



What inhabits the South Sandwich Islands deep-sea? Biodiversity and biogeography of bathyal communities using predators as biological samplers

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ABSTRACT

Understanding the biodiversity of an ecosystem is crucial to determine its structure and resistance to climate change. The South Sandwich Islands (SSI) are located in the Scotia Sea (Southern Ocean), within the South Georgia and the South Sandwich Islands Marine Protected Area. However, the biodiversity of the archipelago remains poorly studied, whilst climate change has the potential for wide-ranging impacts in the Antarctic and Subantarctic regions. Here we used predators as biological samplers to study the bathyal communities of SSI. A total of 61 species including fish, cephalopods and crustaceans, were identified from the diet of 13 predatory taxa (11 fish and two cephalopod). Common Subantarctic and Antarctic species were found, with *Moroteuthopsis longimana* being the species with the highest density (1.74 individuals per stomach at Montagu Island). Eleven fish and one cephalopod species were recorded for the first time at the archipelago. Furthermore, 16 fish species had their bathymetric range increased. Fifteen fish and one crustacean appear to have SSI as the northern or southern limit of their distribution. Community analysis found two major groups at SSI, one in the north and one in the south, with the southern group subdivided into two groups. This separation is related to the environmental conditions at the archipelago that abruptly change at Saunders Islands. Latitude (correlated with sea surface temperature) and sea surface height (proxy for upwelling) both correlated with the dissimilarity between communities. These results suggest that climate change may affect the biodiversity at SSI in the future as warming waters of the Scotia Sea and changes in the upwelling system may favour range extensions of more northerly species into the archipelago. Furthermore, it could lead to local extinctions of some species exclusively found in the southernmost areas of the archipelago.

1. Introduction

Knowledge of the biodiversity of a region is crucial to determine the structure and functioning of the ecosystem and its resilience to global changes (De Broyer et al., 2014; Hattab et al., 2016; Thurber et al., 2014). In marine ecosystems, species distributions are mainly limited by ambient temperature and bathymetry (the latter for demersal species). However, on a smaller scale other habitat characteristics such as productivity may have a major role in determining their presence and abundance (Hattab et al., 2016; Rogers, 2015; Tittensor et al., 2010). Exerting influence on the surrounding environment, climate change is a major threat to such distributions (IPCC, 2018; Pecl et al., 2017;

Poloczanska et al., 2016). To understand the real impacts of external stressors on communities it is important to know the biogeography of the region (De Broyer et al., 2014; De Broyer and Danis, 2011; Rogers, 2015). The impact of climate change is also dependent on whether the species are in the centre of their range or, in contrast, if they are at the edge where conditions are less favourable for survival and proliferation (Gaston, 2009; Sexton et al., 2009). Indeed, individuals living at the edge of the distribution are more vulnerable to climate change (Constable et al., 2014; Hollowed et al., 2013; Pecl et al., 2017).

The South Sandwich Islands (SSI) are located in the Scotia Sea, in the Atlantic sector of the Southern Ocean (Fig. 1). This archipelago is composed of a north-south arc of 11 islands, and it is part of the South

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Georgia and the South Sandwich Islands Marine Protected Area (Collins et al., 2023; Trathan et al., 2014). The marine protected area was established in 2012 and aims to protect and conserve the biodiversity of the region, while allowing a sustainable exploitation of marine living resources (Belchier et al., 2022; GSGSSI, 2013; Trathan et al., 2014). However, baseline data on biodiversity and an understanding of possible impacts from climate change are still needed (Belchier et al., 2022; Trathan et al., 2014). Oceanographically, the SSI are located south of the Antarctic Circumpolar Current yet still under its influence at the north of the archipelago, and within the influence of the Weddell Gyre at south (Murphy et al., 2013; Thorpe and Murphy, 2022). This positions the SSI in the transition between warmer and colder waters, with an abrupt change in temperature around Saunders Island (Thorpe and Murphy, 2022). Moreover, it is within the seasonal sea ice area, with winter sea ice reaching the islands almost every year, but completely retreating before summer (Hart and Convey, 2018; Thorpe and Murphy, 2022). This seasonality is reflected in the productivity of the archipelago, with an increase of chlorophyll *a* concentration during the sea ice retreat (Thorpe and Murphy, 2022). Because of this environmental gradient, the SSI are considered to be the limit of the distributional range for several species acting as a transition zone between Antarctic and Subantarctic regions in respect of demersal fish (Duhamel et al., 2014). The Scotia Sea is one of the regions in the Southern Ocean more affected by climate change (Chown and Brooks, 2019; Sallée, 2018; Turner et al., 2013; Whitehouse et al., 2008). Warming is the most evident effect in the Southern Ocean, yet changes in upwelling, freshening, acidification, and invasion by warmer water species are occurring and can have major impacts on the regions' biodiversity (Chown et al., 2015; Constable et al., 2014; Rintoul et al., 2018; Rogers et al., 2020). To effectively protect this ecosystem, it is necessary to determine the biodiversity of the region and understand which species may be more vulnerable to climate change.

In contrast to its neighbouring South Georgia, the biodiversity of SSI is poorly studied (Belchier et al., 2022; Collins et al., 2023; Rogers et al., 2015). More recently, a series of studies using different techniques (e.g. fishery data, camera traps), started to describe the marine biodiversity at the archipelago (Bamford et al., 2022; Downie et al., 2021; Hogg et al., 2021; Hollyman et al., 2022; Jamieson et al., 2021; Linse et al., 2022; Liszka et al., 2022; Lynch et al., 2016; Soeffker et al., 2022). These studies showed that the SSI holds a great biodiversity, from the sea surface to the deep South Sandwich Trench, with a latitudinal gradient in biodiversity influenced by environmental conditions like temperature, sea ice and productivity (Downie et al., 2021; Hogg et al., 2021;

Hollyman et al., 2022; Liszka et al., 2022; Soeffker et al., 2022). Nonetheless, most of these studies agree that more information is fundamental to better understand the biogeography of this isolated archipelago (Downie et al., 2021; Hogg et al., 2021; Jamieson et al., 2021). For example, the biogeography of fish (except those captured in fishing lines (Hollyman et al., 2022)), cephalopods and crustaceans, especially those inhabiting the bathyal zone, remains poorly known. The absence of research cruises targeting these groups (reviewed in Collins et al., 2023), as well the ability of some species to avoid common sampling methods, e.g. larger size cephalopods easily avoid scientific nets (Cherel, 2020; Rodhouse et al., 2014), explains this gap in knowledge.

The use of top predators as biological samplers to study the biodiversity worldwide, including in the Southern Ocean, is common (Olson et al., 2014; Potier et al., 2007; Queirós et al., 2021). This technique assumes a greater importance in remote locations rarely visited by research vessels such as the SSI and where deep demersal communities would be difficult to sample using traditional techniques. For example, scientific demersal trawling cannot be undertaken at the SSI due to the steep and highly rocky seafloor, and it is often difficult to identify to species level from camera deployments (Downie et al., 2021; Leat et al., 2016). It is important to acknowledge that the use of biological samplers is often dependent on the presence of hard structures that are resistant to digestion, e.g. fish otoliths and cephalopod beaks. Also, the regurgitation or flushing of stomach contents is common, especially in deep-sea species due to barotrauma and/or the ingestion of water associated with hauling from deep-waters, and the time of predation, i.e. the identification and presence of species in the stomach depends if they were eaten recently (Barrett et al., 2007; Bowman, 1986; Drazen and Sutton, 2017). Furthermore, it is dependent on the diet preferences of the predator. The Antarctic (*Dissostichus mawsoni*) and Patagonian toothfish (*D. eleginoides*) are generalist top predators that mostly eat fish and cephalopods, though they are known to predate other taxa as well (Collins et al., 2010; Hanchet et al., 2015). The non-selective foraging behaviour favours the sampling of a wide range of species. Furthermore, these predator species do not have great swimming capability which is ideal for a biological sampler as it guarantees that prey found in their stomach were eaten in the vicinity of the capture location (Collins et al., 2010; Earl et al., 2022; Grilly et al., 2022; Hanchet et al., 2015). Besides their ecological characteristics, both *Dissostichus* species are annually fished in the Southern Ocean, including at the SSI between 700 m and 2250 m deep, which allows easy access to stomach samples (Roberts et al., 2011; Soeffker et al., 2022). These characteristics makes both fish

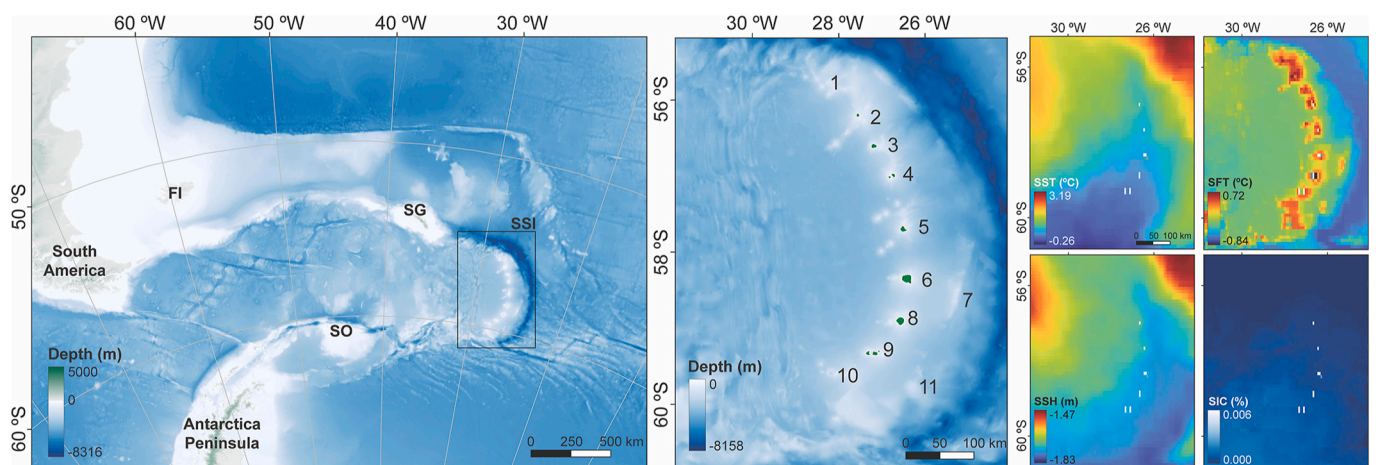


Fig. 1. The South Sandwich Islands (SSI) with the 11 study locations and average environmental conditions during the sampling period. FI- Falkland Islands; SG- South Georgia; SO- South Orkneys; 1- Protector Shoal; 2- Zavadovski Island; 3- Visokoi Island; 4- Candlemas Island; 5- Saunders Island; 6- Montagu Island; 7- Montagu Bank; 8- Bristol Island; 9- Thule Island; 10- Vysokaya Bank; 11- "Southeast seamount". SST - Sea surface temperature; SFT - Seafloor temperature; SSH - Sea surface height; SIC - Sea ice concentration. Bathymetric data was obtained from GBCO (www.gebco.net).

species good biological samplers to study the biogeography at SSI, with a focus on fish and cephalopods species. In addition, the use of other species caught as bycatch or fresh individuals in toothfish stomachs also offer valuable complementary information for lower trophic levels.

The aim of this study was to provide new information on the biogeography of deep-sea bathyal communities at the SSI and discuss the possible effects of climate change. We used fish and cephalopods captured in 2020, 2021 and 2022 at the SSI as biological samplers to: i) study and characterize the communities inhabiting 11 locations (including islands and banks/seamounts) of the SSI; ii) evaluate which environmental conditions may influence the biogeography of the archipelago; and iii) discuss which species may have the SSI as limit of their distribution and which may be more vulnerable to climate change. To evaluate the influence of diet preferences on biogeography, we started the results by analysing the importance of different prey in the diet of *D. mawsoni*, *D. eleginoides* and other predators. We expect a latitudinal pattern with the presence of typically Subantarctic and Antarctic species at the north and south, respectively, of Saunders Islands. Furthermore, we expect that temperature, both at seafloor and sea surface, may be the environmental variables affecting species distributions both spatially and in terms of depth. Though sea ice and sea surface height (proxy for upwelling in the Southern Ocean (Chapman et al., 2020; Yung et al., 2022)) may also have some influence.

2. Materials and methods

2.1. Data collection

Species identified in this study were sampled from 598 stomachs of: *Dissostichus mawsoni* (n = 284), *D. eleginoides* (n = 209), and others (n = 105, including *Amblyraja georgiana*, *Antimora rostrata*, *Artedidraco* sp., *Bathydraco joannae*, *Coryphaenoides armatus*, *Filippovia knipovitchi*, *Lepidonotothen* spp., *Macrourus caml*, *M. whitsoni*, *Moroteuthopsis longimana* and *Muraenolepis evseenkoi*) (Fig. 2). Stomachs were randomly collected from fish captured in the longlines. Predators were captured between 800 m and 2000 m deep onboard licensed longline fishing vessels operating at the SSI - CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) Subarea 48.4. Samples were collected during the 2020, 2021 and 2022 fishing seasons from both captured specimens and fresh prey found in the stomachs of both *D. mawsoni* and *D. eleginoides*. We subdivided the CCAMLR Subarea 48.4 into 11 locations according to geography of SSI (Fig. 1). The 11 locations were distributed across three regions, i.e. north (Protector Shoal, Zavadovski Island, Visokoi Island and Candlemas Island), centre (Saunders Island), and south (Montagu Island, Montagu Bank, Bristol Island, Thule Island, Vysokaya Bank and “Southeast seamount”). Latitude and longitude were obtained from vessels reporting forms (CCAMLR C2). Depth was extracted for each line position from Leat et al. (2016). Stomachs were individually bagged onboard and frozen at -20°C until further analyses in the laboratory.

Using QGIS v3.20 Odense (QGIS.org, 2023) we extracted the environmental data for each line position, i.e. Sea surface temperature (SST in $^{\circ}\text{C}$), Seafloor temperature (SFT in $^{\circ}\text{C}$), Sea surface height (SSH in m) and Sea ice concentration (SIC in %), from monthly average data from E. U. Copernicus Marine Service Information (Global Ocean Physics Reanalysis (2020 (CMEMS, 2023a)) and Global Ocean Physics Analysis and Forecast (2021 and 2022 (CMEMS, 2023b)) at <https://marine.copernicus.eu>) at a $0.083 \times 0.083^{\circ}$ grid (Fig. 1).

2.2. Prey identification

In the laboratory, stomachs were defrosted and opened in a sieve. All prey items were identified to the lowest possible taxa using identification guides (Gon and Heemstra, 1990; Kock, 1992; Reid, 1996; Williams and McEldowney, 1990; Xavier et al., 2020; Xavier and Cherel, 2021) and fish otolith and cephalopod beak reference collections at King

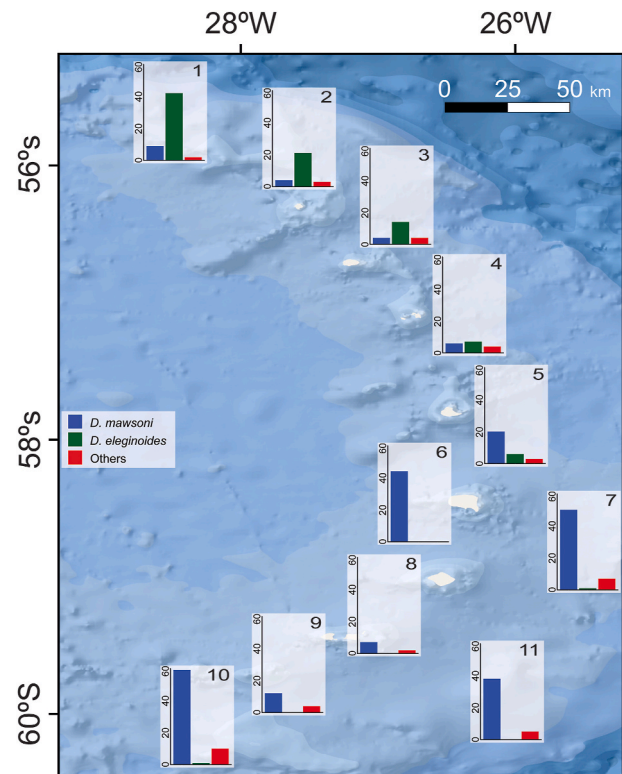


Fig. 2. Number of stomachs sampled per predator for each of the 11 locations. 1- Protector Shoal; 2 - Zavadovski Island; 3 - Visokoi Island; 4 - Candlemas Island; 5 - Saunders Island; 6 - Montagu Island; 7 - Montagu Bank; 8 - Bristol Island; 9 - Thule Island; 10 - Vysokaya Bank; 11 - “Southeast seamount”. Basemap is the Ocean Esri® Basemap.

Edward Point Research Station (South Georgia). Both fresh and non-fresh prey were considered since both toothfish species are largely sedentary, therefore it was assumed that prey found in their stomachs were consumed at the SSI (Collins et al., 2010; Hanchet et al., 2015). Parasites and scavenging crustaceans (e.g. amphipods) were found in several stomachs, but their results are not presented here.

Loose otoliths and heavily digested individuals of *Macrourus* spp. were identified to species level using an otolith shape identification tool (Moore et al., 2022). The right-hand otolith of each pair was photographed against a black background with the rostrum facing left (Fig. S1). Images were taken with a Cannon EOS 600D and a macro lens Cannon EF 100 mm F:2.8 USM. All photos were taken using the same camera settings and with a ruler near the otolith for scale. In R software v2.4.4 (R core team, 2020), we extracted the shape of the otoliths using the *shapeR* package (Libungan and Pålsson, 2015). Otolith images were transformed to grayscale, and contours delineated using a threshold pixel level ranging from 0.2 to 0.4 (Fig. S1). Detected contours of each otolith were visually inspected and repeated if not correct. Using *shapeR*, we extracted the Otolith perimeter (O_P), Otolith area (O_A), Otolith length (O_L), Otolith width (O_W) and 48 Fourier descriptors (Fig. S2). Using these values we calculated the Aspect ratio ($AR = O_L/O_W$), Circularity ($C = O_P^2/O_A$), Ellipticity ($E = (O_L - O_W)/(O_L + O_W)$), Form factor ($FF = 4\pi O_A/O_P^2$), Rectangularity ($Re = O_A/(O_L \cdot O_W)$) and Roundness ($Ro = 4O_A/\pi O_L^2$) (Fig. S2). As otolith size is correlated with fish length (Lombarte and Leonart, 1993; Morley and Belchier, 2002), we standardized otolith measurements with an estimated fish standard length. For that, an allometric equation was created using individuals of *M. whitsoni* and *M. caml* captured and identified onboard. Using the morphometrics of the otoliths we predicted the species using a Linear Discriminant Analysis (LDA) from the *Mass* package (Venables and Ripley, 2002). The training dataset was composed of 233 otoliths of

M. whitsoni and *M. caml* identified onboard and in predator stomachs. A simulation to check the correct % of predictions was performed using the training dataset. Results show a correct prediction of $\approx 77\%$. Predictions were performed for 145 otoliths identified as *Macrourus* spp. in the stomachs.

To evaluate the contribution of different predator diets to the biodiversity of each location, we calculated the Index of Relative Importance (IRI) (Pinkas et al., 1971). IRI was calculated using the formula $IRI = \%O (\%N + \%M)$ where $\%O$ is the frequency of occurrence, $\%N$ is the number and $\%M$ is the mass (the mass found in the stomach, i. e. original prey mass was not reconstructed for IRI). To evaluate the sampling variability between predators and locations and whether maximum biodiversity was reached we did accumulation curves for different predators, regions and locations using the *specaccum* function (method: random, permutations: 1000) (Oksanen et al., 2022). Furthermore, we estimated the maximum richness for the entire archipelago and for each of the 11 locations using the “Chao 2 estimator”, calculated using the function *specpool*. Both functions belong to *vegan* package (Oksanen et al., 2022).

2.3. Biodiversity and community analyses at South Sandwich Islands

All statistical analyses and plots were done using R software v2.4.4 (R core team, 2020). Density (number of individuals per stomach) was calculated for each species in the different locations. To evaluate the biodiversity at each of the 11 locations we calculated Richness (S), Shannon-Wiener Biodiversity Index ($H' = -\sum_{i=1}^S (p_i \cdot \ln p_i)$) and Pielou's Index ($J' = H'/H'_{max}$). These indexes were calculated using prey sampled from all predators.

Because IRI and accumulation curves showed variability between predators (discussed in section 4), only prey identified in the diet of *D. mawsoni* was used in the following community analyses.

Visual differences between communities at each location were investigated using a cluster analysis (function *hclust*, method = Ward) and a NMDS (Non-metric multidimensional scaling; function *metaMDS*). A dissimilarity matrix was calculated using the *vegdist* function (method: Bray-Curtis). Statistical differences between the groups identified in the cluster analysis were tested with a PERMANOVA (Permutational Analysis of Variance; method: Bray-Curtis; permutations: 999) using the *adonis2* function. All these functions are in the *vegan* package (Oksanen et al., 2022). Pairwise comparisons were made using the function *pairwise.adonis* from *pairwiseAdonis* package (Arbizu, 2020). To evaluate the contribution of each species to the dissimilarity between groups we performed a SIMPER (Similarity Percentages) analyses using the function *simper* in the *vegan* package (Oksanen et al., 2022).

The *bioenv* function was used to assess which environmental and geographic variables better correlated with the dissimilarity between locations (Oksanen et al., 2022). The two most correlated variables were plotted using NMDS with the function *ordisurf*. Both functions are from *vegan* package (Oksanen et al., 2022).

3. Results

Considering all predators together, IRI showed that fish was the most important prey group followed by cephalopods (Table 1). A similar pattern was found for *D. mawsoni* with fish comprising $\approx 66\%$ and cephalopods $\approx 34\%$ of the diet (Table 1). In contrast, *D. eleginoides* fed almost exclusively on fish ($\approx 98\%$), and other predators had a diet mainly based on crustaceans ($\approx 86\%$) (Table 1). Similar to IRI, accumulation curves showed that the number of species identified in *D. mawsoni* diet resembles all predators together (Fig. 3). There was substantial variance between regions, i.e. north, centre and south, but more similar across the 11 locations, though larger sampling effort occurred in Montagu Island, Montagu Bank, Vysokaya Bank and “Southeast seamount” (Fig. 3, Fig. S3). Additionally, the identification of

new species never reached a plateau in the number of non-empty stomachs with identifiable prey (Fig. 3).

In total, 60 species were identified, the highest richness was recorded for Vysokaya Bank (S = 30) and the lowest for Visokoi Island (S = 7) (Table 1). Estimated maximum richness for the SSI was 97 species, while for the different locations it varied between 11 at Visokoi Island and 89 at “Southeast seamount” (Table 2). Diversity (Shannon-Wiener) was highest at “Southeast seamount” ($H' = 2.33$) and lowest at Thule Island ($H' = 1.54$), while Candlemas Island ($J' = 0.93$) and Montagu Island ($J' = 0.64$) showed the highest and lowest evenness (Table 2). Overall, the highest densities (n/stomach) were found in the southernmost part of the archipelago with *M. longimana* recording the highest densities, i.e. 1.74 at Montagu Island, 0.91 at Thule Island and 0.76 at Vysokaya Bank (Table 1, Fig. 3). However, when considering predators separately, species identified from *D. eleginoides*' stomachs had higher densities in the north (Fig. S4). Furthermore, aside from *D. mawsoni* whose *M. longimana* had the highest density (2.04 at Montagu Island), the highest densities were different from all predators together, i.e. *Muraenolepis* sp. by *D. eleginoides* (0.22 at Saunders Island) and euphausiids by other predators (0.45 at Montagu Bank) (Fig. S4).

Cluster analyses, supported by the NMDS, showed that communities at SSI divide into three groups: North (Group 1: Protector Shoal, Zavadovski Island, Visokoi Island and Candlemas Island), Banks (Group 2: Saunders Island, Montagu Bank, Vysokaya Bank and “Southeast seamount”) and South (Group 3: Montagu Island, Bristol Island and Thule Island) (Figs. 4 and 5). There were significant differences between the three community groups (PERMANOVA: $F = 2.212$, $p = 0.010$), with the main differences being found to be between “Banks” and “South” (Pairwise PERMANOVA: $F = 3.38$, $p = 0.002$). SIMPER analyses show that *M. longimana*, *Muraenolepis* sp. and *M. whitsoni* were the species that most contributed to the dissimilarity between groups (Table 3).

Latitude (Spearman correlation, $r = 0.40$) and SSH (Spearman correlation, $r = 0.43$) were the environmental/geographical variables that better correlated with the dissimilarity between communities at SSI (Fig. 6).

4. Discussion

The use of biological samplers, captured between 800 m and 2000 m deep, allowed us to study the deep-sea bathyal biodiversity of SSI. Toothfish, the main predators used here, are known to be generalist and opportunistic feeders with a preference for fish and cephalopods (Pilling et al., 2001; Queirós et al., 2022; Roberts et al., 2011). Our results confirmed this diet preference with fish being the main prey for both toothfish species. However, despite cephalopods corresponding to $\approx 34\%$ of the diet of the *D. mawsoni*, they were negligible for *D. eleginoides*. This difference can be found in previous studies, suggesting that *D. mawsoni* have a higher preference for cephalopods than *D. eleginoides* (Goldsworthy et al., 2002; Queirós et al., 2022; Roberts et al., 2011). Therefore, fish and cephalopods were the organisms best sampled in this study. The importance of euphausiids and other crustaceans in the diet of other predators confirmed their usefulness as samplers of lower trophic level species. The diet of important bycatch species such as *Macrourus* spp. and *Muraenolepis* sp. is poorly studied. Nonetheless, our results confirmed that at SSI, as elsewhere in the Southern Ocean, their diet is mainly based on crustaceans (Kompowski, 1993; Pinkerton et al., 2012).

Despite the potential of predator diets to complement other methodologies to assess diversity, e.g. fishing data, camera traps (Hogg et al., 2021; Hollyman et al., 2022), the absence of a plateau in the accumulation curves shows that 300 stomachs with identifiable prey were not enough to provide a complete description of bathyal communities at the SSI. This result contrasts with a previous study in the Ross Sea region that reached the highest number of types of prey and diversity with ≈ 150 *D. mawsoni* non-empty stomachs (Stevens et al., 2014). Furthermore, the difference between the number of species identified in the

Table 1
Diet of the different predators used in this study. %O: occurrence, %N: number; %M: mass; %IRI: Index of Relative Importance. In **bold** are values for the entire group of prey, i.e. fish, cephalopods, crustaceans and others. Species are organized by alphabetical order.

Prey species	All predators				<i>Dissostichus mawsoni</i>				<i>Dissostichus eleginoides</i>				Other predators			
	%O	%N	%M	%IRI	%O	%N	%M	%IRI	%O	%N	%M	%IRI	%O	%N	%M	%IRI
Fish	78.66	55.28	60.91	72.82	83.79	52.03	59.26	65.52	90.22	83.19	88.50	97.50	25.00	23.08	13.30	7.89
<i>Aethotaxis mitopteryx</i>	0.26	0.06	<0.01	<0.01	0.40	0.07	<0.01	<0.01								
<i>Amblyraja georgiana</i>	1.03	0.29	0.94	0.02	1.58	0.36	1.01	0.03								
<i>Anotopterus pharao</i>	0.51	0.12	0.27	<0.01	0.79	0.14	0.30	<0.01								
<i>Antimora rostrata</i>	1.29	0.29	2.11	0.05	1.19	0.21	2.19	0.04	2.17	0.84	1.29	0.05				
<i>Bathyraco joannae</i>	0.51	0.12	0.24	<0.01	0.40	0.07	0.07	<0.01	1.09	0.42	2.59	0.04				
<i>Bathyraco marri</i>	0.51	0.12	<0.01	<0.01	0.79	0.14	<0.01	<0.01								
<i>Bathyraco scotiae</i>	0.26	0.06	<0.01	<0.01	0.40	0.07	<0.01	<0.01								
<i>Bathyraco</i> spp.	0.10	0.12	0.10	<0.01	0.79	0.14	0.11	<0.01								
<i>Chaenocephalus aceratus</i>	0.26	0.06	0.17	<0.01	0.40	0.07	0.18	<0.01								
Channichthyidae	0.26	0.06	0.05	<0.01	0.40	0.07	0.05	<0.01								
<i>Chionodraco rastrospinosus</i>	0.26	0.06	<0.01	<0.01	0.40	0.07	<0.01	<0.01								
<i>Coryphaenoides lecointei</i>	0.26	0.06	0.20	<0.01	0.40	0.07	0.22	<0.01								
<i>Cryodraco antarcticus</i>	0.26	0.06	<0.01	<0.01	0.40	0.07	<0.01	<0.01								
<i>Dacodraco hunteri</i>	0.26	0.06	<0.01	<0.01	0.40	0.07	<0.01	<0.01								
<i>Electrona carlsbergi</i>	0.51	0.12	<0.01	<0.01	0.40	0.07	<0.01	<0.01	1.09	0.42	<0.01	0.01	2.27	1.54	0.02	0.06
<i>Gymnoscopelus bolini</i>	0.26	0.06	0.12	<0.01	0.40	0.07	0.13	<0.01								
<i>Gymnoscopelus braueri</i>	0.26	0.06	<0.01	<0.01	0.40	0.07	<0.01	<0.01								
<i>Gymnoscopelus opisthopterus</i>	0.26	0.06	<0.01	<0.01					1.09	0.42	<0.01	0.01				
<i>Icichthys australis</i>	0.51	0.12	2.11	0.02	0.79	0.14	2.27	0.03								
<i>Krefflichthys anderssoni</i>	0.26	0.06	<0.01	<0.01	0.40	0.07	<0.01	<0.01								
<i>Lepidonotothen larseni</i>	0.26	0.06	0.56	<0.01	0.40	0.07	0.61	<0.01								
<i>Lepidonotothen nudifrons</i>	0.26	0.06	0.23	<0.01	0.40	0.07	0.25	<0.01								
<i>Lepidonotothen</i> spp.	0.51	0.12	0.02	<0.01	0.40	0.07	0.02	<0.01								
<i>Lepidonotothen squamifrons</i>	1.03	0.47	1.00	0.02	1.19	0.43	1.08	0.02	1.09	0.84	<0.01	0.01				
<i>Macrourus caml</i>	5.91	1.52	4.07	0.51	7.91	1.64	3.98	0.58	3.26	1.26	5.72	0.26				
<i>Macrourus</i> spp.	2.83	0.64	0.57	0.05	3.95	0.71	0.62	0.07	1.09	0.42	<0.01	0.01				
<i>Macrourus whitsoni</i>	28.53	9.85	18.05	12.33	36.36	10.41	18.76	13.92	20.65	9.24	9.84	4.45				
<i>Muraenolepis</i> sp.	20.57	7.62	9.80	5.55	25.69	7.98	8.54	5.57	16.30	7.56	28.32	6.60				
<i>Nansenia antarctica</i>	0.26	0.06	0.05	<0.01	0.40	0.07	0.05	<0.01								
<i>Notothenia coriiceps</i>	0.26	0.06	0.51	<0.01	0.40	0.07	0.55	<0.01					2.27	1.54	4.95	0.27
<i>Pogonophryne marmorata</i>	0.26	0.06	0.03	<0.01												
<i>Poromitra crassiceps</i>	0.26	0.06	<0.01	<0.01					1.09	0.42	<0.01	0.01				
<i>Protomyctophum bolini</i>	0.26	0.06	<0.01	<0.01	0.40	0.07	<0.01	<0.01								
<i>Racovitzia glacialis</i>	0.26	0.06	0.05	<0.01	0.40	0.07	0.06	<0.01								
<i>Stomias gracilis</i>	0.26	0.06	0.06	<0.01	0.40	0.07	0.06	<0.01								
<i>Stomias</i> sp.	0.26	0.06	0.23	<0.01	0.40	0.07	0.25	<0.01								
Stomiidae	0.26	0.06	0.02	<0.01	0.40	0.07	0.02	<0.01								
Stomiidae sp. A	0.26	0.06	0.02	<0.01	0.40	0.07	0.03	<0.01								
<i>Trematomus hansonii</i>	0.26	0.06	<0.01	<0.01	0.40	0.07	<0.01	<0.01								
<i>Trematomus loennbergii</i>	0.26	0.06	0.78	<0.01	0.40	0.07	0.84	<0.01								
Zoarcidae	0.51	0.12	0.09	<0.01	0.40	0.07	<0.01	<0.01	1.09	0.42	1.39	0.02				
Unknown fish	61.95	32.12	18.44	48.54	63.64	27.80	17.01	37.41	76.09	60.92	39.33	86.06	22.73	20.00	8.33	11.69
Cephalopod	45.76	39.45	32.54	26.24	60.87	45.05	34.70	34.11	18.48	13.03	2.79	1.84	15.91	15.38	28.79	6.10
<i>Alluroteuthis antarcticus</i>	1.80	1.17	0.68	0.05	2.77	1.43	0.73	0.08								
<i>Filippovia knipovitchi</i>	7.97	2.52	0.50	0.37	9.49	2.57	0.40	0.37	5.43	2.10	1.77	0.24	4.55	3.08	2.57	0.47
<i>Galiteuthis glacialis</i>	4.11	1.06	0.23	0.08	5.93	1.21	0.12	0.10					2.27	1.54	18.68	0.83
<i>Gonatus antarcticus</i>	0.26	0.06	<0.01	<0.01	0.40	0.07	<0.01	<0.01								
<i>Mesonychoteuthis hamiltoni</i>	3.34	0.76	0.72	0.08	5.14	0.93	0.78	0.11								
<i>Moroteuthopsis longimana</i>	27.51	14.19	15.53	12.66	40.71	16.96	16.74	18.00	4.35	1.68	0.06	0.09				
Octopod sp. A	0.26	0.06	<0.01	<0.01	0.40	0.07	<0.01	<0.01								

(continued on next page)

Table 1 (continued)

Prey species	All predators				Dissostichus mawsoni				Dissostichus eleginoides				Other predators			
	%O	%N	%M	%IRI	%O	%N	%M	%IRI	%O	%N	%M	%IRI	%O	%N	%M	%IRI
Octopod sp. B	0.26	0.06	<0.01	<0.01	0.40	0.07	<0.01	<0.01	16.30	9.24	0.95	1.88	2.27	9.23	7.52	3.45
Psychrolutes glacialis	1.29	0.29	0.01	0.01	1.58	0.29	0.01	0.01	23.26	9.24	0.95	1.88	11.36	9.23	7.52	3.45
Unknown cephalopod	35.99	19.28	14.87	19.05	47.43	21.45	15.92	23.26	8.70	3.36	8.66	0.66	84.09	60.00	57.86	85.98
Crustacea	17.48	4.28	1.04	0.74	9.09	1.85	0.10	0.12	1.09	0.42	0.04	0.01	4.55	3.08	1.92	0.41
Decapod	1.03	0.23	0.02	<0.01	0.40	0.07	<0.01	<0.01	1.09	0.42	0.01	0.01	50.00	35.38	45.25	73.17
Euphausiid	6.43	1.58	0.29	0.19	0.79	0.21	<0.01	<0.01	1.09	0.42	0.01	0.01	13.64	9.23	4.45	3.39
Nematocarcinus sp.	4.37	1.11	0.11	0.08	3.95	0.86	0.07	0.05	2.17	0.84	8.49	0.23				
Paralomis sp.	0.51	0.12	0.57	0.01	0.79	0.14	0.01	<0.01								
Pasiphaea sp.	0.51	0.12	0.01	<0.01	0.79	0.14	0.01	<0.01								
Unknown crustacea	4.88	1.11	0.05	0.09	3.16	0.57	0.01	0.02	3.26	1.26	0.01	0.05	18.18	12.31	6.25	6.12
Other	3.86	0.94	5.49	0.20	5.14	1.00	5.91	0.25	1.09	0.42	0.05	<0.01	2.27	1.54	0.04	0.03
Crinoid	0.26	0.06	<0.01	<0.01	0.40	0.07	<0.01	<0.01								
Cnidaria	0.26	0.06	0.23	<0.01	0.40	0.07	0.25	<0.01								
Ophitroid	0.26	0.06	<0.01	<0.01	0.40	0.07	<0.01	<0.01								
Pygoscelis antarctica	2.31	0.53	4.94	0.20	3.56	0.64	5.33	0.28								
Holothurian	0.77	0.23	0.31	0.01	0.40	0.07	0.33	<0.01	1.09	0.42	0.05	0.01	2.27	1.54	0.04	0.07
Unknown chordata	0.26	0.06	0.03	<0.01	0.40	0.07	0.03	<0.01								

predators' stomachs and the estimated maximum richness supports the need for further studies. Indeed, at "Southeast seamount" we found 19 species from a total of 89 species estimated to inhabit this location, suggesting that we just found ≈20% of the species existing here. Accumulation curves also showed variability in the number of species identified from the different predators. *D. mawsoni* was the predator with the highest contribution, and the only predator captured in the 11 locations. Moreover, *D. mawsoni* was the species with the highest % of non-empty stomachs (≈80%) when compared to the other biological samplers used in this study (*D. eleginoides* ≈22%; other predators ≈31%). *D. eleginoides* is more susceptible to regurgitation and/or flushing of the stomach contents when compared to *D. mawsoni* (Pilling et al., 2001; Roberts et al., 2011). Therefore, to reduce the influence of sampling (i.e. the differential capture of predators at specific locations and the differences in regurgitation/flushing rates between species) and diet preferences, we only considered species identified in *D. mawsoni* diet for the community analyses.

4.1. Deep-sea bathyal biodiversity at South Sandwich Islands

In total, 61 species/taxa including fish, cephalopods, crustaceans, crinoids, cnidarians, ophiuroids and holothurians were found to inhabit the bathyal zone of the SSI, confirming the high biodiversity of the archipelago (Downie et al., 2021; Hogg et al., 2021; Jamieson et al., 2021; Lynch et al., 2016). From these, 12 were identified for the first time in the archipelago, and 16 had their known bathymetric distribution increased. This is probably related with the higher sampling effort and techniques used here in comparison to the previous studies (Downie et al., 2021; Hogg et al., 2021; Hollyman et al., 2022). As expected, we identified species typically found in the Subantarctic, e.g. *Lepidotothen larseni*, and Antarctic, e.g. *Cryodraco antarcticus*, environments. Previous studies also found this coexistence at the SSI (Downie et al., 2021; Hogg et al., 2021; Hollyman et al., 2022; Liszka et al., 2022). Only five species/taxa were found at all 11 locations, i.e. *M. whitsoni*, *Muraenolepis* sp., *F. knipovitchi*, *M. longimana*, and euphausiids. Our results indicate a higher species richness at southern locations, contrasting with the more evenly distributed species in the north. This might suggest the dominance of some species in the southern locations. Indeed, the three locations with lower evenness, are those where *M. longimana* had the highest densities, i.e. Montagu and Thule Islands and Vysokaya Bank. Nevertheless, this may also be related to diet preferences of *D. mawsoni*, the main toothfish species at the south of the SSI (Soeffker et al., 2022).

Similarly, the higher densities of species found in the southern locations are probably related with the distribution of toothfish species, i.e. *D. eleginoides* in the north and *D. mawsoni* in the south, and not with more individuals inhabiting these locations (Hollyman et al., 2022; Soeffker et al., 2022). The tendency of *D. eleginoides* to regurgitate/flush when captured in the longlines increases the number of empty stomachs and, ultimately, decrease the density of prey species (discussed above; Pilling et al., 2001; Roberts et al., 2011; Soeffker et al., 2022). This is supported by the highest number of stomachs sampled at Protector Shoal but with a low number of species identified. Moreover, previous studies could not find an increase in the abundance and richness with latitude (Downie et al., 2021; Hogg et al., 2021; Hollyman et al., 2022).

4.1.1. Fish

A total of 41 fish species/taxa inhabiting the SSI were identified. From these, 11 were recorded for the first time at the archipelago, and 16 had their known bathymetric range increased (Table 4). The presence of some species in deeper waters at the SSI when compared to other regions of the Southern Ocean may be related with the absence of a significant shelf around the islands (Leat et al., 2010, 2016) which may allow the fish to inhabit deeper waters. Furthermore, shallow water species may be dispersing towards deeper waters as a response to warming in the Scotia Sea (Pecl et al., 2017; Poloczanska et al., 2016; Whitehouse et al., 2008). However, it may also relate to toothfish species

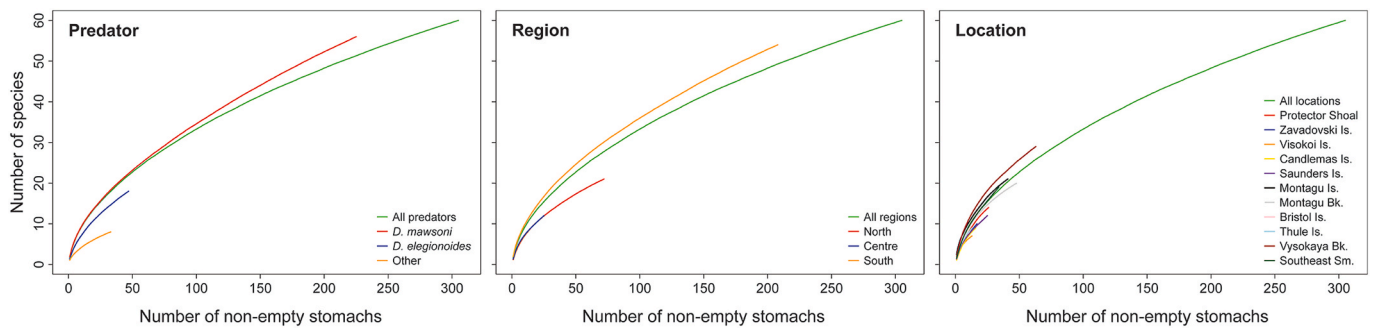


Fig. 3. Accumulation curves for the identification of new species per non-empty stomach with identifiable prey.

moving up slope to feed, a hypothesis that is not new and supported by visual evidence (e.g. camera footage) in the Ross Sea (Eastman and Barry, 2002; Roberts et al., 2011).

The identified species belong to 15 families, all known to inhabit the Southern Ocean (Duhamel et al., 2014; Gon and Heemstra, 1990). Not surprisingly, Nototheniidae, the most abundant and diverse family of fish in the Southern Ocean (Eastman, 2017; Duhamel et al., 2014; Gon and Heemstra, 1990), was the family with the most identified taxa (eight) in this study, followed by Myctophidae and Channichthyidae with six and four, respectively. Myctophids are abundant in the Scotia Sea (Collins et al., 2008, 2012), thus their presence at SSI is not surprising. Yet, it was surprising that species usually associated to the Antarctic Polar Front, e.g. *Electrona carlsbergi*, were found here (Duhamel et al., 2014; Gon and Heemstra, 1990; Saunders et al., 2017). Channichthyids are endemic to the Southern Ocean and are known for their lack of haemoglobin (Kock and Everson, 1997). Mostly distributed in Antarctic waters, it was not surprising that three species (*Chionodraco rastrospinosus*, *Cryodraco antarcticus* and *Dacodraco hunteri*) were identified in the southern area of the SSI (Duhamel et al., 2014; Gon and Heemstra, 1990; Kock and Jones, 2002).

4.1.2. Cephalopods

Nine cephalopod species, including seven squid and two octopods, were identified in this study. From these, only *G. antarcticus* was a new record for the SSI. The beak of *G. antarcticus* was not fresh, though it was found in the stomach of *D. mawsoni* which is a sedentary species, supporting its presence in the archipelago (Hanchet et al., 2015). A previous study suggested that SSI would have a suitable habitat for this species, but not optimal (Xavier et al., 2016). This explains the identification of only one individual over the three years of sampling. All identified species also inhabit South Georgia waters suggesting a similarity between both archipelagos, though with higher diversity at South Georgia (Collins et al., 2004; Xavier et al., 2002). This difference is explained by the presence of warmer water species at South Georgia, e.g. *Martialia hyadesi*, that were not found at SSI (Collins et al., 2004; Rodhouse, 1990; Xavier et al., 2002, 2016).

M. longimana presented the highest densities in the study. This species is one of the most abundant squid species in the Southern Ocean and has a broad distribution in both Antarctic and Subantarctic waters (Cherel, 2020; Collins and Rodhouse, 2006; Queirós et al., 2018; Rodhouse et al., 2014; Xavier et al., 2018). Thus, the highest abundances at SSI were expected. However, this may not indicate that this species is the most abundant at SSI, but it is likely related with *M. longimana* being a main prey for both toothfish (Cherel et al., 2004; Queirós et al., 2022; Roberts et al., 2011).

4.1.3. Crustaceans

As expected, the number of crustaceans was much lower than fish and cephalopods. The only crustaceans present across the archipelago were euphausiids. Euphausiids are some of the most important zooplankton species at the SSI in terms of biomass, with *Thysanoessa*

spp., followed by *Euphausia superba*, being the more abundant (Liszka et al., 2022). The presence of *Paralomis* spp. at Protector Shoal agrees with a previous study that, using bycatch data, only found lithodids in the north of the archipelago (Hollyman et al., 2022). Both *Nematocarcinus* spp. and *Pasiphaea* spp. are common species in the Southern Ocean and were both previously found at SSI in predators' diet and scientific nets (Clarke and Holmes, 1987; Roberts et al., 2011; Xavier et al., 2020). Our results suggest that *Nematocarcinus* spp. is distributed across the archipelago, while the two specimens of *Pasiphaea* spp. were found at Montagu Island and the "Southeast seamount" suggesting a southerly distribution.

The low number of intact specimens or unique hard structures to identify crustaceans to species level precluded a better understanding of the crustacean community. To overcome this and increase the knowledge of crustaceans at SSI we suggest that future studies should use DNA-based techniques (e.g. metabarcoding) to identify the prey in the stomachs (King et al., 2008; Vasiliadis et al., 2023; Yoon et al., 2017).

4.1.4. Other taxa

The presence of crinoids, cnidarians, ophiuroids and holothurians at SSI was previously confirmed using different methodologies, e.g. imaging and fisheries bycatch (Downie et al., 2021; Hogg et al., 2021; Hollyman et al., 2022). The low numbers observed in this study confirm that using predators is not the best approach to study these taxa.

The presence of *Pygoscelis antarctica* in the stomach of *D. mawsoni* is a consequence of scavenging behaviour (Queirós et al., 2022; Roberts et al., 2011). Nevertheless, its presence at Vysokaya Bank and "Southeast seamount" might suggest that some individuals may forage in these areas outside their breeding season (Clucas et al., 2022).

4.2. Biogeography of bathyal communities at South Sandwich Islands

Two major groups of bathyal communities were found at SSI, one comprising northern and one southern (includes Saunders Island) locations. The southern group subdivided into two groups, one with the banks and Saunders Island and the other with the islands. Differences between north and south was previously found for zooplankton, benthic organisms and demersal fish fauna (Downie et al., 2021; Hogg et al., 2021; Hollyman et al., 2022; Liszka et al., 2022). Such differences are attributed to the change in environmental conditions at Saunders Island, with the north being warmer than the south (Thorpe and Murphy, 2022). This is supported by the presence of Subantarctic species in the north and more typical Antarctic species in the south (Downie et al., 2021; Hogg et al., 2021; Hollyman et al., 2022; Liszka et al., 2022). In this study Saunders Island was included in the southern group, contrasting with previous studies where the demersal fish fauna and benthic communities were similar to the northern group (Hogg et al., 2021; Hollyman et al., 2022). The interannual environmental variability at SSI may explain these differences, suggesting that biodiversity found at Saunders Islands may vary across years (Thorpe and Murphy, 2022). This hypothesis is supported by changes in the proportion of toothfish

Table 2
Species inhabiting the deep-sea bathyal region of the South Sandwich Islands. Species identified were sampled from the stomach of all predators. n – number of individuals found in the location; D – density (n/stomach) found in the location. Species are organized by alphabetical order.

	Protector Shoal		Zavadovski Island		Visokoi Island		Candlemas Island		Saunders Island		Montagu Island		Montagu Bank		Bristol Island		Thule Island		Vysokaya Bank		"Southeast seamount"	
	n	D	n	D	n	D	n	D	n	D	n	D	n	D	n	D	n	D	n	D	n	D
Fish																						
<i>Aethotaxis mitopteryx</i>	0		0		0		0		0		1	0.019	0		0		0		0		0	
<i>Amblyraja georgiana</i>	0		0		0		0		0		0		0		0		0		5	0.063	0	
<i>Anotopterus pharao</i>	0		0		0		0		0		0		2	0.028	0		0		0		0	
<i>Antimora rostrata</i>	2	0.015	1	0.016	0		0		0		0		0		0		0		0		2	0.035
<i>Bathyraco joannae</i>	0		0		0		1	0.036	0		1	0.019	0		0		0		0		0	
<i>Bathyraco marri</i>	0		0		0		0		0		2	0.037	0		0		0		0		0	
<i>Bathyraco scotiae</i>	0		0		0		0		0		1	0.019	0		0		0		0		0	
<i>Bathyraco</i> spp.	0		0		0		0		0		2	0.037	0		0		0		0		0	
<i>Chaenocephalus aceratus</i>	0		1	0.016	0		0		0		0		0		0		0		0		0	
Channichthyidae	0		0		0		0		0		0		0		0		0		1	0.013	0	
<i>Chionodraco rastrospinosus</i>	0		0		0		0		0		0		0		0		0		1	0.013	0	
<i>Coryphaenoides lecointei</i>	0		0		0		0		1	0.026	0		0		0		0		0		0	
<i>Cryodraco antarcticus</i>	0		0		0		0		0		0		0		0		0		1	0.013	0	
<i>Dacodraco hunteri</i>	0		0		0		0		0		0		1	0.014	0		0		0		0	
<i>Electrona carlsbergi</i>	1	0.007	0		0		0		0		0		0		0		0		1	0.013	0	
<i>Gymnoscopelus bolini</i>	0		0		0		1	0.036	0		0		0		0		0		0		0	
<i>Gymnoscopelus braueri</i>	0		0		0		0		0		0		0		1	0.077	0		0		0	
<i>Gymnoscopelus opisthopterus</i>	1	0.007	0		0		0		0		0		0		0		0		0		0	
<i>Icichthys australis</i>	0		0		0		0		0		0		1	0.014	0		0		1	0.013	0	
<i>Krefflichthys anderssoni</i>	0		0		0		0		0		0		1	0.014	0		0		0		0	
<i>Lepidonotothen larseni</i>	0		0		0		0		0		1	0.019	0		0		0		0		0	
<i>Lepidonotothen nudifrons</i>	0		0		0		0		0		0		0		0		0		1	0.013	0	
<i>Lepidonotothen</i> spp.	0		0		0		0		0		0		0		0		0		1	0.013	1	0.018
<i>Lepidonotothen squamifrons</i>	0		0		2	0.053	0		0		3	0.056	0		0		0		3	0.038	0	
<i>Macrourus caml</i>	1	0.007	0		1	0.026	1	0.036	2	0.053	8	0.148	6	0.085	0		2	0.087	6	0.075	0	
<i>Macrourus</i> spp.	0		1	0.016	0		0		1	0.026	2	0.037	3	0.042	0		0		2	0.025	1	0.018
<i>Macrourus whitsoni</i>	8	0.059	8	0.131	6	0.158	3	0.107	13	0.342	27	0.500	36	0.507	9	0.692	1	0.043	41	0.513	15	0.263
<i>Muraenolepis</i> sp.	8	0.059	7	0.115	4	0.105	3	0.107	14	0.368	18	0.333	9	0.127	3	0.231	5	0.217	45	0.563	14	0.246
<i>Nansenia antarctica</i>	0		0		0		0		0		0		1	0.014	0		0		0		0	
<i>Notothenia coriiceps</i>	0		0		0		0		0		0		0		0		0		1	0.013	0	
<i>Pogonophryne marmorata</i>	0		0		0		1	0.036	0		0		0		0		0		0		0	
<i>Poromitra crassiceps</i>	0		1	0.016	0		0		0		0		0		1	0.077	0		0		0	
<i>Protomyctophum bolini</i>	0		0		0		0		0		0		0		0		0		1	0.013	0	
<i>Racovitzia glacialis</i>	0		0		0		0		0		0		0		0		0		0		1	0.018
<i>Stomias gracilis</i>	0		0		0		0		0		0		0		0		0		0		1	0.018
<i>Stomias</i> sp.	0		0		0		0		0		0		0		0		1	0.043	0		0	
Stomiidae	0		0		0		0		0		0		1	0.014	0		0		0		0	
Stomiidae sp. A	0		0		0		0		0		0		0		0		0		0		1	0.018
<i>Trematomus hansonii</i>	0		0		0		0		0		0		0		0		0		1	0.013	0	
<i>Trematomus loennbergii</i>	0		0		0		0		0		0		0		0		0		1	0.013	0	
Zoarctidae	0		1	0.016	0		0		0		0		1	0.014	0		0		0		0	
Cephalopoda																						
<i>Alluroteuthis antarcticus</i>	1	0.007	0		0		0		4	0.105	12	0.222	0		0		1	0.043	1	0.013	0	
<i>Filippovia knipovitchi</i>	2	0.015	2	0.033	1	0.026	1	0.036	1	0.026	15	0.278	4	0.056	1	0.077	10	0.435	5	0.063	1	0.018
<i>Galiteuthis glacialis</i>	0		0		0		0		0		3	0.056	2	0.028	0		2	0.087	10	0.125	1	0.018
<i>Gonatus antarcticus</i>	0		0		0		0		0		0		0		0		0		1	0.013	0	
<i>Mesonychoteuthis hamiltoni</i>	0		0		0		0		4	0.105	2	0.037	3	0.042	0		0		3	0.038	1	0.018
<i>Moroteuthopsis longimana</i>	2	0.015	1	0.016	3	0.079	4	0.143	11	0.289	94	1.741	24	0.338	9	0.692	21	0.913	61	0.763	10	0.175

(continued on next page)

Table 2 (continued)

	Protector Shoal		Zavadovski Island		Visokoi Island		Candlemas Island		Saunders Island		Montagu Island		Montagu Bank		Bristol Island		Thule Island		Vysokaya Bank		"Southeast seamount"	
	n	D	n	D	n	D	n	D	n	D	n	D	n	D	n	D	n	D	n	D	n	D
Octopod sp. A	0		0		0		0		0		0		0		0		0		1	0.013	0	
Octopod sp. B	0		0		0		0		0		0		1	0.077	0		0		0		0	
<i>Psychroteuthis glacialis</i>	0		0		0		0		0		2	0.037	0		0		0		2	0.025	1	0.018
Crustacea																						
Decapod	1	0.007	0		0		0		1	0.026	1	0.019	0		0		0		0		1	0.018
Euphausiid	1	0.007	2	0.033	3	0.079	3	0.107	2	0.053	2	0.037	5	0.070	1	0.077	2	0.087	3	0.038	3	0.053
<i>Nematocarcinus</i> sp.	2	0.015	0		0		0		0		0		4	0.056	1	0.077	1	0.043	7	0.088	4	0.070
<i>Paralomis</i> sp.	2	0.015	0		0		0		0		0		0		0		0		0		0	
<i>Pasiphaea</i> sp.	0		0		0		0		0		1	0.019	0		0		0		0		1	0.018
Other																						
Crinoid	0		0		0		0		0		0		0		0		0		0		1	0.018
Cnidaria	0		0		0		0		0		0		1	0.014	0		0		0		0	
Ophiuroid	0		0		0		0		0		0		0		0		0		1	0.013	0	
<i>Pygoscelis antarctica</i>	0		0		0		0		0		0		1	0.014	0		0		4	0.050	3	0.053
Holothurian	0		0		0		0		1	0.026	0		2	0.028	0		0		1	0.013	0	
Number of stomachs	135		61		38		28		38		54		71		13		23		80		57	
Number of non-empty stomachs	27		17		13		16		25		41		48		9		13		63		34	
Number of predators	6		5		7		6		5		5		8		4		4		8		3	
Richness (S)	13		10		7		9		12		20		20		9		10		30		19	
Estimated Richness (Chao 2)	16		18		11		21		36		25		33		17		27		72		89	
Shannon-Wiener Index (H')	2.21		1.90		1.78		2.03		2.00		1.90		2.22		1.61		1.54		2.28		2.33	
Pielou's Index (J')	0.86		0.82		0.92		0.93		0.80		0.64		0.74		0.77		0.70		0.67		0.79	

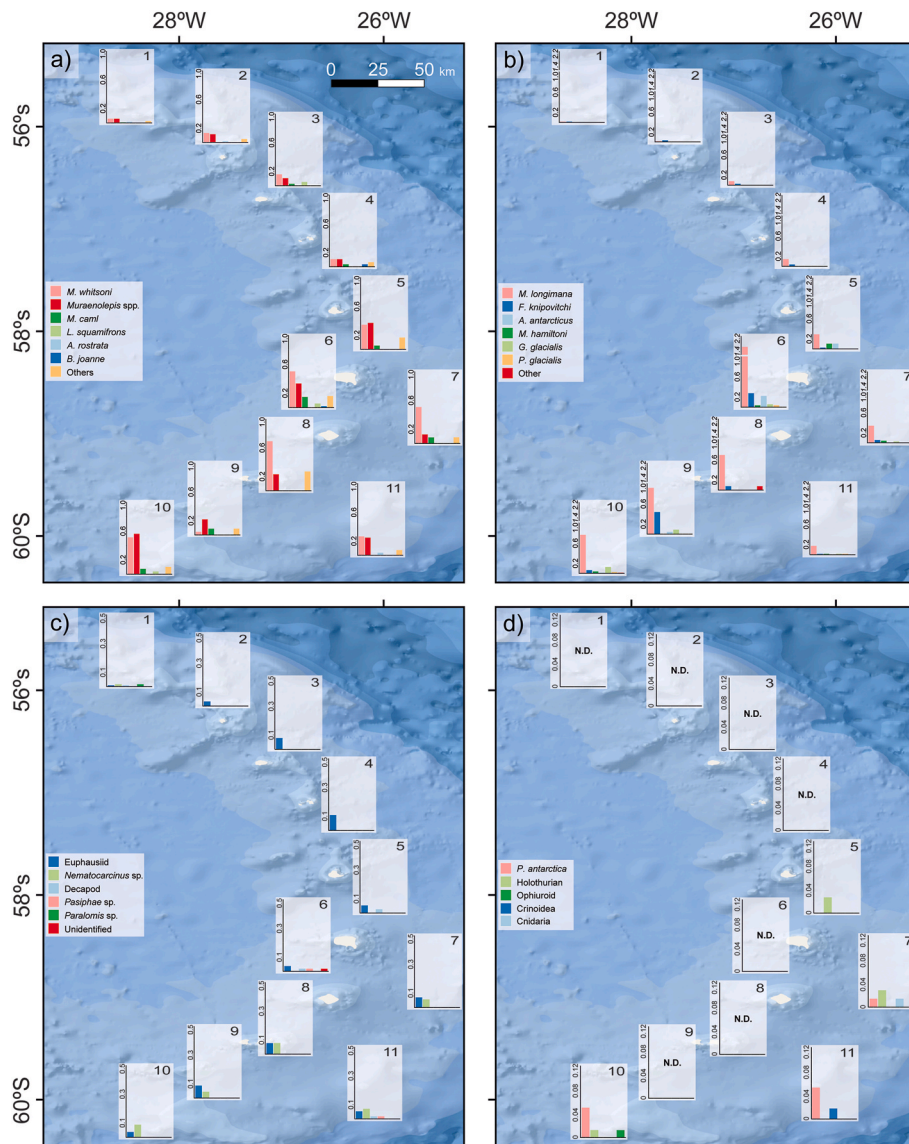


Fig. 4. Distribution and density of prey species at South Sandwich Islands. a) Fish; b) Cephalopods; c) Crustaceans; d) Others. 1- Protector Shoal; 2 - Zavadvoski Island; 3 - Visokoi Island; 4 - Candlemas Island; 5 - Saunders Island; 6 - Montagu Island; 7 - Montagu Bank; 8 - Bristol Island; 9 - Thule Island; 10 - Vysokaya Bank; 11 – “Southeast seamount”. N.D. – No data. Y-axis breaks in Cephalopods’ panel were made using *ggbreak* package (Xu et al., 2021). Densities for each predator can be found at Fig. S4; Detailed view of each plot can be found in Fig. S5. Basemap is the Ocean Esri® Basemap.

captures across years at this location (Soeffker et al., 2022). The subdivision of the southern group into banks and islands could be related to specific environmental conditions that induce changes in the community between them, or the volcanic activity of some islands that may disturb the communities around the islands (Liu et al., 2021).

The differences between north and south communities and the environmental transition at the archipelago suggests that several species, 15 fish and 1 crustacean, might be at the limit of their distribution (Cherel, 2020; Gon and Heemstra, 1990; Hollyman et al., 2022; Liszka et al., 2022; Xavier et al., 2020). Eleven fish have their northern limit distribution at SSI and four their southern (Table 4). *M. whitsoni* is not at the edge of its distribution because some individuals are still caught at South Georgia, though these individuals are small and mostly immature (unpublished data). The presence of *Paralomis* spp. at Protector Shoal, in addition to previous studies finding lithodids in the north of the archipelago, suggest that the SSI might be the southern limit for the distribution of this taxa (Hollyman et al., 2022). Records of lithodid crabs exists at Palmer Deep, though belonging to the genus *Neolithodes* (Smith et al., 2012).

4.3. The influence of environmental conditions in the biogeography of South Sandwich Islands

Latitude and SSH were the environmental variables that best correlated with the distribution of species at SSI. Neither SST nor SFT correlated with the distribution of bathyal communities. However, latitude was correlated with SST which is likely linked to the temperature gradient across the archipelago (Thorpe and Murphy, 2022). The temperature was known to influence the distribution of demersal fish species and benthic fauna at SSI (Hogg et al., 2021; Hollyman et al., 2022). Yet, both Hogg et al. (2021) and Hollyman et al. (2022) found that SFT was more important than SST. The influence of SST, through latitude, in this study may be explained by the presence of several pelagic species, including the squid *M. longimana* whose distribution influences the dissimilarity between the groups. The SSH in the Southern Ocean is a proxy for upwelling areas, as it identifies mesoscale eddies and oceanic fronts (related to productivity) which are known to influence biodiversity in this ocean (Chapman et al., 2020; De Broyer et al., 2014; Leathwick et al., 2006; Rintoul, 2018; Sokolov and Rintoul, 2007;

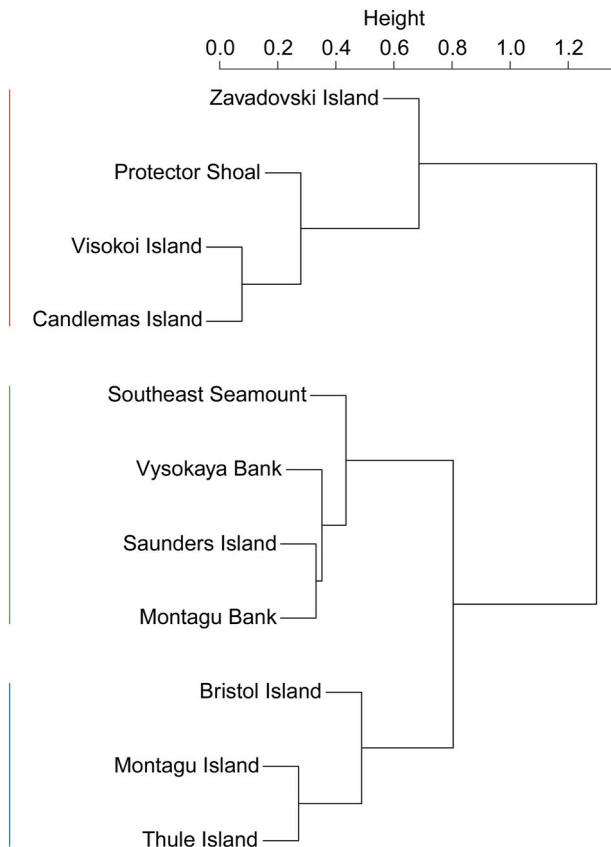


Fig. 5. Cluster analyses showing the three community groups. Colours in the bottom show the different communities.

Table 3

Most influential species for differences between groups determined by SIMPER analyses. Values represent the cumulative influence of the species. **Bold** values indicate species with statistical significance ($p < 0.05$).

Comparison	Species 1	Species 2	Species 3	Species 4	Species 5					
North vs South	<i>M. longimana</i>	0.35	<i>Muraenolepis</i> sp.	0.52	<i>M. whitsoni</i>	0.67	<i>F. knipovitchi</i>	0.76	<i>A. antarcticus</i>	0.84
North vs Banks	<i>Muraenolepis</i> sp.	0.22	<i>M. whitsoni</i>	0.43	<i>M. longimana</i>	0.64	<i>M. caml</i>	0.68	<i>A. antarcticus</i>	0.72
South vs Banks	<i>M. longimana</i>	0.29	<i>M. whitsoni</i>	0.46	<i>Muraenolepis</i> sp.	0.63	<i>F. knipovitchi</i>	0.70	<i>A. antarcticus</i>	0.76

Yung et al., 2022). Previous studies also found productivity influenced the distribution of plankton species at SSI (Liszka et al., 2022).

4.4. Potential impacts of climate change in South Sandwich Islands deep-sea bathyal communities

The presence of several species at the limit of their distribution makes them more vulnerable to environmental change (Gaston, 2009; Sexton et al., 2009). Predictions of warming waters or the poleward movement of the fronts (Rintoul et al., 2018; Rogers et al., 2020; Yamazaki et al., 2021), may indicate that conditions at SSI may become more favourable for northern species. In contrast, communities in the “South” group may be contracted towards the southernmost end of the archipelago, with the potential for some species to become locally extinct, e.g. *Chionodraco rastropinosus* and *Cryodraco antarcticus* which are Antarctic species and were only identified at Vysokaya Bank. Furthermore, the changes in upwelling may also affect the distribution of the species, however, in this case the outcome of the changes is dependent on the intensity of the environmental change (Morley et al., 2020; Rogers et al., 2020). Climate change may also favour the appearance of more northerly species (e.g. species from South Georgia) in the northern part of the archipelago (Rintoul et al., 2018).

Previous studies focused on top predators, plankton, benthic, demersal fish, and trench communities (see references in Collins et al., 2023). This study increases the knowledge for benthopelagic fish and cephalopods within the South Georgia and the South Sandwich Islands Marine Protected Area. These species play an important role in the region as important prey for top predators, e.g. southern giant petrel (*Macronectes giganteus*) (Lynch et al., 2016). Understanding the biogeography and evaluating potential changes due to climate change provides an important baseline for achieving the high-levels of protection designated in this area (Belchier et al., 2022; Trathan et al., 2014). Despite the sampling effort in this study, some taxa and locations (mainly in the northern area) remain poorly sampled. To further

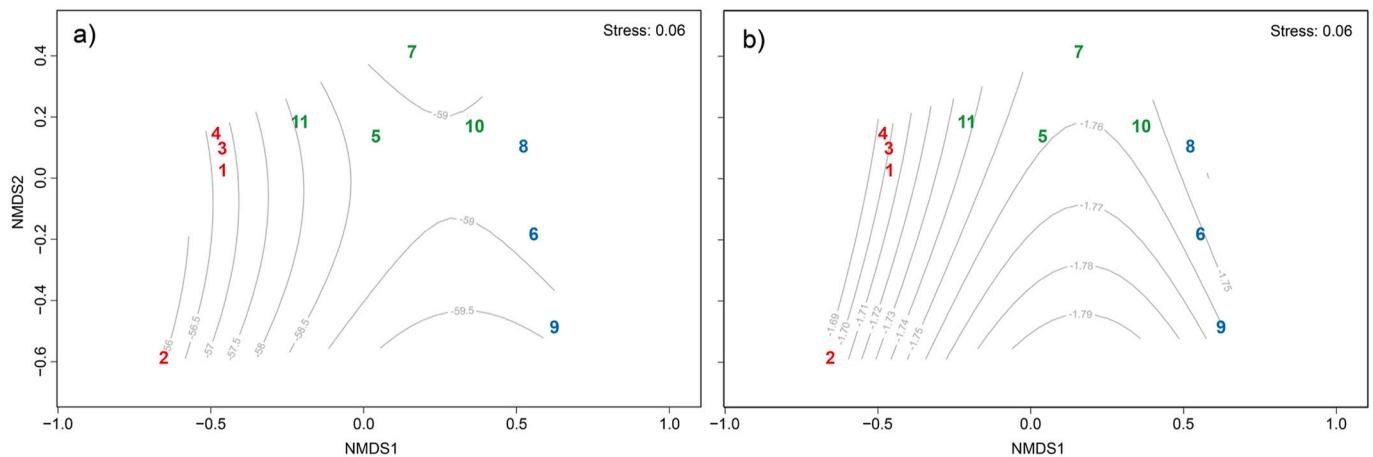


Fig. 6. NMDS ordination based on the density of species overlaid with grey contours of the most correlated geographical/environmental conditions. a) Latitude as overlay grey contour; b) SSH as overlay grey contour. 1- Protector Shoal; 2 - Zavadovski Island; 3 - Visokoi Island; 4 - Candlemas Island; 5 - Saunders Island; 6 - Montagu Island; 7 - Montagu Bank; 8 - Bristol Island; 9 - Thule Island; 10 - Vysokaya Bank; 11 - “Southeast seamount”. The colours represent the three groups of communities identified in the cluster analyses.

Table 4

Fish community at South Sandwich Islands: Family, first record, location at the edge of their distributional range and comparison of the known bathymetric distribution with the capture depth at this study. Y – yes; ↓ indicate that it was captured in deeper waters than previously known; ↑ indicate that it was captured in shallower waters than previously known. Previous information was found in Eastman (2017), Gon and Heemstra (1990), Jones et al. (2008), Kock and Jones (2002), Liszka et al. (2022), Roberts et al. (2011) and Targett (1981).

Species	Family	First record	Edge Limit	Known bathymetric distribution (m)	Depth (m) (this study)	New range
<i>Aethotaxis mitopteryx</i>	Nototheniidae			400–1500	1479	
<i>Amblyraja georgiana</i>	Rajidae			20–1130 ^b	966–1418	
<i>Anotopterus pharao</i>	Anotopteridae		North	>1000 ^a	1273–1382	
<i>Antimora rostrata</i> *	Moridae			<3000 ^a	946–1482	
<i>Bathydraco joannae</i>	Bathydraconidae			230–1800	1168–1443	
<i>Bathydraco marri</i>	Bathydraconidae	Y	North	300–1250	1240–1452	↓
<i>Bathydraco scotiae</i>	Bathydraconidae		North	2100–2950	1452	↑
<i>Bathydraco</i> spp.	Bathydraconidae					
<i>Chaenocephalus aceratus</i>	Channichthyidae			5–820 ^d	1442	↓
Channichthyidae	Channichthyidae					
<i>Chionodraco rastrorpinosus</i>	Channichthyidae	Y	North	0–1000	1441	↓
<i>Coryphaenoides lecointei</i>	Macrouridae	Y	North	2100–3900	1407	↑
<i>Cryodraco antarcticus</i>	Channichthyidae	Y	North	250–820 ^d	966	↓
<i>Dacodraco hunteri</i>	Channichthyidae	Y	North	300–800	1382	↓
<i>Electrona carlsbergi</i> *	Myctophidae		South	100 – >650 ^{a,d}	1375–1441	
<i>Gymnoscopelus bolini</i> *	Myctophidae			200–800	1366	↓
<i>Gymnoscopelus braueri</i> *	Myctophidae			0 – >200 ^a	1655	
<i>Gymnoscopelus opisthopterus</i> *	Myctophidae			>500	1368	
<i>Icichthys australis</i> *	Centrolophidae	Y	South	0–2000	1412–1446	
<i>Krefflichthys anderssoni</i> *	Myctophidae			0 – >1000 ^a	1553	
<i>Lepidonotothen larseni</i>	Nototheniidae			30–650 ^d	1471	↓
<i>Lepidonotothen nudifrons</i>	Nototheniidae			5–650 ^d	966	↓
<i>Lepidonotothen</i> spp.	Nototheniidae					
<i>Lepidonotothen squamifrons</i>	Nototheniidae			5–900 ^c	966–1427	↓
<i>Macrourus caml</i> **	Macrouridae				1185–1730	
<i>Macrourus</i> spp.	Macrouridae					
<i>Macrourus whitsoni</i>	Macrouridae			600–1500 ^b	935–1655	
<i>Muraenolepis</i> sp.	Muraenolepididae			>1600 ^a	935–1655	
<i>Nansenia antarctica</i> *	Microstomatidae	Y	South	500–5000	1390	
<i>Notothenia coriiceps</i>	Nototheniidae			0–650 ^d	1412	↓
<i>Pogonophryne marmorata</i>	Artedidraconidae	Y	North	140–1405	1216	
<i>Poromitra crassiceps</i> *	Melamphidae	Y	South	>1000 ^a	1435–1747	
<i>Protomyctophum bolini</i> *	Myctophidae			360–730	1389	↓
<i>Racovitzia glacialis</i>	Bathydraconidae		North	219–867	1213	↓
<i>Stomias gracilis</i> *	Stomiidae	Y	South	400–1250	935	
<i>Stomias</i> sp.	Stomiidae					
Stomiidae	Stomiidae					
Stomiidae sp. A	Stomiidae					
<i>Trematomus hansonii</i>	Nototheniidae			5–650 ^d	1641	↓
<i>Trematomus loenbergtii</i>	Nototheniidae	Y	North	0–1243	1557	↓
Zoarcidae	Zoarcidae					

*Species also found north of the Antarctic Polar Front.

**Records of *M. whitsoni* in the Falkland Islands might be from this species (only described in 2012).

^a The upper or lower limit was not possible to define.

^b Published material suggest this vertical distribution though we have evidence that *M. whitsoni* and *A. georgiana* inhabit deeper waters thus we will not consider having increased its depth range.

^c Vertical distribution for both *L. squamifrons* and *L. kempi*.

^d Based on the maximum depth reported for the sampling method, e.g. depth range of demersal trawl.

increase our knowledge, we suggest that future studies focus also on the north of the archipelago and use other predators. For that, we advise the use of DNA-related techniques to capture easily digested prey items where visual identification may not be possible (King et al., 2008). Besides the continuous study of biodiversity, future studies should also focus on understanding how these communities are structured, as such structure plays a major role in determining resistance to climate change (Hette-Tronquart et al., 2013).

CRedit authorship contribution statement

José P. Queirós: Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization, Writing – review & editing. **José C. Xavier:** Writing – original draft, Supervision, Methodology, Conceptualization. **José Abreu:** Writing – original draft, Methodology. **Martin A. Collins:** Writing – review & editing, Writing – original draft, Methodology. **Mark Belchier:** Writing – original draft, Supervision, Conceptualization. **Philip R. Hollyman:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr.2024.104260>.

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