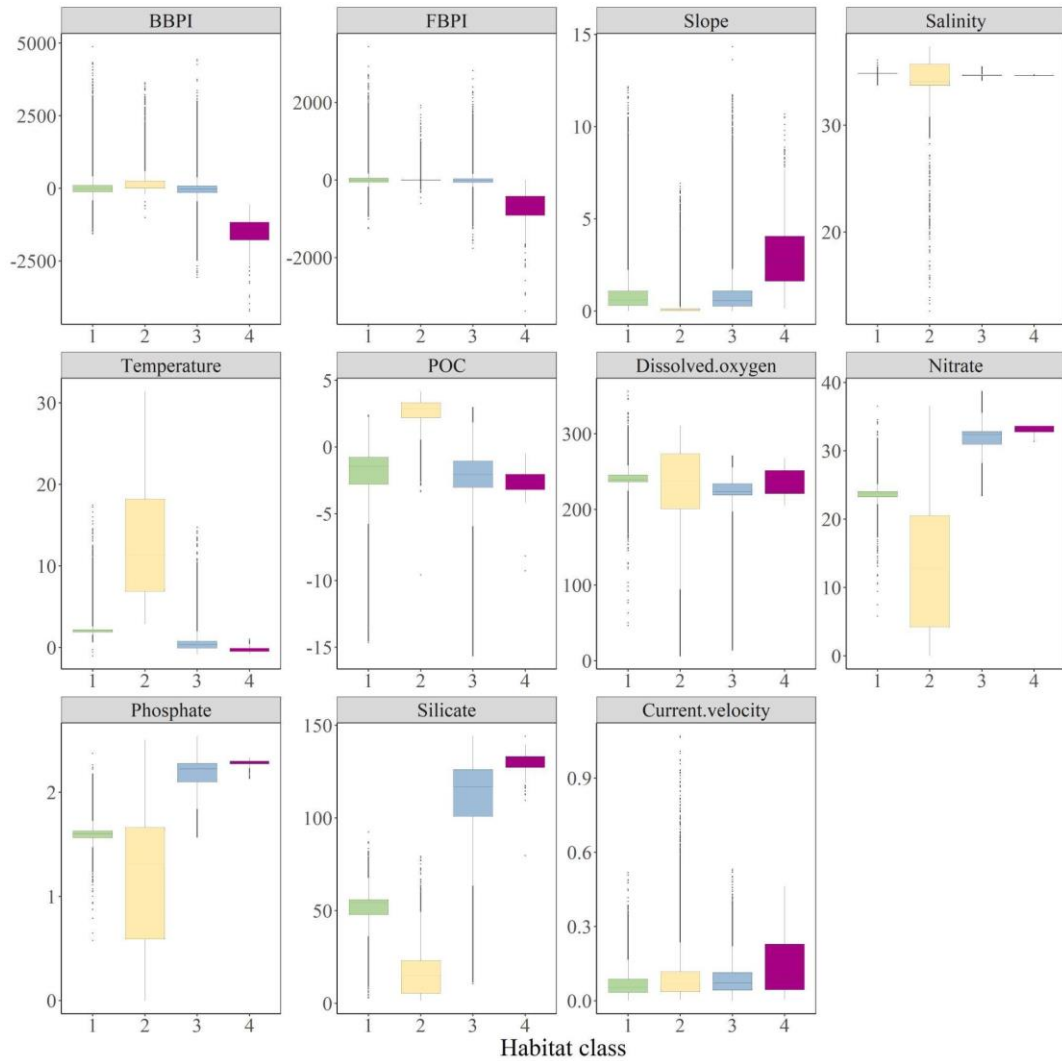


Figure 6. Boxplots showing environmental characteristics of the four habitat classes in level 1 produced through clustering of PCAs for the hierarchical approach. Boxplots show the median, first and third quartiles as well as the maximum and minimum observed values. Units for each variable are described in Table 1; POC has been log transformed to better show patterns. [Colour, 1.5 or double column]

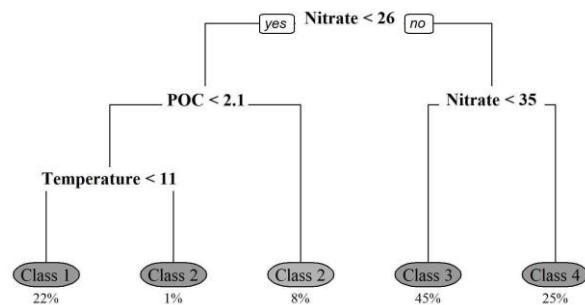


Figure 7. Decision-tree for clustering Principal Components of environmental data in level 1 of the hierarchical approach. Units are given in Table 1. Percentages indicate the percentage of observations in each Class. [Colour not required, single column]

3.2.2 Final nested hierarchical classification

The PCA explained a high proportion of total variance for repeated clustering of Classes 1 to 4 produced in the first and second levels of the hierarchical approach (>70% and >64%, respectively). See

supplementary material for the resultant PCA eigenvalues, percent variance explained, clustering solutions and key environmental drivers (Tables S3 and S4), and environmental properties of habitat classes in the first two levels of nested clustering (Table S5). As with the non-hierarchical approach, in most cases the highest scoring iterations were those with two clusters. In these cases, the second highest scoring iterations were selected.

At the second level of clustering, subdivisions in Class 1 were driven by nutrient concentrations. Owing to the global nature of the classification, some classes did not show much additional variation in the South Atlantic when re-clustered (i.e. greater variation was observed in other parts of the world), and this was the case for Class 1 (Figure 5b). Nutrient concentration was also the most important factor driving level 2 clustering of Class 2, a shelf habitat class, followed by oceanographic variables, productivity and slope. This was reflective of the high variability in these environmental drivers in shallower waters on continental margins. Subdivisions in Class 3 were driven first by temperature, and then nutrient concentrations and BBPI, as this class stretched from polar to temperate and even tropical waters (Figure 5b). Finally, Class 4 showed no further differentiation in the South Atlantic.

A third level of clustering produced a more detailed classification layer, with a total of 132 habitat classes in the South Atlantic (Figure 5c). This re-clustering split a large habitat class to the east of the MAR and north of the Walvis Ridge into several new classes associated with varying topography around the MAR, Rio Grande Rise and the Walvis Ridge. Habitat classes with complex topography were also identified on transverse ridges to the west of the MAR and around the Agulhas Ridge in ABNJ off South Africa. The third level of clustering showed two large habitat classes in both the Brazil and Cape Basins characterised by flatter topography, one with higher current velocity and nutrient concentrations than the other. A large habitat class occurring in subpolar frontal regions and the Argentine Basin was also further divided, exhibiting latitudinal and longitudinal splits of the higher-level class, with bottom temperature being the primary driver of habitat differentiation (Figure 5c). Observations within the Argentine Basin clustered together to produce a single cluster characterised by low temperatures and high current velocity (reflecting circulation of Antarctic Bottom Water in this area), and flat topography with very little variability. To the south of this was a warmer class around 45-55°S, with higher dissolved oxygen and lower nutrient concentrations, and finally a selection of habitat classes around the Subantarctic front. This latitudinal pattern was also split longitudinally, with different classes between South Georgia and the South Sandwich Islands, and another broad split around 10-20°E.

The final habitat classifications are available to download at: <https://github.com/DeepSeaCRU/South-Atlantic-Benthic-Habitat-Classification>.

3.3 Confidence maps

Confusion index confidence maps revealed which areas are less or more certain in their assignment to cluster groups. For the non-hierarchical approach, areas of greater uncertainty for topography clusters were located at the boundaries between clusters, which was to be expected (Figure 8a). This was evident particularly between the ‘plains and shallow slopes’ cluster and both the ‘hills and ridges’ and ‘seamounts and other complex features’ clusters, which had smaller spatial extents. Clustering of water mass structure had the greatest extent of high confusion index values (Figure 8b). Although much of it was focussed around transitions between classes, particularly around the Subantarctic Front system, there were also large areas of uncertainty in the Cape and Angola Basins and around the Falkland Islands. Finally, clusters of POC flux to the seafloor showed areas of greater uncertainty (shown in white in Figure 8c) close to land masses, where there is higher variability in POC, and again on and near boundaries between clusters.

For the first level of the hierarchical cluster approach, the highest confusion index values were again observed at boundaries between the four classes (Figure 8d). However, there was also uncertainty within classes. Class 2, particularly, showed high uncertainty on the continental margins of Africa and South

America, which may likely be linked to high environmental variability in these areas and therefore difficulty placing observations in a single cluster.

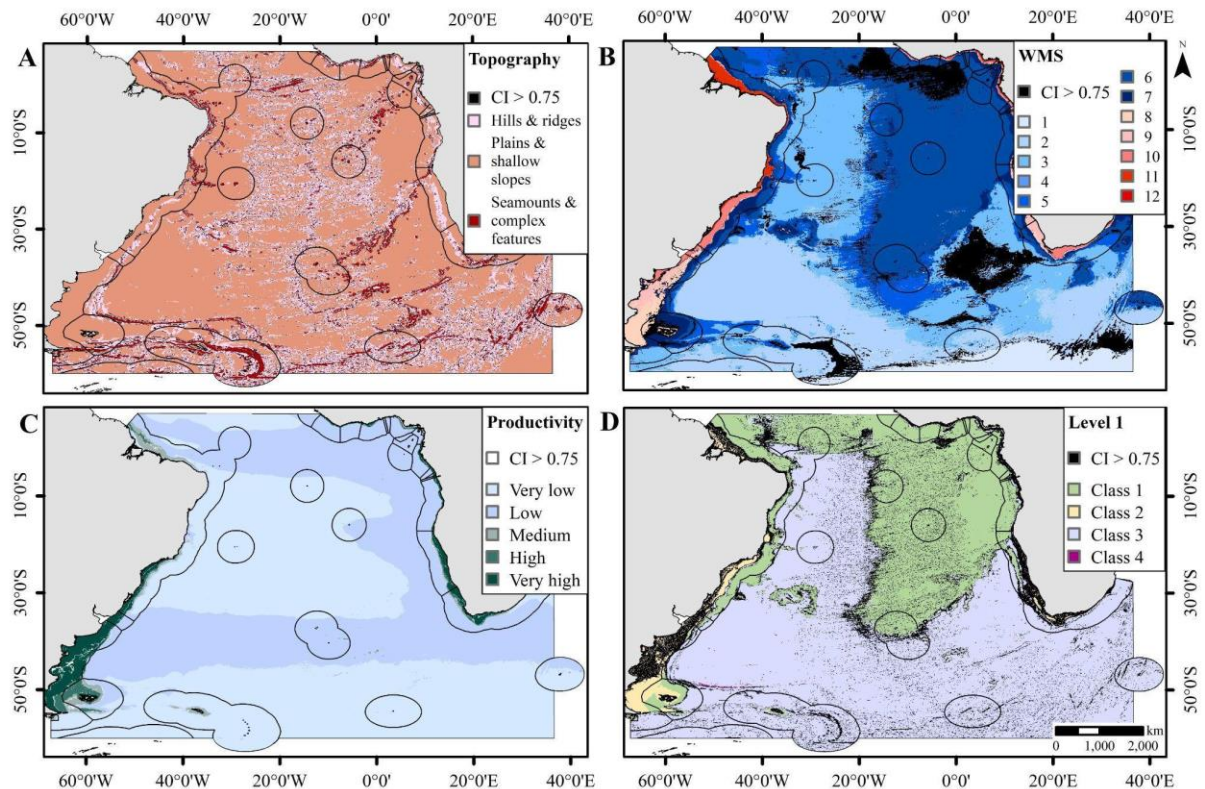


Figure 8. Confidence maps for clustering of initial input data for the non-hierarchical approach (a-c) and Principal Components for the hierarchical approach (d). Confusion index (CI) values are mapped over clustering outputs, showing areas of greater uncertainty at transitions between clusters and within-cluster uncertainty. High CI values (>0.75) are shown in black (and white for POC) and indicate lower confidence in clustering. For the non-hierarchical approach, maps show CI for clustering (a) FBPI, BBPI and slope to produce a topography layer, (b) salinity and temperature to produce a water mass structure (WMS) layer, and (c) POC flux to seafloor to produce a productivity layer. For the hierarchical approach, map shows CI for clustering (d) Principal Components at the highest level of the classification. [Colour, double column]

4 Discussion

We produced two broad-scale benthic habitat classifications of the South Atlantic using different approaches. Here we reflect on their potential validity by identifying areas of agreement between the two approaches and comparing the outputs with previously published patterns of biological diversity and relevant global, national and finer-scale classifications.

4.1 Areas of agreement

4.1.1 Cape and Angola Basins

Differentiation between the Cape and Angola Basins was consistently identified through this study and is supported by knowledge of water bodies (Kopte et al., 2017), examination of macro- and megabenthic communities (Kröncke et al., 2013; Brix et al., 2015), previous global biogeographies (Watling et al., 2013; Sayre et al., 2017; Watling & Lapointe, 2022) and a recent Atlantic-scale seafloor classification (Schumacher et al., 2022). Class boundaries highlighted a sharp division in water masses, marked at the African coast by the Angola-Benguela Front situated between 15° and 17°S off the coast of Angola and Namibia (Kopte et al., 2017). The hydrographic boundary between classes may be caused by the

isolation of the majority of Antarctic Bottom Water from the deep eastern South Atlantic by the Walvis Ridge and MAR (Connary & Ewing, 1970; Shannon & Chapman, 1991) and the extension of North Atlantic Deep Water into the southern hemisphere (Larqué et al., 1997). Strong differences in macro- and megafaunal communities have been recorded between the Guinea, Angola and Cape Basins, linked to differences in water mass structure and food availability (Kröncke et al., 2013). Habitat differentiation closely mirrored the bottom-occurring Ecological Marine Units of a global clustering of oceanographic variables (Sayre et al., 2017) and a global biogeographic classification (Watling et al., 2013). The latitudinal split in nearshore habitat classes between Angola and Namibia was also identified in a global biogeographic classification by Costello et al. (2017), who analysed the largest available biological dataset from the Ocean Biodiversity Information System (OBIS), as well as in a classification of coastal and shelf areas based on biological data by Spalding et al. (2007). It is worth noting that Costello et al. (2017) included both benthic and pelagic records, with a high proportion of the latter. This nearshore differentiation was not reflected in Schumacher et al. (2022), although their Atlantic-scale classification identified only 9 classes across the Atlantic. High CI values were located at class boundaries, which is to be expected as habitat classes include a transition zone between classes. High CI values were also recorded in southern parts of the Cape Basin for the water mass structure layer of the non-hierarchical approach.

4.1.2 Argentine Basin

Both approaches classified abyssal habitats in the Argentine Basin together with colder waters of the Subantarctic and Polar fronts. This delineation is supported by Costello et al. (2017) and a study of abyssal tunicates from the Argentine Basin showing that these were more similar to Antarctic fauna than other Atlantic basins (Monniot & Monniot, 1976). Increased diversity of bivalves, gastropods, and isopods has also been observed in the Argentine compared to the Cape Basin, although this was potentially linked to high and variable POC flux to seafloor recorded in the latter (Rex et al., 1993). Although distinction between the Cape and Argentine Basins was not proposed by Watling et al. (2013) or Schumacher et al. (2022), these were based on environmental, and not biological, data. Low CI values in the Argentine Basin indicated high confidence around this classification.

4.1.3 Patagonian and Brazilian shelf split

Distinction between habitat classes on the Patagonian Shelf and adjacent continental slope, and those on the Brazilian shelf and slope between 33 and 38°S, was identified by both classifications and is supported by knowledge of water mass structure in the region. Class boundaries are likely linked to the Subtropical Shelf Front (Piola et al., 2000) and probably represent the limit for the Northern Argentine Mound Province, the largest coral mound province worldwide (Steinmann et al., 2020). This latitudinal split in nearshore habitat classes was reflected in Costello et al. (2017) and although Watling & Lapointe (2022) did not propose separate biogeographic provinces for this region, their analysis of anthozoan data using Infomap Bioregions (Edler et al., 2017) did differentiate between two different 'Bioregions'. Low CI values supported this split, although there was low confidence in Habitat Class 2 in the EEZs of Uruguay and Argentina at level 1 of the hierarchical approach.

4.1.4 Frontal systems

The two approaches in this study showed habitat differentiation between 40 and 50°S, reflecting the dynamic Subtropical, Subantarctic and Polar fronts (Giglio & Johnson, 2016). This mirrored previous classifications that proposed latitudinal splits from the South Atlantic into Subantarctic and Antarctic or Southern Ocean classes (Watling et al., 2013; Costello et al., 2017; Watling & Lapointe, 2022; Schumacher et al., 2022). These fronts potentially drive latitudinal differences in benthic communities owing to different bottom water masses and productivity (e.g., Clarke et al., 1992; Mackensen et al., 1993; von der Meden et al., 2017); however, the high variability in environmental conditions and the lack of biological data from this area, with a focus on the pelagic and Southern Ocean (e.g., Petryashev,

2007; De Broyer et al., 2011; Kaiser et al., 2013), preclude definitive statements. In both approaches of the current study, the habitat classes represented a transition to sub-zero temperatures. In the North Atlantic, distinct benthic faunal communities have been observed in cold (sub-zero) and warm (above zero) waters (Bett, 2001; Narayanaswamy et al., 2005; Howell et al., 2007), suggesting that this distinction between classes may be biologically relevant. Therefore these class boundaries could represent some change in benthic communities, although the exact location of the front boundaries is not clear (see high CI values in the water mass structure layers of the non-hierarchical approach). As the locations of the fronts migrate seasonally, transition zones in the benthic habitats and assemblages may be pronounced in these areas. The potential driving role of these front systems for benthic communities should be investigated, including the collection of more data.

4.1.5 Seamounts, hills and ridges

Both classifications showed a clear influence of topography, identifying habitat classes for elevated or depressed topographic features that were distinct from adjacent, flatter habitat classes. This is supported by biological studies where hills, ridges, seamounts and trenches have different fauna from adjacent plain areas (e.g., Molodtsova et al., 2008; Durden et al., 2015; Cuvelier et al., 2020; Jamieson et al., 2021). Both classifications also differentiated between habitat classes on the flanks and summits of seamounts, which is expected to mirror biodiversity patterns (e.g., Baco, 2007; Clark et al., 2011). The classifications showed some distinction between seamounts in different geographic areas, aligning with a global classification of seamounts (Clark et al., 2011) and examination of seamount image data from UK Overseas Territories in the South Atlantic (Bridges et al., 2021). Clark et al. (2011) proposed different classes of seamounts in the Angola Basin, MAR, Walvis Ridge, South Georgia, and at approximately 52°S south of South Africa. This was mirrored in the non-hierarchical approach and, to a lesser extent, the hierarchical approach. Bridges et al. (2021) showed distinct benthic assemblages associated with seamounts around Tristan da Cunha compared to those around the tropical Ascension Island and Saint Helena. The small and localised habitat classes around these topographic features could exaggerate transition zones, explaining the high CI values.

4.2 Areas of less certainty

While there are patterns of agreement between the two approaches presented here and previously published classifications, many areas of uncertainty remain that require further interrogation of environmental data, classification approaches and, most importantly, biological data. One of the key differences between the approaches was the number of habitat classes produced (204 vs 132), but the outputs also diverged in other ways.

4.2.1 Abyssal basins

There is some evidence that suggests different faunal communities may occur in the Cape and Angola Basins (Kröncke et al., 2013; Brix et al., 2015) and that variations occur in a range of faunal groups across the Atlantic at 31°30' S (Vinogradova et al., 1990). However, there are very little data available in the South Atlantic to resolve biological patterns among other abyssal basins, and there is a lack of consistency both in outputs of this study and previous global scale biogeographies as to whether they should be considered different habitats. The separation of the Brazil, Angola and Argentine Basins has been thought to occur in the abyssal fauna, based on sample data (Vinogradova, 1997). Watling et al. (2013) distinguished between abyssal biogeographic provinces north and south of the equator and between the Cape and Brazil Basins. The former was not observed in either classification from this study, while the latter was reflected in the non-hierarchical approach. Both approaches and Watling et al. (2013) proposed different habitat classes north and south of the Rio Grande Rise. None of these aforementioned boundaries were reflected in Costello et al. (2017). Analyses based on different dissimilarity matrices by Costello et al. (2017) did show some differentiation between the Cape and Brazil basins, but this appears to be driven by a low number of data points and included pelagic records.

The non-hierarchical approach proposed a longitudinal division of habitat classes in ABNJ between Angola and the MAR driven by POC flux to the seafloor. While this pattern was partly reflected in the Atlantic-scale classification (Schumacher et al. 2022), it was not captured by the hierarchical approach nor any global classifications. In addition, large patches of high CI values were observed in the southern Cape and Guinea Basins for water mass structure clustering in the non-hierarchical approach, leading to uncertainty over these habitat classes. To our knowledge, no broad-scale analysis of benthic biodiversity patterns in abyssal ecosystems has been undertaken in the South Atlantic. Biological data is required to determine whether deep areas across the South Atlantic support different benthic communities.

4.2.2 Mid-Atlantic Ridge

Our study, together with existing biogeographic classifications (Watling et al. 2013; Sayre et al., 2017; Schumacher et al., 2022), proposed different habitat classes either side of the MAR north of approximately 40°S, driven predominantly by oceanographic variables and related nutrient concentrations (for the hierarchical approach). This pattern came out strongly in both classifications, with high CI values associated only with class boundaries or transition zones. While some studies suggest that the MAR limits dispersal (e.g., Etter et al., 2011; Bober et al., 2018; Zardus et al., 2015), others do not (e.g., Brix et al., 2015). Broad community-level studies of benthic fauna are required to better understand whether or how these communities differ to the east and west of the MAR, and among the oceanic islands.

4.2.3 Shelf and slope habitats

Towards the continental slope and shelf, both classifications reflected changing environmental conditions between deeper and shallower waters, as well as increased variability in conditions over smaller spatial scales compared to the large ABNJ. For example, both classifications captured the substantial gradients in POC flux between shallow, inshore waters and deep offshore waters that drive patterns in benthic biomass (Rex et al., 2006; Smith et al., 2008; Ramirez-Llodra et al., 2010). Our classifications showed some depth-related differentiation between bathyal habitats in the South Atlantic, unlike Watling et al. (2013), but several of the same habitat classes were observed off both South America and Africa (particularly in the hierarchical approach). Spalding et al. (2007), Costello et al. (2017) and Sayre et al. (2017) differentiated between shelf and slope classes off these continents, and analysis of hydromedusae, whose life cycle includes a benthic stage, showed that 40-50% of species recorded on one coast of the South Atlantic were not recorded on the other (Bouillon, 1999). There was also some divergence in shelf and slope classes between approaches. For example, on the South African western shelf, the non-hierarchical approach presented a mosaic of different habitats, whereas in the hierarchical approach there were fewer classes and these were more strongly related to depth bands. In some cases, there were also high CI values associated with shelf and slope habitat classes (e.g., Patagonian Shelf). National datasets could play an important role in determining which approach, if either, best represents patterns of biodiversity, but also in exploring whether shelf and slope habitats on either side of the Atlantic are the same. This highlights another key knowledge gap in the region.

4.3 Performance at a finer scale

In this section we compare our results with the outputs of national and finer-scale classifications (Table S1) and knowledge of biodiversity.

4.3.1 South Africa

Both the hierarchical and non-hierarchical approaches aligned broadly with the South African national ecosystem classification performed by Sink et al. (2019), although there were areas of disagreement. A key boundary in the South African classification was the separation between areas influenced by the southern Benguela and southwest Indian Ocean Currents. This was present in the non-hierarchical

approach, owing to the biogeography layer that was informed by Sink et al. (2019). The hierarchical approach did not capture this separation as distinctly in deeper waters, where the influence of those ocean currents may become less pronounced. Both classifications reflected class boundaries for deep waters reasonably well, and differentiated between inshore and offshore waters. The spatial distribution of classes on the western margin broadly mirrored the national classification, but in southern and eastern parts of South Africa's EEZ, classes were less well-matched. Similar to the national classification, the outputs of this study also identified the Agulhas Bank, seamounts and the Agulhas plateau, although in some cases they grouped with other areas that differed from the national classification.

4.3.2 Prince Edward Islands

Both classifications proposed latitudinal class boundaries representing the Subantarctic and Polar fronts present in the Prince Edward Islands (PEI) EEZ and captured by an ecosystem classification of this area (von der Meden et al., 2019). However, the classifications did not reflect changes in habitat class resulting from the Indian Ocean temperate current to the north and the Ob and Lena Polar Front to the south, as captured in the PEI classification. Key topographic features of the region included rift valleys and troughs, although our classifications did not differentiate shelf habitat classes from spreading ridges and seamounts, as is seen in the PEI classification.

4.3.3 Falkland Islands

An unsupervised classification of the Falkland Islands Conservation Zones (FCZ) (Pearman, 2021) was based upon the same GEBCO-derived variables and physical oceanographic variables as our classifications, although the latter were derived from different models. The non-hierarchical approach picked up slope and broad bathymetric variation, but there were many classes compared to the FCZ classification. The hierarchical approach distinguished broad-scale bathymetric changes such as the slope, the Falklands Trough and the Burwood Bank.

4.3.4 Brazil

While the non-hierarchical approach delineated the continental slope and shelf break well, shelf habitat classes were not reflective of the national classification (Magris et al., 2020) and were driven particularly by water mass structure. Overall, the hierarchical approach performed better, differentiating known features on the shelf break and deep ocean; phosphate, dissolved oxygen and current velocity played an important role in separating shelf classes, although shelf ecosystems fell mainly under the same class.

4.3.5 Uruguay

A national marine ecosystem classification has not yet been developed for Uruguayan waters. However, some advances have been made in the identification and mapping of coastal and marine areas of high relevance for biodiversity conservation (Freplata, 2004; Brazeiro & Defeo 2006; Defeo et al., 2009; MVOTMA, 2016) and the spatial extent and evolution of more than 30 human activities and associated use conflicts (Marín et al., 2021). Our classification system may be used as a start to advance national-level MSP, since some preliminary cross-validation results suggest that known broad-scale distribution patterns of benthic biodiversity fit reasonably well within both the hierarchical and non-hierarchical approaches (Alvar Carranza, pers. comm.). Nevertheless, some spatially discrete elements of ecological relevance, such as submarine canyons and the influence of discharge from the Río de la Plata, were not captured in the current classifications.

4.3.6 South Georgia and the South Sandwich Islands

Habitat classification and mapping work at South Georgia and the South Sandwich Islands is advanced compared to many areas of the South Atlantic. This comparison draws from unsupervised hierarchical

classifications at South Georgia (Hogg et al., 2016a; 2018), regional bathymetric data (Hogg et al., 2016b), a bioregionalisation of the South Sandwich Islands (Hogg et al., 2021; Hollyman et al., 2022) and expert knowledge of the wider Scotia region. Both approaches effectively delineated broad-scale topographic features such as the islands' continental shelves, submarine banks such as the North Georgia Rise and Tyrell and Herdman Banks, the South Sandwich Trench and the East Scotia Ridge. To a lesser extent they also reflected some of the region's oceanographic discontinuities (e.g., different water masses). For the non-hierarchical approach, the classification did not correspond to previous attempts to classify habitats in this region or to known biological discontinuities. There was however some differentiation between the shelf, shelf break and slope at South Georgia, and some of the geomorphological features of the shelf were picked out (e.g., some of the glacial cross-shelf troughs). There was differentiation between habitat classes around northern and southern South Sandwich Islands, and this was in-line with the most recent assessment of the region (Hogg et al., 2021; Hollyman et al., 2022). The hierarchical approach picked up major topographic features. The inner and outer South Georgia shelf and slope were represented, potentially identifying some regions of topographic complexity, seamounts, topographic peaks and areas of steeper slope. There were however also clusters that didn't appear to correspond to any known bathymetric, biological or oceanographic discontinuities.

4.3.7 Tristan da Cunha

The Tristan da Cunha EEZ has a variable oceanographic regime, spanning the South Atlantic Gyre, the subtropical convergence zone, and into Subantarctic waters. This is a strong driver of local differences in habitat type, especially of pelagic and demersal species, and some distinction between benthic seamount communities has been observed, likely driven by the spatial distribution of different water masses (Bridges et al., 2021). Both approaches closely represented the position of these two fronts (Figure 5). However, the relative position of these fronts changes seasonally (Smythe-Wright et al., 1998), highlighting that the classifications presented here are averaged over longer periods and that their accuracy depends on the level of inter-annual variability in a given location. Seasonal changes in riverine input and sea surface temperature can substantively shift oceanographic properties, resulting in more or less similar adjacent areas between seasons (Bell et al., 2021).

4.4 Application to broad-scale marine spatial planning

The South Atlantic is heavily utilised for a number of different activities (see review by Bridges et al., in press). Pelagic and demersal fisheries are active on both the continental shelves of Africa (FAO, 2004) and South America (e.g., Brewin et al., 2020; Marin et al., 2020), as well as in ABNJ (FAO, 2020). Maritime transport is important along Africa, South America and connecting the Indian Ocean with the Atlantic (UNCTAD, 2021), and oil exploration is increasing (Zhang et al., 2019). Marine pollution (Ryan et al., 2019; Hatja et al., 2021) and factors affecting human health (Escobar et al., 2015) are also on the rise, and seabed mining, having occurred for decades off the coast of Namibia (Schneider, 2020), is increasingly imminent elsewhere in the South Atlantic (SBEC, 2018; Montserrat et al., 2019; Perez et al., 2020). Climate change is also impacting ocean circulation and resource distribution and availability (Gianelli et al., 2019; Franco et al., 2020), with deep-water species ranges expected to be disproportionately affected by warming (Brito-Morales et al., 2020). Initiatives to manage these pressures cover a broad but patchy spectrum of activities and offer protection at varying levels, from MPAs within EEZs (e.g., RSA 2019b), to fisheries restrictions for highly migratory species (e.g., through the International Commission for the Conservation of Atlantic Tunas, or the Commission for the Conservation of Southern Bluefin Tuna), agreements and management bodies for specific regions (e.g., the South East Atlantic Fisheries Organisation, or the Convention for the Conservation of Antarctic Marine Living Resources), or transboundary arrangements (e.g., the Joint Technical Commission for the Maritime Front in the area of mutual interest for Uruguay and Argentina).

Ocean basin scale MSP is required to support these organisations and initiatives, and manage multiple, cumulative pressures, and sustainable use and conservation of BBNJ through a holistic, multi-sector

approach. In the absence of comprehensive biological data, as is the case in the South Atlantic, approaches such as those proposed here can act as an indicator to identify important biological and ecological areas. This could be through identification of regions of habitat heterogeneity used as a proxy for biological diversity, key topographic or oceanographic features that may be considered priorities for MSP, or a representative range of essential habitat types for protection. This first step of mapping to implement large-scale MSP (Ehler & Douvère 2009; Gandra et al., 2020) could support ocean basin scale management aspirations under a new BBNJ agreement (Wright et al., 2021). The comparative reflections presented here highlight areas of agreement between the two approaches that could be used to inform decision-making in a marine spatial planning context; in other areas where there was disagreement the outputs should be treated more cautiously. The two models could be used to explore other questions and scenarios, with decision-making guided by commonalities in the results. Their use may also be determined by specific needs; for example, the non-hierarchical approach is easier to interpret as clusters capture information on environmental conditions while the hierarchical approach relies on PCs. The former also limits the number of variables based on ecological relevance, as is common in the selection of variables for species distribution modelling (e.g., ICES, 2021).

While this study made use of the best available global datasets for input variables understood to influence benthic habitats, there remains nonetheless a level of unquantified error in such broad-scale, modelled spatial datasets, particularly in areas with little scientific exploration or monitoring. The impacts of such potential errors are expected to decline as the quality and resolution of data improve with time. What is more, the absence of biological data and the broad scale of the classifications (10 km) prevent the identification of habitat variation at finer scales. This is relevant when considering features where strong gradients in environmental conditions and hence biological variation may occur at scales less than 10 km. Validation of such classifications with biological data is essential to ensure that models used in decision-making are representative of biologically relevant variation in environmental conditions. The difficulties of gathering enough meaningful biological data to capture variation at a scale relevant to the models or classifications highlight the importance of a precautionary approach in assessment and decision-making processes in the South Atlantic. Concerted effort to collate such a dataset from benthic OBIS records, national datasets or new, targeted exploration under a coordinated programme (e.g., Challenger 150³) would help to address key questions in the South Atlantic and support validation going forward.

While acknowledging these uncertainties and limitations, we are confident that some of the patterns found likely represent real biogeographic differences in biodiversity. Importantly, the broad-scale classifications presented here do not overwrite national or regional efforts but can act as a starting point in areas where finer scale efforts are still in development, empowering nations to make progress towards achieving SDGs by providing insight into the potential distribution of habitats and thus supporting national-level MSP. Such classifications can also provide a broader context for understanding national-level mapping, where transboundary habitats or species may be of importance.

Author contributions

Conceptualisation: KH, KM, AB; Methodology: All authors; Software: KM, AB, OH, TG, NP; Formal Analyses: KM, AB, KH; Investigation: KM, AB, KH, TG, VS, TP, AC, JC, KS, LA, AL, OH, JB; Resources: AY; Data Curation: KM, AB, AY, NP; Writing - Original Draft: KM, KH, AB; Writing - Review & Editing: All authors.

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³ <https://challenger150.world/>

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