# Bioregionalization of the South Sandwich Islands through community analysis of bathyal fish and invertebrate assemblages using fishery-derived data

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## ABSTRACT

The South Sandwich Islands (SSI) are a volcanic archipelago in the Atlantic sector of the Southern Ocean; they are a biologically rich area, home to a range of benthic habitats such as hydrothermal vents and seamounts. A commercial longline fishery for two congeneric species of deep-sea fish, the Patagonian (*Dissostichus eleginoides*) and Antarctic (*D. mawsoni*) toothfish has been in operation annually at the SSI since 2005 and throughout its history has employed scientific observers to collect detailed information on the species caught during fishing operations. Previous studies have investigated the distributions and communities of benthic invertebrates, sampled via scientific cruises. Here we highlight the utility of demersal longlines as spatially extensive sampling tools to investigate both invertebrate and fish communities at the SSI. A clear gradient in the distribution of many fish and invertebrate species is evident across the latitudinal range of the archipelago, these distributions result in clear differences in fish communities between the north, mid, and south of the islands, whilst the invertebrate communities are less clearly delineated. Environmental variables were investigated as drivers in these communities, and seawater temperature appears to be a key abiotic factor in mediating the distributions of species and communities. As many of these communities are structured based on temperature dependent species distributions, it is likely climate change will alter these communities with poleward shifts in the ranges of many species.

## 1. Introduction

The South Sandwich Islands (SSI) are an archipelago of emergent volcanoes, comprising eleven islands or island groups, located in the Atlantic sector of the Southern Ocean between 56 and 60°S (Smellie et al., 1998). The SSI span from Zavodovski Island in the north to the Southern Thule island group in the south and form the eastern boundary of the Scotia Sea (Fig. 1). They are part of the United Kingdom Overseas Territory (UKOT) of South Georgia and South Sandwich Islands (SGSSI) and fall within the SGSSI Marine Protected Area (established in 2012), one of the largest in the world at 1.24 million km² (GSGSSI, 2018). The archipelago is part of the Scotia Arc, a topographical feature stretching from the tip of the Antarctic Peninsula to Tierra Del Fuego at the southern tip of South America. The islands are on the leading edge of the South Sandwich plate, under which the South American plate is being

subducted (Leat et al., 2016; Liu et al., 2020), creating the deep South Sandwich Trench to the east of the islands (Leat et al., 2016; Smalley et al., 2007). Volcanic activity in this area has also resulted in the formation of several seamounts and calderas (Leat et al., 2013; Liu et al., 2020; Smellie et al., 1998). Hydrothermal vents have been found at several of these sites at the SSI, supporting chemosynthetic communities that are hotspots of endemic and often abundant species (Linse et al., 2019; Rogers et al., 2012; Roterman et al., 2016). The benthic environment around these volcanic peaks is dominated by soft substrates on the slopes, from which exposed rock surfaces emerge steeply to form the islands (Downie et al., 2021). The topography of the soft substrates suggests a mass-transport of sediments down-slope with sediment waves and landslide scars both present (Leat et al., 2010), consistent with a highly perturbed sea floor. Hard rock communities at the SSI, consisting of glacial and volcanic deposits and exposed bedrock, are typically

characterised by sessile filter and suspension feeders such as corals, bryozoans and sponges (Downie et al., 2021; Hogg et al., 2021). More sediment-laden environments at the SSI demonstrate greater abundances of mobile predators, filter feeders and detritivores such as brittlestars, sea stars and holothurians (Downie et al., 2021; Hogg et al., 2021). In addition to distinct communities associated with available habitat at the SSI, the taxonomic and functional composition of benthic communities varies both with depth and from north to south along the island chain (Downie et al., 2021; Hogg et al., 2021). Previous research has shown that faunal abundances, composition and diversity around the SSI can be depth dependent (Downie et al., 2021; Griffiths et al., 2008; Hogg et al., 2021; Kaiser et al., 2008; Rogers et al., 2015), however this relationship is not necessarily linear. Relatively shallow waters <600 m are dominated by large ascidians (family Molgulidae), asteroids and ophiuroids (Ramos, 1999).

The hydrography of the Scotia Sea region is dominated by several major oceanographic fronts (Fig. 1)(Park et al., 2019; Thorpe and Murphy, 2022). The Southern Boundary (SB) of the Antarctic Circumpolar Current (ACC) passes between South Georgia and the SSI which results in differences in the water masses between these two locations (Fig. 1a). To the west of the SSI in the Scotia Sea, relatively warm Circumpolar Deep Water lies between the surface layer and the colder Weddell Sea Deep Water (WSDW) beneath it (Meredith et al., 2008; Naveira Garabato et al., 2002; Orsi et al., 1999; Roterman et al., 2016). The SSI trench is supplied with deep waters from the Weddell Gyre, which may also sporadically bisect the SSI through the deeper areas to the north and south of Saunders Island (Naveira Garabato et al., 2002). The northern boundary of the Weddell Gyre (the Weddell Front) may also periodically cross the SSI from the east at roughly the same location (Orsi et al., 1993).

The SSI are a biologically rich area, home to globally important populations of several bird species, including over a third of the global population of chinstrap penguins (*Pygoscelis antarctica*), with a recent census estimating ~1.35 million breeding pairs at SSI (Strycker et al., 2020), and major populations of Antarctic fulmars (*Fulmarus glacialoides*), cape petrels (*Daption capense*), and snow petrels (*Pagodroma nivea*) (Convey et al., 1999). An array of demersal fish species are found at the SSI, including two congeneric species of toothfish: Patagonian toothfish (*Dissostichus eleginoides*), found predominantly in the northern

half of the archipelago; and Antarctic toothfish (*D. mawsoni*) predominantly found in the south (Roberts, 2012; Soeffker et al., 2022). A survey of the demersal fish community across the northern Scotia Arc (between 46 m and 503 m) found that the diversity of fish at the SSI is lower than that of nearby South Georgia (31 and 42 species respectively), with the vast majority of species reported from the SSI also found at South Georgia (Jones et al., 2008). A commercial longline fishery has operated annually at the SSI targeting both *D. eleginoides* (since 2005) and *D. mawsoni* (since 2009) (Agnew and Payne, 2005; Earl and MacLeod, 2019; Earl and Riley, 2019; Roberts, 2012; Soeffker et al., 2022), although some fishing was conducted in the early 1990s (Soeffker et al., 2022). This fishery is monitored by independent scientific observers, deployed on all vessels under the CCAMLR (Convention for the Conservation of Antarctic Marine Living Resources) Scheme of International Scientific Observation (SISO) to collect catch and effort data for scientific purposes and monitor fishing operations. The *D. mawsoni* population at the SSI are believed to be part of a larger stock extending into the Weddell Sea and western South Atlantic (Soeffker et al., 2018, 2022). The *D. eleginoides* stock is believed to be part of a larger stock connected to South Georgia (Soeffker et al., 2018, 2022). The main species caught as bycatch during fishing operations at SSI include grenadiers (*Macrourus* spp., (Fitzcharles et al., 2012)), skates (genus *Amblyraja* (Goodall-Copestake et al., 2018)), blue antimora (*Antimora rostrata*) and eel cods (*Muraenolepis* sp. (Fitzcharles et al., 2021; Roberts, 2012)).

Considering the uniqueness of the SSI in their location, ecology, hydrography and benthic gradients, understanding the grouping of geographical areas based on differences in biological communities and environmental variables (bioregionalization (Grant et al., 2006)) provides scientific underpinning to management decisions related to marine communities (Grant et al., 2006). Recent work on benthic communities at the SSI suggests this archipelago could be considered its own biogeographic province (Hogg et al., 2021). This supports previous work which also concluded that the SSI differ biogeographically from surrounding areas (Grant et al., 2006; Longhurst, 2007; Spalding et al., 2007). Much of the previous work at the SSI has focussed on sessile benthic organisms and planktonic species, based on available data. Far less is known about the more mobile species communities such as fish in this region, outside of initial analyses by Roberts (2012) on which this paper builds.
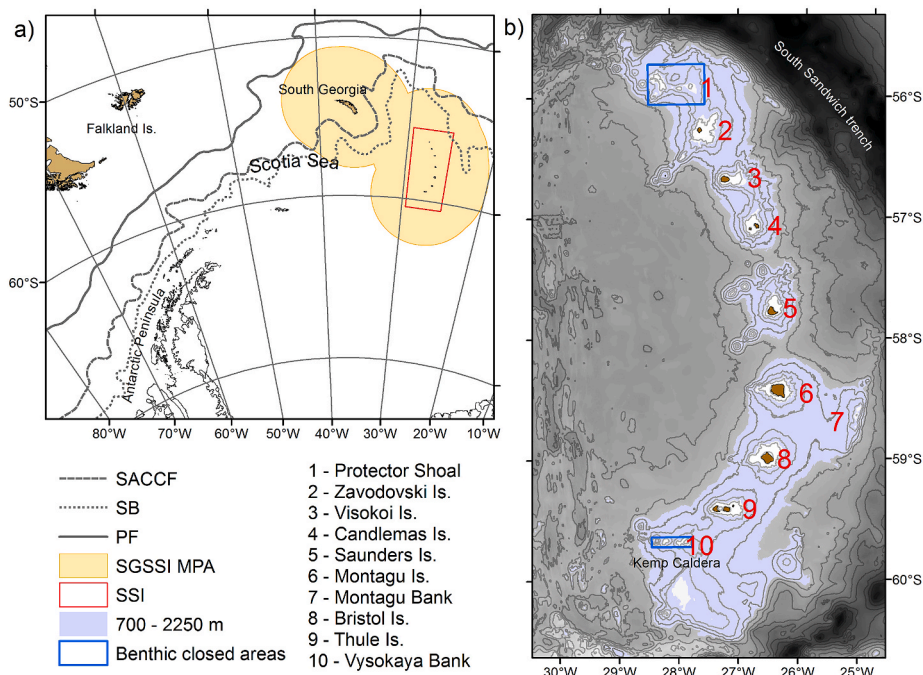


**Fig. 1.** a) Location of the South Sandwich Islands (red box) in the Atlantic sector of the Southern Ocean and the major current systems in the region. PF – Polar Front; SACCF - Southern Antarctic Circumpolar Current Front; SB - Southern ACC Boundary (Park and Durand, 2019; Park et al., 2019). b) A detailed map of the SSI, showing the major islands and areas used in this study are numbered 1–10 and identified on the map. Areas 1, 2, 3 & 4 are classed as 'North', areas 6, 7, 8, 9 & 10 are classed as 'South'. Number 5 (Saunders Is.) is classed as 'Mid'. Contour lines are displayed at 500 m intervals to a depth of 8000 m in the South Sandwich Trench. The shaded blue area is the depth zone between 700 and 2250 m, in which fishing is permitted although not all of this area is suitable. There is a prohibition on fishing in certain areas denoted by the blue boxes.

To address this gap, we used data obtained during commercial longline fishing operations at the SSI to describe spatial differences in the bathyal (700–2250 m) fish assemblage available to the fishery. Alongside data for fish, we assessed spatial variability in the incidental capture rate of invertebrate species. We also assessed potential relationships between observed spatial differences and environmental variables to understand the drivers of spatial differences in communities.

## 2. Methods

### 2.1. Fishery data

Fishery derived data were collected by scientific observers on board commercial fishing vessels fishing in the SSI between 2006 and 2020. Two different types of longline gear were used by vessels within the time series (Spanish longlines and autoline longlines). As autoline longlines constituted the vast majority of the fishing effort, only data arising from this gear type was used to avoid any potential influence of gear type on the data (1340 line sets in total). To investigate spatial differences, data were grouped in to the ten areas identified in Fig. 1b based on discrete islands and surrounding fishable area. The catch weight of each species was calculated from vessel reporting forms (CCAMLR C2), which detail the total catch of all species for each line. All data manipulation and analyses were performed in R version 4.1.0 (R Core Team, 2021).

During observation periods, observers identified fish and invertebrates to the lowest possible taxonomic level (e.g. species, genus) and recorded their catch (numbers caught and weight) along with the number of observed hooks on a line-by-line basis. These data were used to calculate a Standardised Abundance Index (SAI, n/1000 hooks) by extrapolating the abundances of the observed hooks to the total number of hooks per line. Spatial differences in SAI were investigated visually by aggregating the data to $0.2 \times 0.2°$ grid cells. The influence of depth on SAI was investigated by splitting the data into fine scale depth bands (200 m bands between 300 m and 2100 m) and plotting the aggregated SAI.

Grenadiers were grouped together due to difficulties in the identification of species (Fitzcharles et al., 2012; McKenna et al., 2014). Within the data there were several different classifications for a common skate genus *Amblyraja*, which were aggregated together. This followed recent work highlighting that only one species is present in GSGSSI waters (*A. georgiana*), with distinct populations at South Georgia and the SSI (Goodall-Copestake et al., 2018).

### 2.2. Environmental data

Monthly means of environmental data (bottom temperature, sea surface temperature and sea ice cover) were obtained from the Copernicus Marine Environment Monitoring Service (Global Ocean Biogeochemistry Hindcast and Global Ocean Physical Reanalysis products) at a $0.83 \times 0.83°$ resolution. Rasters for each environmental variable were created for the months of February–April (the months of fishery operations) between 2006 and 2020. These rasters were cropped to the area of interest (Fig. 1b) and averaged over the whole time series to create single average rasters for each variable.

### 2.3. Community analysis

For each of the ten areas (Fig. 1b), data were split in to three different depth zones spanning the full depth range of the available data (801–1200 m, 1201–1600 m and 1601–2000 m) creating 30 area-depth band subsets. Each depth subset with fewer than 15 lines was removed from the community analysis for fish species, and fewer than 10 lines for invertebrates due to a paucity of data. A total of 18 subsets were removed from the fish community analysis (with 19 remaining) and 19 were removed from the invertebrate community analysis (with 14 remaining). Some data were present for lines set between 400 and 800 m, however, none of the ten areas had more than 15 lines in this depth zone. For each subset pair, data were log-transformed and Bray-Curtis similarities were calculated using the average SAI values to create a similarity matrix, this was done separately for fish and invertebrates. Structure in the communities of fish and invertebrates was then investigated using non-metric multidimensional scaling (nMDS) and hierarchical agglomerative cluster analysis with the *vegan* package (ver. 2.5–7) (Oksanen et al., 2020). This approach was used to investigate between subset differences in the species assemblages.

A similarity percentages (SIMPER) analysis was used to determine which species were the most influential in the resulting groupings from cluster and nMDS analyses. A permutational multivariate analysis of variance (ADONIS) was used to investigate whether observed groups were statistically different.

Environmental variable data were extracted on a point-by-point basis for each individual line from the average rasters described above. The resulting data were then averaged by subset. A BIO-ENV function was used to assess which of these environmental variables had the best correlation with community dissimilarities. Environmental variables identified as important were then used to overlay smooth surface contours on the nMDS ordination the *envfit()* function in *vegan*, to visually show relationships between groupings and environmental variables.

## 3. Results

### 3.1. Catch over time

Between 2006 and 2020, the two target toothfish species dominated catches comprising 88.5% (SD ± 6.6) of the total fish catches around SSI by weight. The main bycatch species were *Macrourus* spp., *Amblyraja georgiana*, *Antimora rostrata* and *Muraenolepis* sp., comprising 9.7% (±5.4), 1.3% (±1.3), 0.2% (±0.05), and 0.15% (±0.09) of the total catch weight, respectively. The catch weight of *A. georgiana* presented here only represents those brought aboard vessels (hence weight measurements could be taken). The number of *A. georgiana* hooked but released alive represented a higher percentage of the total number of fish caught (21.4% (±8.5)). Over time, the total percentage of catch represented by toothfish has risen from 75% in 2006 to 95.3% in 2020 (Fig. 2). Fishing for *D. mawsoni* was prohibited before 2009, with any incidental captures released alive.

### 3.2. Spatial distribution

Line haul observations were performed by scientific observers for an average of 42.8% (±16.1 SD) of all deployed/hauled hooks for the duration of fishing at the SSI (maximum 100%, minimum 10%). The two toothfish species display differing distributions across the latitudinal range of the SSI (Fig. 3). *Dissostichus eleginoides* were predominantly caught in the northern regions, although their distribution extends throughout the island chain. Conversely, *D. mawsoni* dominated catches in the southern regions although this species too was found throughout the island chain. Both species mixed in the regions around Saunders Island where the catches are approximately equal for both species (Fig. 3). A combined comparison of toothfish catches is presented in SM Fig. 1.

Some of the major bycatch species also exhibit differences in the spatial distribution of catch rate (Fig. 4), with *Antimora rostrata*, *Amblyraja georgiana* and *Macrourus* spp. all displaying generally higher SAI in the northern half of the island chain. In the case of *A. rostrata*, there were few records of catches south of Montagu Island except for Montagu Bank to the east of the island, where this species was consistently found. In contrast, *Muraenolepis* sp. were found almost ubiquitously throughout all the explored areas around the SSI, although the SAI is low throughout.
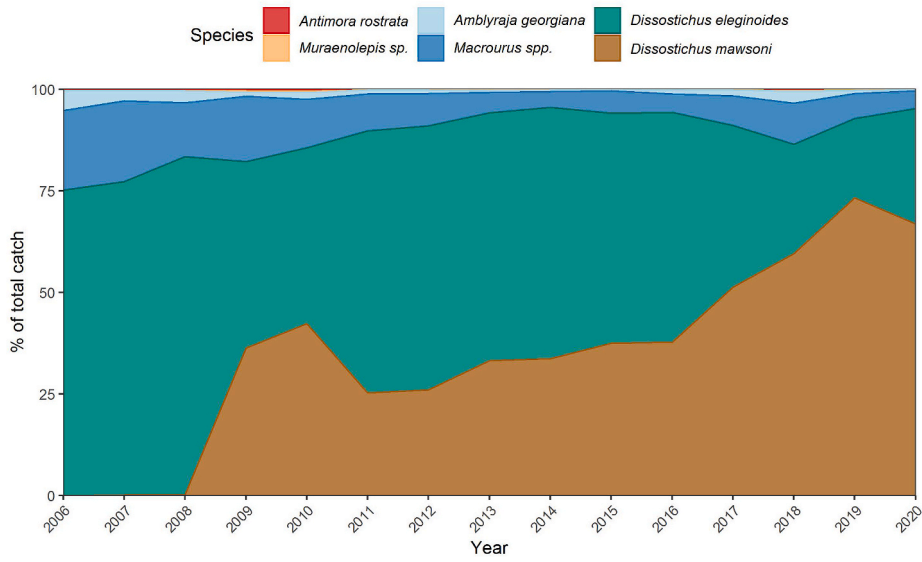
**Fig. 2.** Proportional fish catches over time by weight at the South Sandwich Islands. Only species with consistent annual catches are included, and sporadic catches of *Notothenia* spp., *Bathyraja maccaini* and *Icichthys australis* were also recorded. Fishing for *D. mawsoni* was prohibited before 2009.
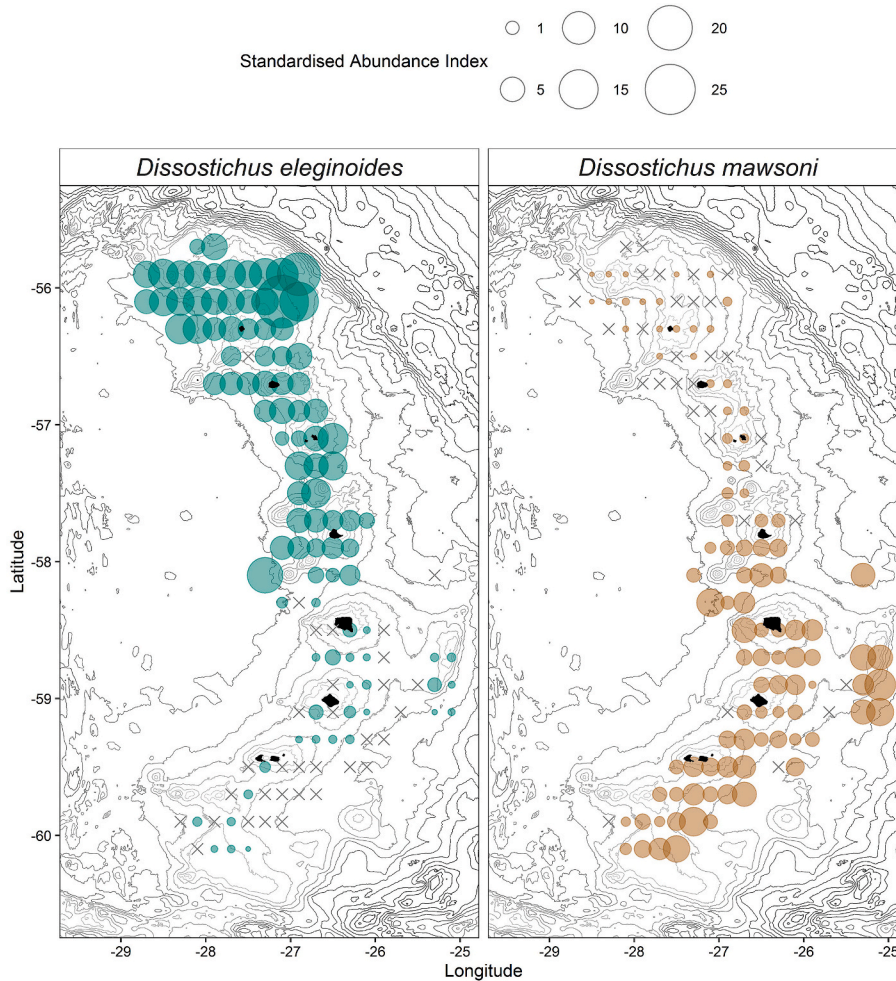


**Fig. 3.** Distribution and SAI (n/1000 hooks) of both toothfish species at the South Sandwich Islands. Data are aggregated by 0.2 × 0.2° grid cells. Black crosses represent cells where no catch of the respective species has been recorded.

**Fig. 4.** Distribution and SAI (n/1000 hooks) of major fish bycatch species at the South Sandwich Islands. Data are aggregated by 0.2 × 0.2° grid cells. Black crosses represent cells where no catch of the respective species has been recorded.

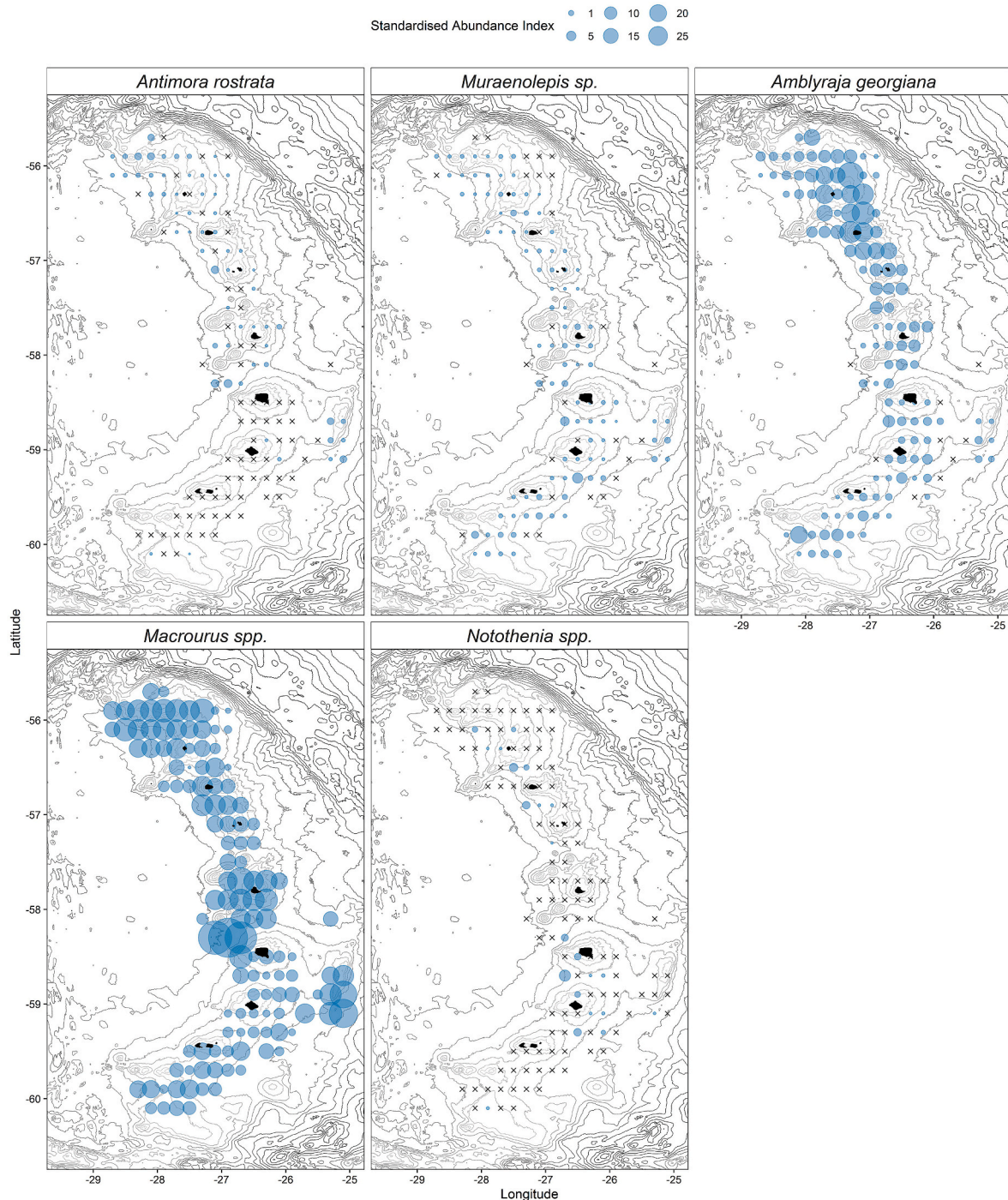The SAI for *A. georgiana* was highest in the north-eastern section of the SSI, east of Protector Shoal, Zavodovski Island and Visokoi Island, which coincides with an area of sloping topography leading to the South Sandwich Trench (Fig. 4; see also Fig. 1). While *Macrourus* spp. were found throughout the SSI, species-specific distributions for the different macrourid species known from SSI were not possible to determine due uncertainties in species identification. There are sporadic records of *Notothenia* spp. in both the north and south with no clear distributional pattern. It is unclear which species these data points represent as they were not identified to species in the observer data aside from a couple of entries identified as *Lepidonotothen squamifrons*. However, Roberts

(2012) reported that the marbled rock cod (*Notothenia rossii*) was also caught as bycatch by longlines at the SSI.

Invertebrate bycatch data were split in to mobile and sessile organisms prior to analysis. Whilst many benthic invertebrate species display both mobile and sessile life stages, we split the data based on the life stages of the organisms when they were caught. As with fish, the distribution of mobile invertebrate bycatch showed strong latitudinal patterns (Fig. 5). Stone crabs (*Lithodidae*) were found almost exclusively in the north and intermediate regions, with only one recorded individualsouth of Saunders Island. Several species were reported in certain years, most likely when the observers on board had the required

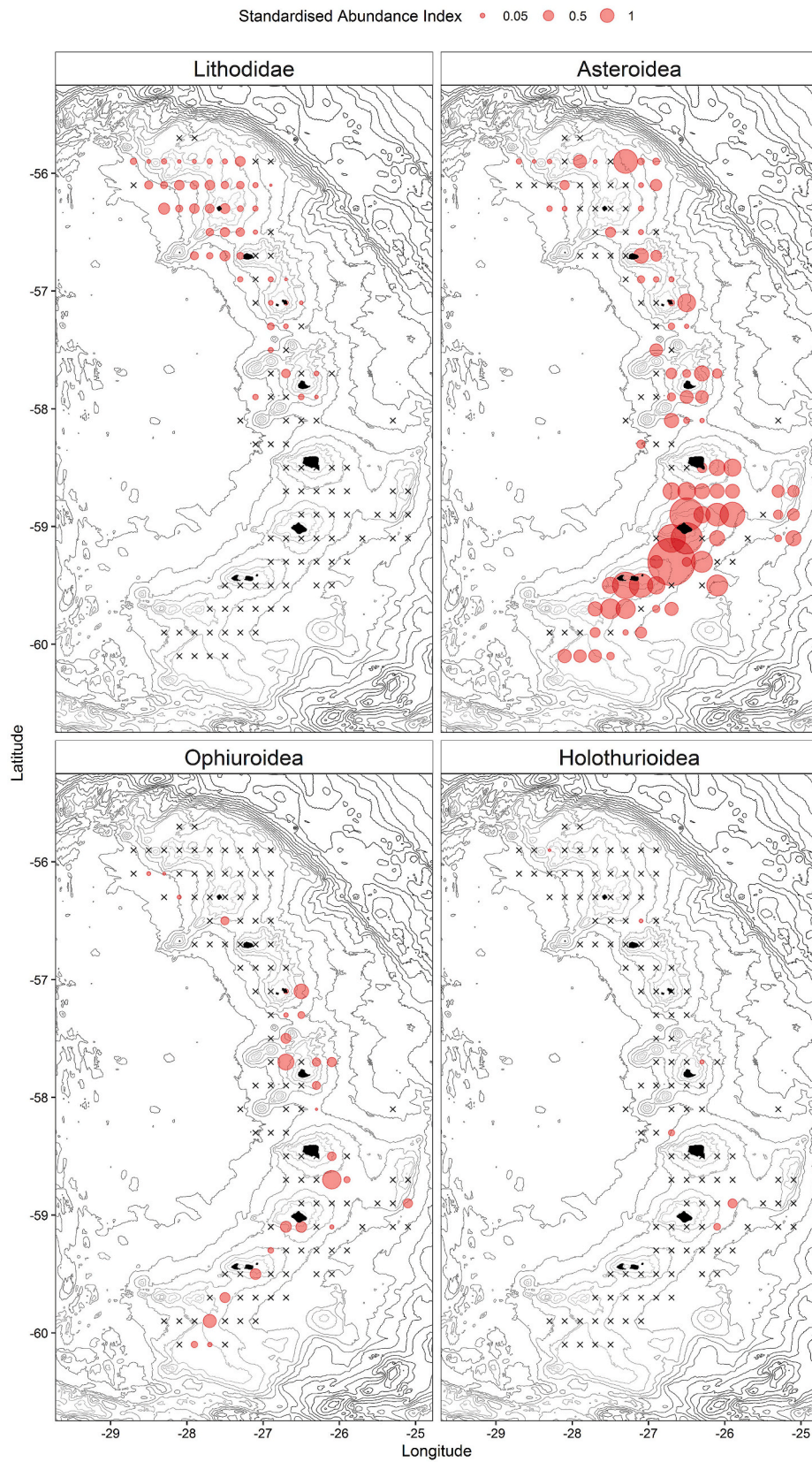**Fig. 5.** Distribution and SAI (n/1000 hooks) of mobile invertebrate groups at the South Sandwich Islands. Data are aggregated by $0.2 \times 0.2°$ grid cells. Black crosses represent cells where no catch of the respective species has been recorded.

experience to identify these species. In those years, the reported species included *Paralomis formosa*, *P. aculeata* and *P. spinosissima*. Conversely, both ophiuroid and asteroid starfish were more frequently caught in locations south of Candlemas Island, with generally lower catches in the northern half of the island chain. Data for sessile invertebrate bycatch (Fig. 6) were limited due to the nature of the sampling gear not being designed to sample this species group. Sessile invertebrate data often had low levels of identification to family level and instead was identified as 'Invertebrate', which was likely caused by differences in observer experience. These data were removed from the main analysis.

Data for sessile invertebrate bycatch distributions (Fig. 6), revealed a similar north-south gradient as seen in fish and mobile invertebrates.

Several groups of sessile species were more readily found at the northern group of islands (anemones - Actiniaria, sea lilies - Crinoidea, soft corals - Alcyonacea). Sea pens (Pennatulacea) and sponges (Porifera) whilst uncommon, have been found in both the north and south of the SSI.

The distribution of aggregated, unidentified invertebrates also followed a similar pattern to that seen in many of the sessile species with higher SAI values in the northern half of the archipelago (SM Fig. 2). Whilst we cannot be certain of what species constitute these catches, they are likely to be comprised in part by Alcyonacea and Actiniaria based on a comparison of distributions.

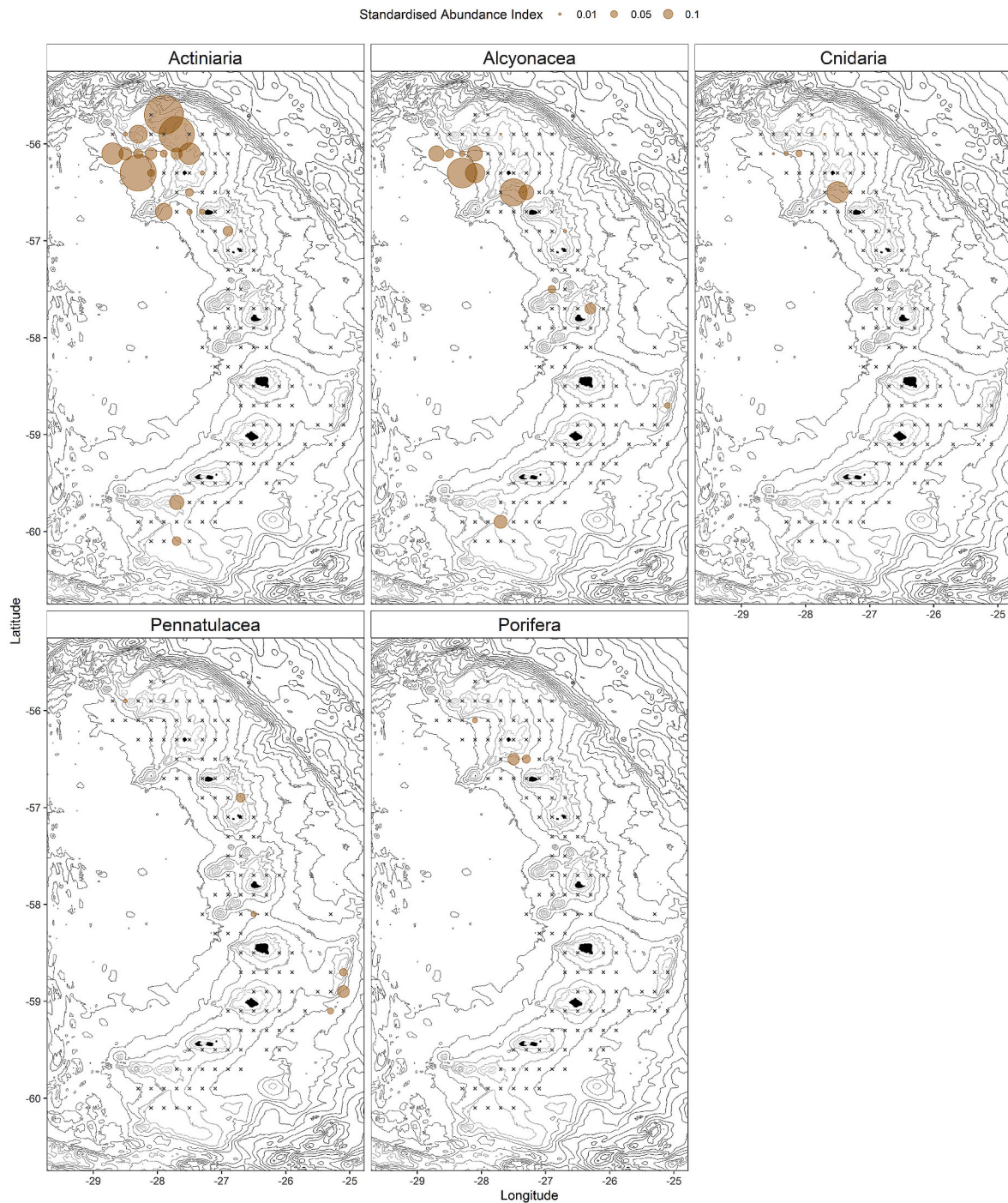

**Fig. 6.** Distribution and SAI (n/1000 hooks) of sessile invertebrate groups at the South Sandwich Islands. Data are aggregated by 0.2 × 0.2° grid cells. Black crosses represent cells where no catch of the respective species has been recorded.
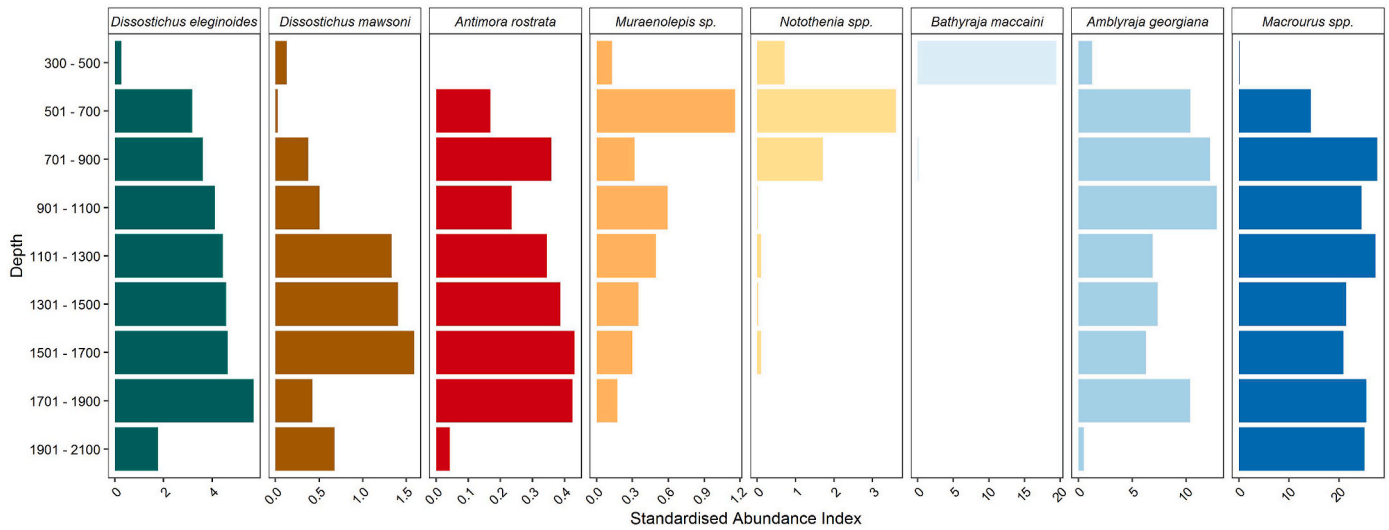
**Fig. 7.** Average SAI (n/1000 hooks) by depth for key species/species groups. Data are aggregated in to 200 m depth zones between 300 and 2100 m.

### 3.3. Depth distribution

The SAI of the examined fish species varied across the depth gradient (Fig. 7). The two toothfish species both showed single peaks in catches between 1500 and 1900 m (see also Soeffker et al., 2022). Several other fishes had a bimodal or multimodal depth distributions (*A. rostrata*, *Macrourus* spp., *Muraenolepis* sp. and *A. georgiana*). *Bathyraja maccaini* was only recorded in shallower sets (<700 m), similar to *Notothenia* spp. which exhibits a peak at 500–700 m with few occurrences below 1300 m. The catch rate information for invertebrate species was too sparse to

complete a comparable analysis of depth distribution. Information on depth gradients in benthic invertebrate species around the South Sandwich Islands can be found in Downie et al. (2021).

### 3.4. Bioregional communities

#### 3.4.1. Fish

The non-metric multi-dimensional scaling (nMDS) ordination displayed clear grouping of subsets between the north, mid and south of the archipelago (Fig. 8). For the southern group of islands, data from
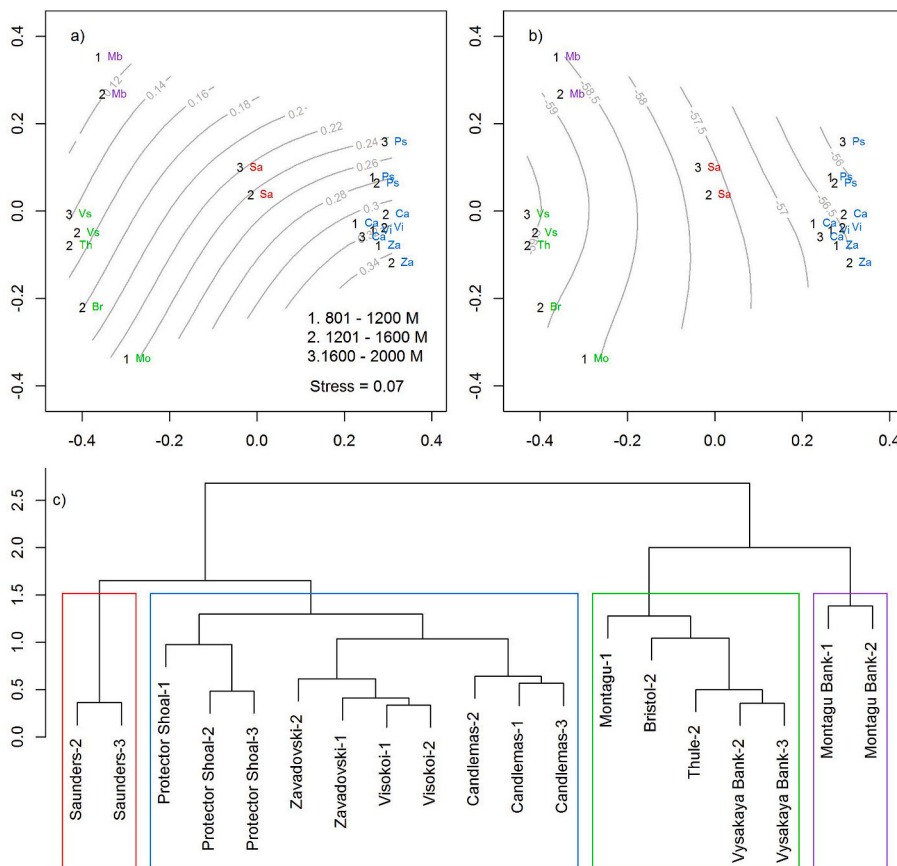


**Fig. 8.** a) nMDS ordination based on the SAI of all major fish species groups from longlines set at different areas and depth zones. Labels are areas: Br – Bristol, Ca – Candlemas, Mo – Montagu, Mb – Montagu Bank, Pr – Protector Shoal, Sa – Saunders, Th – Thule, Vb – Vysokaya Bank, Vi – Visokoi & Za – Zavodovski. Overlaid grey contours represent average sea floor temperature at each site fitted to the ordination. b) The same nMDS ordination seen in a) overlaid with latitude of site. c) Cluster plot of the four main community groups. Groups identified using cluster analysis were used to map colours on to the ordination plots (a & b).

Montagu Bank are further away from the main group, suggesting the catch composition in this location may be distinct from the broader southern group. A cluster analysis confirmed the groups shown in the nMDS plot, with data from Montagu Bank being different to all other groups. Significant differences between the four areas were confirmed using a permutational multivariate analysis of variance (p < 0.01). A SIMPER analysis between areas highlighted the SAI for *A. georgiana*, *Macrourus* spp., *Muraenolepis* sp. and both toothfish species were the most important in driving the dissimilarity between north, mid and south taxonomic composition (Table 1). It was mainly differences in bycatch species that drove the observed dissimilarity between Montagu Bank (801–1200 m) and the other three areas (Table 1).

The BIO-ENV analysis highlighted several enviornmental variables as correlated to community groupings. Seafloor temperature and latitude are overlaid as smooth surface contours on the nMDS ordinations in Fig. 8a and b. This shows a clear gradient in seafloor temperature between the north, mid and south groupings (Fig. 8a) and a similar pattern in latitude (Fig. 8b). Latitude was used here in place of both sea surface temperature and sea ice thickness, both of which are strongly correlated to latitude. nMDS ordinations overlaid with both sea surface temperature and sea ice thickness can be found in SM Fig. 3.

### 3.4.2. Invertebrates

A nMDS ordination displayed a clustering of groups that did not follow the same pattern as fish (Fig. 9a). The taxonomic composition for Saunders Island as well as several of the subsets from the northern areas were more closely grouped with the southern areas. Visually there appear to be groups on the right hand and left hand sides of the plot (Fig. 9a). However, cluster analysis suggests the groups are not as clearly delineated (Fig. 9c). Group 1 was identified as the largest with a majority of northern subsets, group 2 contains mainly southern subsets but only four in total. Similar to the fish community analysis, shallower sets at Montagu Bank (801–1200 m) are different to both main groups. A SIMPER analysis between groups highlighted the SAI of asteroid and ophiuroid starfish and Lithodidae crabs as most influential in driving the dissimilarity between groups (Table 2).

The BIO-ENV analysis of invertebrate communities suggested that seafloor temperature was more strongly correlated with the groupings than it was for fish and latitude was also important (Fig. 8a and b). nMDS ordinations overlaid with both sea surface temperature and sea ice thickness can be found in SM Fig. 4.

The two key environmental variables (sea floor temperature and sea ice thickness; Fig. 10), vary between the northern and southern extents of the SSI, indicting that spatial variation in environmental variables mediates the distribution of many of the species considered here.

## 4. Discussion

This study, which builds on the work of Roberts (2012), uses data derived from longlines to investigate spatial patterns in bathyal fish assemblages and invertebrate bycatch in the South Sandwich Islands. Distinct latitudinal patterns were identified in species distributions and communities, which likely reflect environmental and bathymetric gradients. The geographically distinct communities in the fish assemblage correlate well with environmental variables, many of which correlate to latitude. Invertebrate communities did not show clear spatial differences, although they did still correlate well with seafloor temperature, an environmental variable which is likely to be influential for sessile benthos and linked to sea ice cover. The use of commercial longline data has resulted in a spatially and temporally extensive analysis, which would not have been possible via traditional scientific surveys. However, whilst the data are temporally and spatially extensive, the accuracy of the data is likely not as high as data resulting from a targeted scientific cruise. As an example, the taxonomic resolution of invertebrate bycatch data was poor, and with more accurate or improved data the spatial patterns in these species and communities may have been better resolved.

Previous studies of species distributions at the SSI have focussed on Vulnerable Marine Ecosystem (VME) indicator species (Downie et al., 2021), bioregionalisation based on functional groupings of benthic invertebrates and environmental gradients (Hogg et al., 2021), and chemosynthetic fauna of deep-sea hydrothermal vents (Linse et al., 2019; Marsh et al., 2012). The species found at the SSI have also featured in research on the Scotia Sea or wider Antarctic (Griffiths et al., 2009; Howe et al., 2004; Lockhart and Jones, 2008; Malyutina, 2004; Ramos, 1999) as well as studies with a tighter geographical focus around single islands (Griffiths et al., 2008; Kaiser et al., 2008). A previous survey of shallower demersal fish also showed that the SSI had a similar ichthyofaunal community to nearby South Georgia (Jones et al., 2008). This study adds a valuable aspect by defining the patterns and distributions of the most commonly caught bathyal fish and invertebrate species throughout this region.

### 4.1. Fish distributions

The longline gear used to fish for toothfish is designed with hooks to retain fish that take bait and to target large, mobile species, making them reliable and consistent sampling gear for toothfish species in their demersal life stage. Longlines are likely to have an an inherent bias towards a particular fish size defined by the size of hooks, and larger, faster swimming fish are likely to encounter bait quicker. While the configuration of the longlines makes them selective towards toothfish, their attraction and catchability of non-target species remains spatially consistent and provides insights into the abundances and distributions of bathyal fish species susceptible to longline gear. For all examined fish, seafloor water temperature was an important abiotic factor mediating their distributions, with southward range expansions of several Southern Ocean fish limited by cold thermal stress (Eastman, 1990). Distinct changes in the fish communities as well as the distributions of individual species were evident around Saunders Island (Fig. 1) following a latitudinal gradient. Future work could focus on latitudinal assessment of biological parameters of all target and non-target fish species, evaluating whether there are temporal changes resulting from the longline fishery.

### 4.2. Distribution of toothfish species

The distributions of both toothfish species had clear latitudinal differences typified by increasing abundance of *D. mawsoni* and decreasing abundance of *D. eleginoides* from north to south (Fig. 3) and this latitudinal change was among the key drivers of the observed changes in fish communities (Table 1). Cold stress is not a likely limiting factor for *D. mawsoni* which produce several antifreeze glycopeptides (AFGPs)

**Table 1**
SIMPER analysis summary of the most influential species driving the dissimilarity observed between locations.

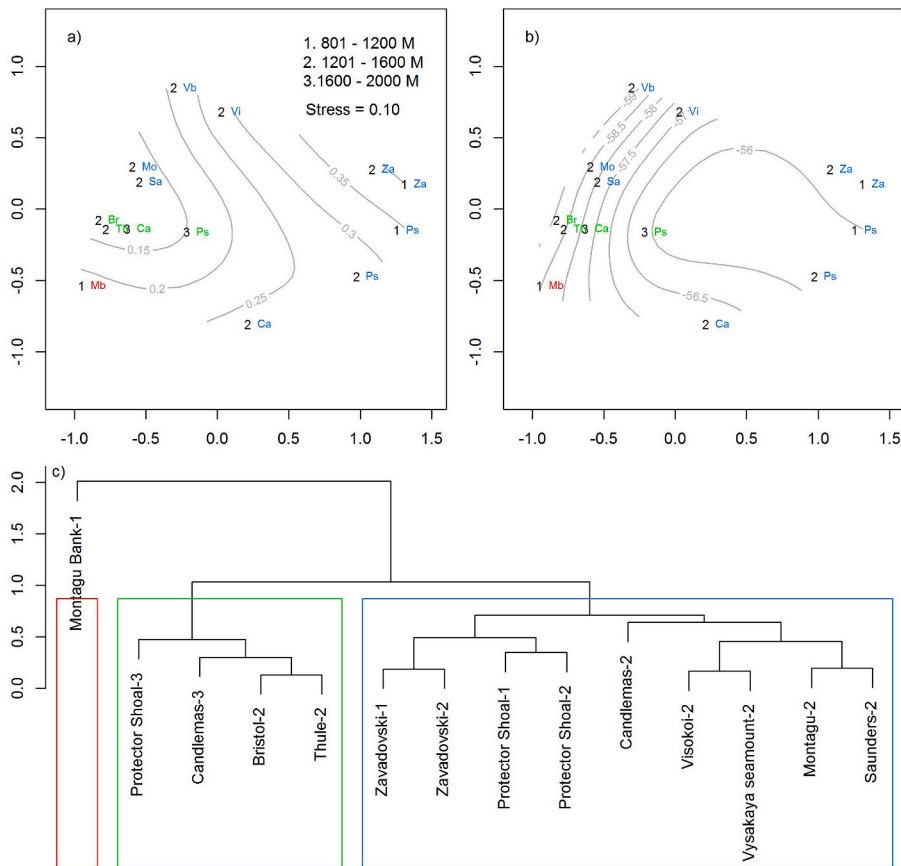| Cumulative contributions of most influential species | | | |
|---|---|---|---|
| Comparison | 1 | 2 | 3 |
| North vs. South | *D. eleginoides* | *Amblyraja georgiana* | *D. mawsoni* |
| | 0.30 | 0.56 | 0.76 |
| South Vs. Mid | *Macrourus* spp. | *D. eleginoides* | *D. mawsoni* |
| | 0.40 | 0.57 | 0.72 |
| North vs. Mid | *Amblyraja georgiana* | *D. eleginoides* | *D. mawsoni* |
| | 0.34 | 0.56 | 0.78 |
| North vs. Montagu Bank | *Macrourus* spp. | *Amblyraja georgiana* | *D. eleginoides* |
| | 0.29 | 0.52 | 0.72 |
| Mid vs. Montagu Bank | *Macrourus* spp. | *Muraenolepis* sp. | *D. eleginoides* |
| | 0.41 | 0.60 | 0.74 |
| Mid vs. Montagu Bank | *Macrourus* spp. | *Muraenolepis* sp. | |
| | 0.61 | 0.74 | |

**Fig. 9.** a) nMDS ordination based on the SAI of all major invertebrate bycatch species groups from longlines set at different areas and depth zones. Labels are areas: Br – Bristol, Ca – Candlemas, Mo – Montagu, Mb – Montagu Bank, Pr – Protector Shoal, Sa – Saunders, Th – Thule, Vb – Vysokaya Bank, Vi – Visokoi & Za – Zavodovski. Overlaid grey contours represent average sea floor temperature at each site fitted to the ordination. b) The same nMDS ordination seen in a) overlaid with latitude of site. c) Cluster plot of the four main community groups. Groups identified using cluster analysis were used to map colours on to the ordination plots (a & b).

**Table 2**

SIMPER analysis summary of the most influential invertebrate species groups driving the dissimilarity observed between locations.

| Cumulative contributions of most influential species | | | |
| --- | --- | --- | --- |
| Comparison | 1 | 2 | 3 |
| Group 1 vs. Group 2 | Asteroidea 0.81 | Lithodidae 0.88 | Actiniaria 0.93 |
| Group 1 vs. Montagu Bank 2 | Ophiuroidea 0.78 | Asteroidea 0.93 | Lithodidae 0.97 |
| Group 2 vs. Montagu Bank 2 | Ophiuroidea 0.69 | Asteroidea 0.97 | |

(Chen et al., 1997; Cheng and Detrich, 2007), preventing them from freezing when they come in to contact with ice (Collins et al., 2010). Conversely, *D. eleginoides* does not appear to produce AFGPs (Cheng and Detrich, 2007; Ghigliotti et al., 2006) and thus temperature is likely to be the main limiting factor of the distribution of this species at the SSI. This distinction likely plays a major role in the latitudinal mirroring of the distributions for the two toothfish species at the SSI. The southern regions of the archipelago are likely to be the edge of the habitable range for *D. eleginoides* (Soeffker et al., 2022) which is generally found in waters 1.4–11 °C (Collins et al., 2006, 2010; Eastman, 1990).

*4.3. Distribution of non-target species*

The only other species showing a clear and consistent decrease in SAI with increasing latitude (along with *D. eleginoides*) was the deep-sea morid cod *Antimora rostrata* (Fig. 4). This species was encountered more frequently to the north of Saunders Island and also displayed relatively high SAI at Montagu Bank. It is not clear whether this species is capable of producing AFGPs but its widespread distribution (Gon and

Heemstra, 1990) may suggest that the southern regions of the archipelago do not provide suitable habitat.

All four southern hemisphere species of *Macrourus* grenadiers were recorded in the dataset (*M. whitsoni, M. holotrachys, M. carinatus & M. caml*). Southern hemisphere *Macrourus* spp. can be difficult to identify to species level (McKenna et al., 2014) and one species was not described until recently. *Macrourus caml* was first described in 2012 (McMillan et al., 2012) and while it may have been caught prior to that date around the SSI, it cannot retrospectively be identified as such from the dataset. Preliminary genetic evidence suggests that neither *M. holotrachys* nor *M. carinatus* are present in SSI waters despite being recorded in observer data, and that potentially, *M. caml* and *M. whitsoni* have latitudinal distribution differences between them (Fitzcharles et al., 2012). No *M. holotrachys* or *M. carinatus* were found in the line observation data after 2011, suggesting that the visual identification of these two species has improved in recent years and historical records of these species at the SSI are likely incorrect. This change is likely due to increased understanding of species distributions (Fitzcharles et al., 2012) and improved identification materials (McKenna et al., 2014). Alongside this, for specimens kept for biological sampling, no incidences of unidentified *Macrourus* spp. have been recorded since 2015, with only *M. caml* and *M. whitsoni* identified. Similar to *D. mawsoni*, AFGPs have been found in *M. holotrachys* (Wöhrmann, 1996) and due to the distribution of *M. caml* and *M. whitsoni* into cold waters (Pinkerton et al., 2013) it can be assumed that these species are either also able to synthesize AFGPs or have other coping mechanisms for cold water stress. Due to these uncertainties and difficulties with consistent identification (Fitzcharles et al., 2021; Gon et al., 2021; McKenna et al., 2014), the macrourid species were grouped in our analyses. *Macrourus* spp. are found ubiquitously throughout the SSI, with catches recorded in every individual $0.2 \times 0.2°$ grid cell. Whilst no clear latitudinal gradient is present in their SAI, higher SAI values were observed at Montagu Bank
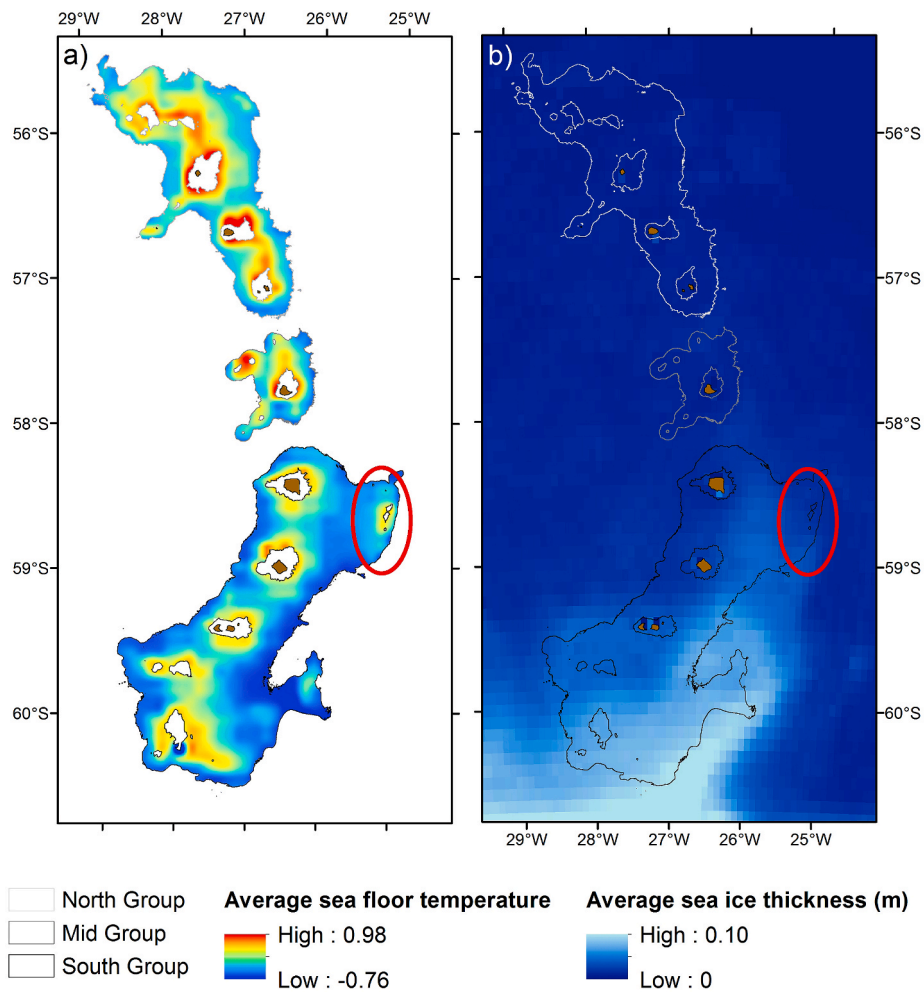
**Fig. 10.** a) Average sea floor temperature from February–March 2006–2019, cropped to depths between 700 and 2250 m. b) Average sea ice thickness from February–March 2006–2019, overlaid with 700 and 2250 m depth contours. The north, mid and south areas which had different communities of fish are outlined in different shades of grey. The red ellipse denotes Montagu Bank, with communities that fall into their own group.

when compared to surrounding areas and consistently high SAIs were observed from Protector Shoal down to Saunders Island. It is possible that the subtle difference in SAI between the north-mid area and the southern area are indicative of different distributions of the two species (*M. caml* and *M. whitsoni*). The depth distribution of *Macrourus* spp. SAI with depth (Fig. 7) could further indicate differences in bathymetric distribution between macrourid species, which has previously been observed in the Ross Sea where only a single *M. holotrachys* was identified out of a total of 864 *Macrourus* spp., but *M. whitsoni* and *M. caml* were found to be sympatric (Pinkerton et al., 2013). Proportionally *M. whitsoni* was more prevalent with increasing depth (Pinkerton et al., 2013).

The uncertainties around *Macrourus* spp. identification and subsequent grouping at genus level in our study reduced the power of the resulting community analyses, which may well have been stronger with additional species distributions displaying latitudinal patterns, highlighting the need for further research into macrourid species, their identification and distribution patterns around the SSI. With *Macrourus* spp. being the largest bycatch species complex around the SSI, it is important to understand explicitly how longline fishing may affect individual species as opposed to an aggregate group. In the Ross Sea, 74% of bycaught macrourids were identified as *M. caml*, although it was unclear whether this was due to a large local *M. caml* population, competition between macrourid species for bait, or specifics of deployed gear (Pinkerton et al., 2013). With morphological identification

difficult, further genetic work is needed to clarify the distributions of *Macrourus* spp. around the SSI to improve our understanding of the ecology of these fish.

The Antarctic starry skate (*Amblyraja georgiana*) was found throughout the latitudinal range of the SSI with increased SAI over the sloping topography to the north east of Zavodovski Island (Fig. 4). It is possible that this area represents a good habitat for this species, as this habitat has been shown to accommodate a comparatively high richness in benthic species when compared to other areas in the SSI (Hogg et al., 2021). Recent genetic analysis of this species at South Georgia and the SSI confirmed that only a single species is present, with genetically distinct populations in the two areas and little gene flow between (Goodall-Copestake et al., 2018). As the introduction of guidelines on skate bycatch in 2004 in the CCAMLR area pre-dated the longline fishery at the SSI, most skates are released alive and in good condition (Endicott and Agnew, 2004). Therefore the total landed catch weights of this species are generally low, even though they make up ~21% of catches by number.

Eel cods (*Muraenolepis* sp.) were found throughout the SSI with no apparent latitudinal pattern. A recent study clarified the identification of this genus at the SSI finding that one species, assumed to be *M. evseenkoi*, was the predominant species in the north of the island chain with a single specimen of *M. marmorata* identified close to Southern Thule (Fig. 1b)(Fitzcharles et al., 2021). In *M. marmorata* the presence of AFGPs has been identified (Wöhrmann, 1996), but not specifically in

*M. evseenkoi.* However, the presence of *M. evseenkoi* around continental Antarctica further south (Balushkin and Prirodina, 2010) would suggest this species can synthesize AFGPs.

### 4.4. Fish communities and depth distributions

The distinct fish assemblages (or communities) identified by MDS and cluster analyses appear to be driven by environmental factors with a latitudinal gradient, namely water temperature. These communities are delineated well by the seafloor topography of the region, with deeper water splitting the north, mid and south groups (Fig. 10). Several species shown to be important drivers in community differences by the SIMPER analysis displayed clear latitudinal variation in SAI. The presence or absence of AFGPs within the sampled fish species is likely important in driving differences in communities based on temperature gradients. Abrupt changes in distributions of several species are observed close to Saunders Island, it is possible this is not only due to temperature but also due to the Weddell Front sporadically crossing the island chain at this location (Naveira Garabato et al., 2002; Orsi et al., 1993; Thorpe and Murphy, 2022). This may result in more abrupt temperature barriers to species already at the edge of their thermal tolerance, as well as physical barriers to dispersal for benthic species which may rely on north-south currents for dispersal along the archipelago.

Montagu Bank was distinct from all other areas. This dissimilarity appears to be driven largely by bycatch species (*Marcourus* spp. and *Muraenolepis* sp.) and *D. eleginoides*. In fact, all target and bycatch species (aside from *Notothenia* spp.) were found at Montagu Bank, even if their distributions may be patchy throughout the rest of the southern archipelago. This distinctly different community suggests that Montagu Bank exhibits a different environmental setting to other nearby areas. This is likely due to differences in oceanography providing suitable habitat for the prey of target and bycatch species. Tag recapture data of *D. mawsoni* shows that many tagged animals remain around Montagu Bank (Soeffker et al., 2022), suggesting this area provides valuable habitat for this species.

Both toothfish species showed broad peaks in SAI between 1500 m and 1900 m, a depth range over which only one other species displayed a peak in SAI (*A. rostrata*). As toothfish are the largest species within this community and are targeted by the fishery, their depth distributions may be accurately represented as they may out-compete all other species for available bait, resulting in a capture reduction of other species over the peak of their depth distribution. Toothfish at the SSI have also been shown to predate on all of the main bycatch species (aside from *Bathyraja maccaini*), with *Macrourus* spp. being the dominant fish prey for both toothfish species (Roberts et al., 2011).

### 4.5. Invertebrate distributions and communities

The distributions of many of the invertebrates showed clear spatial variation with lithodid crabs and several groups of suspension feeding organisms (e.g. anemones (Actiniaria) and soft corals (Alcyonacea)) all showing a preference for northerly latitudes, and starfish (Asteroidea and Ophiuroidia) displaying a preference for colder latitudes (Figs. 5 and 6). Recent studies have found similar latitudinal relationships in the benthic fauna at the SSI (Downie et al., 2021; Hogg et al., 2021). Hogg et al. (2021) used a gradient forest approach based on environmental data and species distributions to identify 12 spatial groupings of benthic communities at the SSI. One of these clusters corresponds to shallower habitats around the northern grouping of locations (Protector Shoal – Candlemas Island; Fig. 10) and another to the mid- and southern grouping outlined in Fig. 10 (Saunders Island – Vysokaya Bank). Similarly to the communities of fish investigated in this study, sea floor temperature appeared to be influential in the delineation of these groups. Downie et al. (2021) analysed video transects and still imagery taken throughout the SSI, to assess the distribution and abundance of invertebrate groups (specifically VME indicator species, which many of

the sessile invertebrate groups in this study are classed as). Their study indicated that there is a change in benthic fauna between the north and south of the archipelago. Fewer observations of soft corals (Alcyonacea) were noted at higher latitudes around Southern Thule, with changes in their morphotype to less branching species further south, and our findings in this study are consistent with these observations (Fig. 6). Downie et al. (2021) also reported low abundances of sponges (Porifera) and sea pens (Pennatulacea) throughout the island chain, which is also consistent with our findings.

Sessile invertebrates with branching structures (e.g. some Alcyonacea) are more likely to be hooked by lines due to the complexity of their structure, which may bias the results presented here to branched morphotypes of some species groups. This has been observed previously for branched cold water corals (Pham et al., 2014). Mobile invertebrates such as crabs have been seen feeding on bait (Yau et al., 2002), and are probably caught when lines are hauled. The same is likely true for other mobile invertebrates such as asteroid starfish. These species are not hooked in the same manner as fish, and thus they are likely underrepresented in our dataset as many may simply not be hauled to the surface. Many of the invertebrate species reported in this paper are also found less frequently at depths >700 m (Downie et al., 2021), and therefore would be sampled less frequently with gear operating mainly between 700 and 2250 m. The depth restriction on the longline fishery (Belchier et al., 2022), as well as the innate inefficiently of longline gear for capturing sessile invertebrates, therefore provides substantial protection to benthic invertebrates around SSI.

The distribution of suspension feeders in the north (e.g. Alcyonacea, Actiniaria) may be consistent with environmental conditions other than seawater temperature. Current speed plays an important role in determining habitat suitability for suspension feeders (Eckman and Duggins, 1993; Lim et al., 2020), and the concurrent distribution of actiniarians and alcyonaceans (as well as the generic 'Invertebrates' in SM Fig. 2) may suggest the current flows in the northern half of the archipelago are more suited to suspension feeding. Evidence of current activity on the seabed can be seen in the form of sediment waves which are a prominent feature of the bathymetry in the northern half of the island chain around Protector Shoal and Zavodovski Island (Leat et al., 2010). There is also a requirement for many sessile invertebrates to have a stable substrate (such as hard rock) to attach to. Zavodovski and Saunders have reported areas of exposed rock that appear to host a greater diversity of suspension feeding organisms (Downie et al., 2021). But for many areas, repeated disturbance from slumping of soft substrates (Leat et al., 2010) and volcanic activity (Liu et al., 2020) likely limit colonisation opportunities for sessile organisms. It is also possible that the proliferation of sessile benthic organisms with larval phases may also be impeded by currents crossing the SSI around Saunders Island (Naveira Garabato et al., 2002; Orsi et al., 1993; Thorpe and Murphy, 2022). The abundance of opportunistic actiniarians suggests relatively high levels of disturbance amongst the benthic communities at the SSI, consistent with previous surveys along the Scotia Ridge (Arntz and Brey, 2003; Ramos, 1999).

The distributions of mobile invertebrate fauna are likely to be mediated by water temperature. Lithodid crab species distribution in the subantarctic and Antarctic is controlled by temperature, which would be consistent with the findings of this study (Arntz et al., 2005). The populations of mobile ophiuroids and asteroids are more prevalent in the southern half of the archipelago, often in areas where other benthic invertebrates are absent which may be due to competition for access to bait from crabs in the north of the archipelago. It is possible that the species present in these populations originate in cooler Antarctic waters and therefore are restricted to the colder latitudes within the SSI. It is well established that ophiuroids are often associated with branching coral species (Mosher and Watling, 2009), but in this case, the distribution of alcyonacea does not overlap well with that of ophiuroids (Figs. 5 and 6). While species-specific information was not available in our dataset, Downie et al., (2021) do report large ophiuroids at Montagu

Island and communities dominated by ophiuroids at Southern Thule.

While distributions of several invertebrate groups individually display a clear latitudinal gradient, the communities identified through cluster analysis did not follow the same pattern (Fig. 9). Although capture by longlines of these species can be considered consistent and comparable, the efficiency of this gear for sampling sessile invertebrates is poor as it is designed to target mobile, scavenging fish species. However, the similarity in distributions of many taxa between this study and Downie et al. (2021) shows consistency between the two different methods of data collection (video transects/photographic surveys and longline fishing). This suggests that the expected poor catchability of invertebrates via longlines is at least consistent, therefore, we can use these data to look at distributions of invertebrate taxa. Together, these studies are building up a multi-layered picture of the benthic environment around the SSI and the latitudinal changes throughout.

*4.6. Climate change*

As the distributions of many of the species reported here are influenced by temperature, changes to temperature may have a drastic impact, both on the ranges of individual species and the associated communities. The polar regions surrounding the Antarctic Peninsula have warmed twice as much as the average for the globe since the end of the 19th century (Siegert et al., 2019), with significant warming of surface water environments also reported at South Georgia (Whitehouse et al., 2008). In association with this warming, the Southern Ocean is also experiencing a range of other climate stresses, such as reductions in sea ice cover, shifts in key oceanic fronts and freshening of seawater (Meredith et al., 2019; Morley et al., 2020). Whist many impacts of climate change focus on the surface layers of the ocean, deeper waters are also affected, with a predicted increase of up to 1.7 °C by 2100 in waters between 200 m and 3000 m (Sweetman et al., 2017). Warming is likely to result in a pole-ward shift of many species based on their thermal tolerance (Constable et al., 2014; Sweetman et al., 2017). At the SSI, shifts in distributions of cold-water species with narrow thermal tolerances will likely result in changes and shifts in the fish and invertebrate communities identified here. Fish species lacking AFGPs (e.g. *D. eleginoides*) may expand further south as restrictive colder waters shift pole-ward. However, there is limited availability of juvenile habitat for *D. eleginoides* at the SSI which may make it difficult for it to establish a self-sustaining population (Soeffker et al., 2022). *D. mawsoni* has been identified as particularly vulnerable to climate change impacts due to its narrow thermal tolerance (FAO, 2018). Whilst there is evidence of enhanced spawning activity in *D. mawsoni* at slightly elevated temperatures (Roberts, 2012), regional warming will likely impact on other aspects of their life history and potentially increase competition with Patagonian toothfish. Fertilised eggs of *D. mawsoni* are thought to be retained and nurtured by association with sea ice (Parker et al., 2021). In the Ross and Weddell seas, which are thought to be spawning locations for *D. mawsoni* (Hanchet et al., 2008, 2015; Parker et al., 2021; Soeffker et al., 2018) sea ice had been increasing between 1979 and 2014, although a steep decline was observed over the subsequent three years (Parkinson, 2019). Whilst the sea ice extent appears to now be back in line with the established 40-year increasing trend (NASA, 2021), the potential inter-annual variability in the sea ice extent is likely to have an impact on the reproductive success of *D. mawsoni* populations in these locations.

In conclusion, the distributions of fish species and communities show a clear latitudinal gradient with an abrupt change around Saunders Island. Community analysis suggests there are three distinct communities of scavenging fish delineated by toprgraphy, with a fourth group present at Montagu Bank. The observed latitudinal differences are likely driven by seawater temperature and the ability of particular species to produce AFGPs (Eastman, 1990; Wöhrmann, 1996). Similarly, invertebrate species display clear latitudinal gradients in distribution, which are likely to be driven by a gradient in seawater temperatures, disturbance,

suitability of available habitat and possibly the influence of current systems in the region restricting dispersal. With many of the species distributions reliant on temperature, the prospect of climate change induced warming (along with changes in the strength and positions of ocean fronts) is likely to result in pole-ward contractions in the ranges of many cold water species along with shifts and changes in their communities.

## Author statement

PRH - Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Validation; Visualization; Writing - original draft; Writing - review & editing. MS - Conceptualization; Investigation; Validation; Writing - review & editing. JR - Conceptualization; Methodology; Investigation; Writing - review & editing. OTH - Roles/Writing - original draft; Writing - review & editing. VVL - Roles/Writing - original draft; Writing - review & editing. JQ - Conceptualization; Writing - review & editing. MB – Conceptualization; Writing - review & editing. CD - Conceptualization; Writing - review & editing. MAC - Conceptualization; Roles/Writing - original draft; Writing - review & editing.

## 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.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr2.2022.105054.

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