Ecosystems (2025) 28:72
https://doi.org/10.1007/s10021-025-00984-7

ECOSYSTEMS

ORIGINAL ARTICLE

Benthopelagic Deep-Sea Food Webs Along a Latitudinal Gradient in the Scotia Sea (Southern Ocean)

José P. Queirós,[1,2,8]* Mark Belchier,[2] José Abreu,[1,2] Paco Bustamante,[3] Martin A. Collins,[2] Ana M. M. Gonçalves,[4,5] Irene Bermúdez-Gutiérrez,[1] Gabriele Stowasser,[2] Diana Vaz,[6] Philip R. Hollyman,[2,7] and José C. Xavier[1,2,5]

[1]MARE—Marine and Environmental Sciences Centre/ARNET—Aquatic Research Network, Department of Life Sciences, University of Coimbra, 3000-456 Coimbra, Portugal; [2]British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK; [3]Littoral Environnement et Sociétés (LIENSs), UMR 7266 CNRS –La Rochelle Université, 2 rue Olympe de Gouges, 17000 La Rochelle, France; [4]Department of Biology and CESAM—Centre for Environmental and Marine Studies, University of Aveiro, Campus Universitário de Santiago, 3810-193 Aveiro, Portugal; [5]CFE– Centre for Functional Ecology: Science for People & Planet, Department of Life Sciences, University of Coimbra, 3000-456 Coimbra, Portugal; [6]Department of Physics, University of Aveiro, Campus Universitário de Santiago, 3810-193 Aveiro, Portugal; [7]School of Ocean Sciences, Bangor University, Askew Street, Menai Bridge LL59 5AB, UK; [8]Present address: Present Address: CIIMAR/CIMAR LA, Interdisciplinary Centre of Marine and Environmental Research, University of Porto, Terminal de Cruzeiros Do Porto de Leixões, 4450-208 Matosinhos, Portugal

ABSTRACT

Understanding food-web structure is crucial to determine the functioning of ecosystems and sustainably manage resources. The Scotia Sea is an important area for Antarctic krill and toothfish fisheries, and one of the regions most impacted by climate change in the Southern Ocean. Whilst the pelagic Antarctic krill-centric food web has been investigated in reasonable detail, the structure of deep-sea food webs associated with toothfish fisheries remain largely unknown. Utilising stable isotopes and fatty acids as trophic proxies, we studied the deep-sea food-web structure in three locations of the Scotia Sea, from South Georgia (SG) to the South Sandwich Islands (SSI; divided into north and south). Our analyses indicate that all food webs were similar, presenting high trophic redundancy and similar vertical structure. All food webs had five trophic levels, with the 5th and 4th trophic levels mainly constituted of fish and the 3rd trophic level of cephalopods and crustaceans. However, some differences existed with the SG food web presenting larger diversity of producers and the bigeye grenadier *Macrourus holotrachys* in the highest trophic position, while Patagonian toothfish *Dissostichus eleginoides* and both Patagonian and Antarctic toothfish *D. mawsoni* were the top

---

Received 26 October 2024; accepted 4 June 2025

Supplementary Information: The online version contains supplementary material available at https://doi.org/10.1007/s10021-025-00984-7.

Author Contributions: JPQ: Conceptualisation, formal analysis, funding acquisition, investigation, methodology, visualisation, writing—original draft, writing—review and editing; MB: Conceptualisation, resources, supervision, writing—original draft; JA: Methodology, writing—original draft; PB: Resources, validation, funding acquisition, writing—original draft, writing—review and editing; MAC: Methodology, resources, writing—original draft, writing—review and editing; AMMG: Methodology, resources, funding acquisition, writing—original draft, writing—review and editing; IBG: Methodology, validation, writing—original draft; GS: Writing—original draft; DV: Methodology, writing—original draft; PRH: Conceptualisation, supervision, writing—original draft; JCX: Conceptualisation, supervision, writing—original draft, writing—review and editing.

*Corresponding author; e-mail: jqueiros@student.uc.pt

predators at SSI-North and SSI-South, respectively. Compared to coastal and pelagic food webs in the Southern Ocean, our results suggest that deep-sea food webs, including the benthic/demersal components, have a longer food-chain length. This study provides essential knowledge of the ecological variability of Southern Ocean deep-sea food webs while contributing to the management of resources within the SG and SSI Marine Protected Area.

Key words: Antarctica; Bathyal zone; Fatty acids; Food-chain length; Marine protected area; Stable isotopes; Trophic web.

HIGHLIGHTS

- Benthopelagic food webs in the Southern Ocean are composed by five trophic levels.
- Two trophic pathways are found in benthopelagic food webs: pelagic and benthic.
- Southern Ocean deep-sea benthopelagic food webs are longer than pelagic and coastal.

INTRODUCTION

South Georgia (SG) and the South Sandwich Islands (SSI) are part of the Scotia Arc and form the northern and eastern boundaries of the Scotia Sea, in the Atlantic sector of the Southern Ocean (Figure 1). South Georgia is approximately 500 km to the northwest of the SSI, yet several environmental differences exist between these regions. South Georgia is crossed by the warmer waters of the Antarctic Circumpolar Current (ACC) and thus connected to a larger system including the Amundsen and Bellingshausen seas and the western Antarctic Peninsula (Whitehouse and others 2008; Murphy and others 2013; Trathan and others 2014). The SG region is one of the most productive areas of the Southern Ocean and holds a great diversity and abundance of species (Gaston 2009; Sexton and others 2009; Stowasser and others 2012a; Murphy and others 2013; Trathan and others 2014). In contrast, the SSI are located south of the Southern Boundary of the ACC (though with some influence at the northern end of the archipelago), and within the influence of the Weddell Gyre in the south (Thorpe and Murphy 2022). This creates a strong latitudinal gradient along the north-south arc of the archipelago, with warmer waters to the north and cold Antarctic

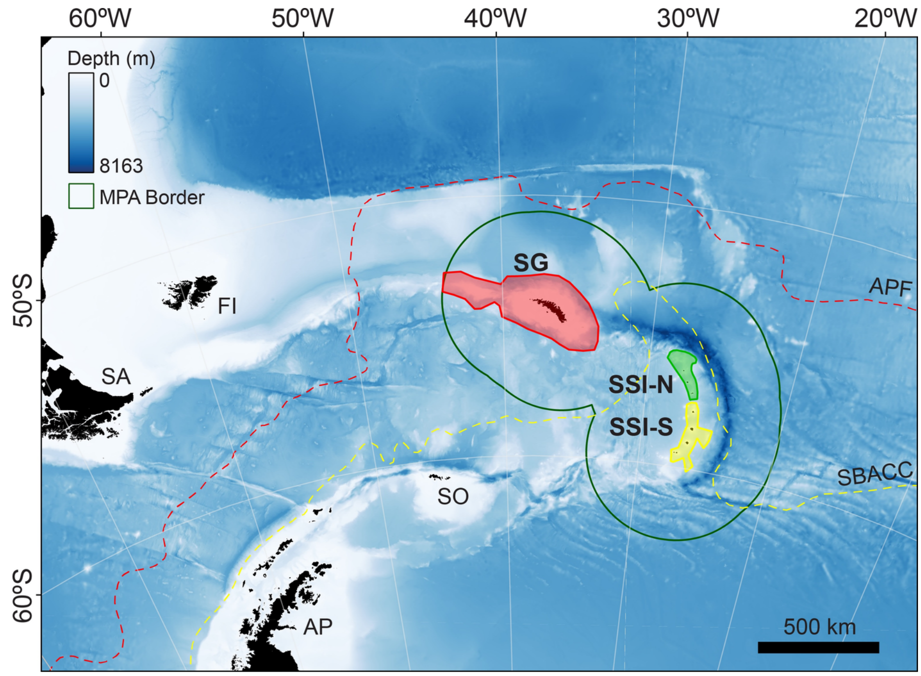

Figure 1. Study areas in the South Georgia and the South Sandwich Islands Marine Protected Area. SG: South Georgia; SSI-N: South Sandwich Islands—North; SSI-S: South Sandwich Islands—South; APF: Antarctic Polar Front; SBACC: Southern Boundary of the Antarctic Circumpolar Current; SA: South America; FI: Falkland Islands; SO: South Orkneys; AP: Antarctic Peninsula

waters to the south (Thorpe and Murphy 2022). Such a gradient is reflected in the biological communities, with typical subantarctic species in the north and Antarctic species in the south, and whose populations present range-edge characteristics (Gaston 2009; Sexton and others 2009; Roberts 2012; Downie and others 2021; Hogg and others 2021; Hollyman and others 2022; Soeffker and others 2022; Queirós and others 2024b).

Both archipelagos are within the SG and SSI Marine Protected Area (SGSSI MPA), the second largest MPA in the Southern Ocean and one of the largest in the world. It was established in 2012 and comprises a total area of 1.24 million km^2, including 283 000 km^2 of no-take zones (Brooks and others 2020; GSGSSI 2023b). The SGSSI MPA aims to protect the ecosystem while maintaining a sustainable and highly regulated use of its marine living resources (Trathan and others 2014; Belchier and others 2022; GSGSSI 2023b). More specifically, it aims to protect biodiversity, representative and rare habitats, facilitate recovery of populations from past overexploitation, maintain robustness and resilience against climate change, and protect ecosystem processes such as the food-web interactions (Trathan and others 2014; Hollyman and others 2021; Belchier and others 2022).

Four fisheries occur within the MPA, including fisheries targeting Antarctic (*Dissostichus mawsoni*; exclusively at SSI) and Patagonian (*D. eleginoides*) toothfish (Trathan and others 2014; Brooks and others 2018; GSGSSI 2023a). These fisheries operate in the deep-sea and are limited to depths between 700 and 2250 m (Belchier and others 2022; GSGSSI 2023a). Fisheries within the MPA are managed following a precautionary and ecosystem-based approach as applied by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) in its convention area (CAMLR 1980). The ecosystem-based management aims to use scientific knowledge in decision making, acknowledge uncertainty, and consider the biodiversity and the ecosystem connections (Trochta and others 2018). However, to fully implement this management approach, knowledge about the marine food web is crucial.

The Scotia Sea is one of the regions most affected by climate change in the Southern Ocean, with changes in environmental conditions (for example, warming) being recorded over recent decades (Whitehouse and others 2008; Murphy and others 2013; Fabri-Ruiz and others 2020; Rogers and others 2020; Xavier and others 2022). These changes are not limited to surface waters but are also altering and impacting the deep-sea and its communities (Rogers 2015; Rintoul 2018; Rogers and others 2020; Constable and others 2023; Li and others 2023). However, the communities' response to climate change is highly dependent on the structure of its marine food web (Post 2002a; Hette-Tronquart and others 2013; Pinsky and others 2020). Among food-web properties (for example,-connectance, modularity, etc), the food-chain length assumes a major role in determining the response of the community to climate change (Post 2002a). The food-chain length can be defined as the number of links between the primary producer and the top predator or simply as the highest trophic position in a food web, with the latter being able to be determined using trophic markers such as stable isotopes (Post 2002b, 2002a).

Food webs represent the predator–prey interactions in an ecosystem, and its structure underpins the function of the ecosystem (Dunne and others 2002). Previous research on the marine food web within the SGSSI MPA focussed on the pelagic and/or shelf environments but the demersal deep-sea component of the ecosystem, including benthopelagic coupling, remains largely overlooked (Stowasser and others 2009b, 2012a, 2012b; López-López and others 2022). Furthermore, there is generally scarce information on trophic interactions in the deep-sea ecosystems in this region (for example, Pilling and others 2001; Roberts and others 2011; Seco and others 2016; Queirós and others 2018).

Studying deep-sea marine food webs raise specific challenges compared to other marine food webs, due to the difficulty of direct observation of predator–prey interactions and the technical challenges related to deep-sea sampling (for example, costs, spatial resolution, organisms damaged by changes in pressure) (Iken and others 2001; Choy and others 2017; Parzanini and others 2018). Trophic proxies such as stable isotopes (mainly δ^{13}C and δ^{15}N) and fatty acids have been commonly used to overcome these challenges (Post 2002b; Newsome and others 2007; Stowasser and others 2009a; Kelly and Scheibling 2012; Drazen and Sutton 2017; Horswill and others 2018; Parzanini and others 2019; Queirós and others 2025). Values of δ^{13}C are relatively stable throughout the trophic levels and are used to determine the carbon source of the food web (DeNiro and Epstein 1978; McCutchan and others 2003; Cherel and Hobson 2007). In contrast, consumers are enriched in δ^{15}N in relation to their prey, so δ^{15}N values are used to determine the species' trophic position (McCutchan and others 2003; Vanderklift and Ponsard 2003; Bearhop and others 2004). Fatty acids are used on the principle that each organism presents a unique fatty acid profile, with some fatty acids being incorporated by the consumer without changes (Dalsgaard and others 2003; Kelly and Scheibling 2012; Drazen and Sutton 2017). Polyunsaturated $\omega3$ and $\omega6$ fatty acids are exclusively de novo synthesised by primary producers, with heterotrophic organisms being only capable of slightly modifying them through elongation and desaturation (Dalsgaard and others 2003; Couturier and others 2020; Graeve and Greenacre 2020). These modifications are limited by the presence of fatty acids desaturase, enzyme responsible to introduce double bounds between carbons, in organisms (Dalsgaard and others 2003). In contrast, saturated and monounsaturated fatty acids up to C18:0 can be synthesised by consumers, for example, fish (Dalsgaard and others 2003; Graeve and Greenacre 2020). Differences in the synthesis and modification of fatty acids enable the attribution of specific fatty acids to organisms such as C18:1ω7 which is produced by phytoplankton or bacteria whereas C18:1ω9 can be produced by several organisms, odd chain saturated fatty acids (for example, C15:0, C17:0) are characteristic from bacteria, or long chain monounsaturated fatty acids (for example, C20:1ω9, C22:1ω11) being characteristic of calanoid copepods (Dalsgaard and others 2003; Maar and others 2023; Papadimitraki and others 2023). Therefore, fatty acid profiles can provide information on the feeding strategy of the species such as carnivory, herbivory, or detritivory, and on the phytoplankton community, i.e. diatoms or dinoflagellates (Dalsgaard and others 2003; Kelly and Scheibling 2012; Papadimitraki and others 2023).

This study aims to determine the structure of Southern Ocean deep-sea food webs on a latitudinal gradient from SG to SSI (divided into north and south) and to consider how food-chain length varies across different Southern Ocean ecosystems. To accomplish these, we analysed stable isotopes and fatty acids in muscle of fish, and of prey species, found in their stomachs captured during toothfish fishing operations in the SGSSI MPA.

MATERIALS AND METHODS

Data Collection

Samples were collected during the 2020 toothfish fishing season at the SSI (March and April—CCAMLR Subarea 48.4) and SG (from May to August—CCAMLR Subarea 48.3) (Figure 1). Due to the environmental and ecological differences found along the north–south arc at SSI (Hollyman and others 2022; Thorpe and Murphy 2022; Queirós and others 2024b), we considered two different study areas, that is, the South Sandwich Islands—North (SSI-N) and South Sandwich Islands—South (SSI-S) (Figure 1).

Samples were obtained from fish captured between 600 and 1900 m depth aboard the *FV Nordic Prince* using an autoline longline system baited with Humboldt squid (*Dosidicus gigas;* (Fenaughty 2008)). As a conservation measure, fisheries are limited to depths between 700 and 2250 m, but some shallow fishing research lines (from 500 to 700 m) are undertaken by licensed vessels operating in the MPA, explaining the samples collected at 600 m. Additional samples were collected by scientific observers aboard *FV San Aspiring* (at SSI) and *FV Argos Froyanes* (at SG) using the same capture method and during the same period. Muscle samples of skates (*Amblyraja* sp.; presumably *A. georgiana* as this is the most common species by caught in these fisheries (Goodall-Copestake and others 2018)), blue antimora (*Antimora rostrata*), *D. eleginoides*, *D. mawsoni*, Caml grenadier (*Macrourus caml*), ridge scaled rattail (*M. carinatus*), bigeye grenadier (*M. holotrachys*), Whitson's grenadier (*M. whitsoni*), eel cod (*Muraenolepis* sp.) (and occasionally other fish species) were collected from the wing (*Amblyraja* sp.), the head (*Dissostichus* sp.), and the lateral body region (all other species). Muscle samples were preserved at −30 °C aboard fishing vessels.

Stomachs (n = 1268) from individuals captured in the longlines were also collected, bagged individually, and frozen at −30 °C. Most of the stomachs (≈ 85%) were collected from both *D. mawsoni* (at SSI) and *D. eleginoides* (both SSI and SG) though stomachs from non-target species (for example, *Amblyraja* sp., *Macrourus* spp., *A. rostrata*) were collected when non-everted. In the laboratory, stomachs were defrosted, and prey items identified to the lowest taxonomic level using published identification guides (for example, Gon and Heemstra 1990; Reid 1996; Xavier and others 2020; Xavier and Cherel 2021) and reference collections at King Edward Point Research Station (South Georgia), at British Antarctic Survey (United Kingdom) and at the University of Coimbra (Portugal). Muscle from fresh prey found in stomachs was sampled from the lateral body region (fish), buccal mass (cephalopods), abdomen and legs (crustaceans) and pectoral muscle (chinstrap penguin, *Pygoscelis antarctica*). Samples of Holothuria (body wall), Antipatharia (polyps) and Asteroidea (body) were also collected. Samples collected aboard and from prey species were transferred to freezers at −20 °C for stable isotopes and at −80 °C for fatty acids.

Stable Isotope Analyses

Muscle samples were lyophilised for 36 h. Once dry, samples were ground to powder and delipidated using three successive rinses of cyclohexane following Chouvelon and others (2011). Lipids are enriched in ^{13}C and due to different lipid content between species, delipidation is necessary to allow species comparison (DeNiro and Epstein 1977; Post and others 2007). However, chemical delipidation may influence δ^{15}N values, thus these values may be ≈0.25 ‰ higher than if non-delipidated (Post and others 2007). After delipidation, samples were dried overnight in an oven at 45 °C. No prior acidification was performed to remove inorganic carbon from Antipatharia and Asteroidea samples, therefore these are likely to be enriched in ^{13}C (Kolasinski and others 2008). Between 0.2 and 0.4 mg of sample were weighed into a tin capsule using a Mettler Toledo® XPR6UD5 microbalance. Isotope values of carbon (δ^{13}C) and nitrogen (δ^{15}N) were determined with a Continuous Flow Mass Spectrometer (Thermo Scientific® Delta V Plus—Isotope Ratio Mass Spectrometer) coupled with an elemental analyser (Thermo Scientific® Flash 2000). Results are presented following the conventional δ-notation in ‰. Values were calculated using Vienna Pee Dee Belemnite (VPDB) and atmospheric nitrogen (Air-N_2) as reference materials for carbon and nitrogen, respectively. Replicates of the certified reference materials USGS-61 and USGS-63 (Caffeine, United States Geological Survey) were performed throughout the analyses to assess the precision of the analyses (always < 0.10 ‰ and < 0.14 ‰ for δ^{13}C and δ^{15}N, respectively). Stable isotope analyses were performed at La Rochelle Université—Littoral, Environnement et Sociétés Laboratory (France).

Fatty Acid Analyses

Fatty acids were analysed in the same individuals used for stable isotopes. However, this analysis was not done for all individuals nor species as it requires, for example, a larger amount of sample which was not always possible to collect (for example, small sized individuals). Muscle for fatty acids was lyophilised for 72 h (Telstar, USA) and homogenised prior to fatty acid extraction and methylation following Gonçalves and others (2012). Briefly, 100 mg of sample were incubated with methanol to methylate the lipids. N-hexane was added to the samples and Fatty Acid Methyl Esters (FAMEs) extracted and separated from total lipids by centrifugation. The FA C19:0 in *n*-hexane (at 2 µg mL^{-1}) was added to each sample as an internal standard for FAME quantification. FAMEs were identified by Gas Chromatography—Mass Spectrometry (GC–MS) (Thermo Scientific®—Trace 1310 Gas Chromatographer) equipped with a Trace™ TR-FFAP GC Column (0.32 mm × 0.25 µm × 30 m, Thermo Scientific®). 1.00 µL of each sample was injected in spitless mode. GC-MS was performed using the following program: column temperature at 80 °C for 3 min; heating to 160 °C at a rate of 20 °C min^{-1}; heating up to 190 °C at a rate 2 °C min^{-1}; final heating to 220 °C at a rate 5 °C min^{-1}; and temperature of 220 °C hold for 10 min. Helium was used as carrier gas at a flow rate of 1.4 mL min^{-1}. Selective ion monitoring (SIM) acquisition was performed using a Thermo Scientific® ISQ 7000 targeting specific m/z. SIM allows the ions to be scanned multiple times increasing the signal to noise ratio, though it precludes the identification of peaks not included in the certified reference standard (Couturier and others 2020). FAME identification was performed by comparing the retention times of samples with those of the certified reference standard Supelco® 37 Component FAME Mix (CRM47885, Sigma-Aldrich®). Analyses were performed at Laboratório MAREFOZ—Universidade de Coimbra (Figueira da Foz, Portugal).

Peaks were integrated using the Thermo Xcalibur Quan Browse v4.1 software. Before quantification, peaks were cleaned for background contamination using the nearest instrument blank and normalised using the C19:0 peak area. FAME concentrations were calculated with a specific equation built for each peak using the chromatographic areas and corresponding known concentrations of the certified reference material. All concentrations are presented in dry weight. Throughout the analyses duplicates were performed to evaluate the accuracy of the readings (Coefficient of variation = 5.7%). Fatty acids were classified according to the number of double bonds: saturated fatty acids (SFA, zero double bonds), monounsaturated fatty acids (MUFA, one double bond), polyunsaturated fatty acids (PUFA, two or three double bonds) and highly unsaturated fatty acids (HUFA, four or more double bonds).

Data Analyses

Stable Isotopic Analyses

Layman metrics were calculated for each of the three studied food webs using the function *communityMetricsML* from the *SIBER* package (Jackson and Parnell 2023) in R Software (Layman and others 2007; R core team 2022). These metrics were used to determine the structure of the studied food webs and included the range of δ^{15}N (NR) and δ^{13}C (CR) values which represents the vertical and the horizontal structure of the web, respectively (i.e. larger NR represents more trophic levels and, consequently, higher trophic diversity, whereas larger CR suggest higher diversity in the base of the food web, suggesting different carbon sources); total area (TA) which is the convex hull area including all species in the δ^{15}N-δ^{13}C biplot space and represent the extent of the trophic diversity in the food web; mean distance to centroid (CD) which represents the average degree of trophic diversity within the food web and is calculated as the mean Euclidean distance of each species to the δ^{15}N-δ^{13}C centroid considering all species in the web (this metric is less sensible to the presence of outlier species in comparison with TA); mean nearest neighbour distance (MNND) which is the average of all species Euclidean distance to the nearest neighbour species in the web and measures the density of species packing in the web, being a measure for trophic redundancy, i.e. species with similar trophic niche; and standard deviation of nearest neighbour distance (SDNND) which measures the evenness of species distribution across the trophic niches (Layman and others 2007).

The trophic position of each individual was estimated using the equation: $TP = \frac{\delta^{15}N_{Individual} - 3.5}{3.4} + 2$, where 3.4 is the average increase in δ^{15}N that a marine predator exhibits in relation to its prey (Minagawa and Wada 1984; Post 2002b); 3.5 is the average δ^{15}N value for salp (*Salpa thompsoni*; primary consumer) measured in the last two studies in the Scotia Sea (Stowasser and others 2012a; Seco and others 2021); and 2 is the trophic position of *S. thompsoni*. We must be aware that *S. thompsoni* is a pelagic species and may exhibit some food preference, thus its use as a baseline organism may not be the most appropriate for deep-sea benthopelagic food webs (Pakhomov and others 2019). Yet, considering that *S. thompsoni* occurs in our three studied sites, as well across the Southern Ocean (Atkinson and others 2004; Liszka and others 2022; Yang and others 2022), its isotopic values are not affected by different chlorophyl *a* concentration such as the case of our study region and the entire Southern Ocean (Deppeler and Davidson 2017; Thorpe and Murphy 2022), and being commonly used in Southern Ocean food-web studies (for example, Cherel and others 2008, 2010; Stowasser and others 2012a), this species is appropriate to compare the food-web structure between our three study sites and with other food webs in the Southern Ocean.

Statistical tests were performed in GraphPad Prism v9.5.1 and considering α at 5%. Normal distribution and homogeneity of variances of δ^{13}C and δ^{15}N values for each species in each of the three study areas was tested using a Shapiro–Wilk normality test and a Bartlett's test. Differences in δ^{15}N values of species with a minimum of four samples in two of the three studied areas were tested to evaluate changes in trophic position with location. Differences between individuals of *M. caml* and *M. whitsoni* in the three study areas were tested using an ANOVA followed by a Tukey's multiple comparison test, while *A. rostrata* and *Muraenolepis* sp. were tested using a Kruskal–Wallis' test. Differences in *D. mawsoni*, *Nematocarcinus* sp. and euphausiids were tested with a *t*-test, whereas a Mann–Whitney test was used for *D. eleginoides* and *M. longimana*. Considering all species together, differences in δ^{13}C values between study areas were tested using a Kruskal–Wallis test proceeded by a Dunn's multiple comparison test. To evaluate the trophic enrichment of δ^{13}C values and the number of carbon sources in the studied food webs we did a Spearman correlation between δ^{13}C and δ^{15}N values.

Fatty Acids

In R software v4.2.2 (R core team 2022), we tested differences in species fatty acids signatures. We considered three divisions between species, that is, study area (SG, SSI-N, and SSI-S), taxonomic group (fish, cephalopods, crustaceans, and ''others'') and trophic level (that is, considered groups of 0.5 trophic level based on stable isotopes). Significant differences between groups were tested using a Permutational Analysis of Variance (PERMANOVA) using the function *adonis2* (method: Bray–Curtis; permutations: 999) from the *vegan* package (Oksanen and others 2022). Multiple comparisons were done by a Pairwise-PERMANOVA using the function *pairwise.adonis* (method: Bray–Curtis; permutations: 999) from *pairwiseAdonis* package (Arbizu 2020). To evaluate which fatty acids contributed to the differences between groups we did a Similarity Percentage (SIMPER) analysis using the

Table 1. δ^{13}C and δ^{15}N Values Measured in the Muscle (Except for Asteroidea, Antipatharia and Holothurian) of the Studied Species in the Three Study Areas

Species	South Georgia				South Sandwich Islands—North				South Sandwich Islands—South			
	n	δ^{13}C (‰)	δ^{15}N (‰)	C/N mass ratio	n	δ^{13}C (‰)	δ^{15}N (‰)	C/N mass ratio	n	δ^{13}C (‰)	δ^{15}N (‰)	C/N mass ratio
Fish												
Amblyraja sp.	11	−19.9 ± 0.3	12.7 ± 0.5	3.0 ± 0.2	0				2	−23.7 ± 0.1	11.2 ± 0.1	3.0 ± 0.2
Anotopterus pharao	0				0				1	−25.4	9.8	3.3
Antimora rostrata	11	−21.9 ± 0.5	11.5 ± 0.7	3.2 ± 0.0	4	−23.5 ± 0.1	11.2 ± 0.4	3.3 ± 0.0	5	−23.5 ± 0.2	11.6 ± 0.1	3.2 ± 0.0
Artedidraco sp.	0				0				1	−24.6	11.4	3.4
Bathydraco sp.	12	−21.2 ± 1.5	11.7 ± 1.0	3.4 ± 0.1	1	−23.0	12.4	3.3	0			
Bathylagus sp.	0				1	−23.4	11.5	3.3	0			
Champsocephalus gunnari	2	−21.0±0.8	10.2 ± 0.0	3.3 ± 0.0	0				0			
Channichthyidae	0				0				1	−24.3	11.9	3.2
Chionodraco rastrospinosus	1	−24.4	10.1	3.5	0				0			
Coryphaenoides armatus	0				0				10	−23.3±0.6	12.5 ± 0.3	3.2 ± 0.0
Dissostichus eleginoides	10	−21.3 ± 0.8	14.1 ± 1.3	3.3 ± 0.0	11	−22.5 ± 0.6	15.4 ± 0.6	3.3 ± 0.1	1	−23.2	14.8	3.3
Dissostichus mawsoni	0				6	−24.1 ± 0.5	13.5 ± 0.8	3.3 ± 0.1	13	−24.3 ± 0.5	14.7 ± 0.6	3.3 ± 0.1
Gymnoscopelus sp.	3	−22.4 ± 1.6	10.9 ± 0.4	3.5 ± 0.1	0				0			
Idiacanthus atlanticus	2	−20.1 ± 0.7	11.7 ± 0.2	3.3 ± 0.1	0				0			
Lepidonotothen sp.	6	−22.5 ± 0.6	10.0 ± 0.4	3.3 ± 0.1	0				0			
Lycenchelys antarctica	1	−21.0	11.4	3.4	0				0			
Macrourus caml	10	−22.1 ± 0.7	12.1 ± 0.7	3.3 ± 0.0	11	−23.2 ± 0.2	11.7 ± 0.4	3.2 ± 0.1	10	−23.8 ± 0.6	12.1 ± 0.6	3.3 ± 0.0
Macrourus carinatus	11	−20.7 ± 1.4	13.6 ± 1.0	3.2 ± 0.1	0				0			
Macrourus holotrachys	8	−20.3 ± 1.1	14.9 ± 0.4	3.2 ± 0.0	0				0			
Macrourus whitsoni	8	−20.3 ± 1.5	12.9 ± 0.6	3.3 ± 0.1	10	−23.3 ± 0.2	11.6 ± 0.3	3.2 ± 0.0	11	−23.9 ± 0.3	11.8 ± 0.4	3.3 ± 0.1
Melanostigma sp.	1	−22.0	13.0	3.5	0				0			
Muraenolepis sp.	9	−20.4 ± 1.3	12.2 ± 0.5	3.5 ± 0.1	8	−23.5 ± 0.2	12.0 ± 0.2	3.3 ± 0.1	17	−24.0 ± 0.5	12.4 ± 0.9	3.3 ± 0.1
Paraliparis sp.	1	−25.0	8.8	3.6	0				0			
Pogonophryne sp.	1	−21.7	12.0	3.5	0				0			
Stomiidae	2	−22.2 ± 0.5	12.1 ± 0.7	3.5 ± 0.0	0				0			
Unidentified	1	−21.2	14.0	3.2	0				0			
Cephalopoda												
Batoteuthis abyssicola	1	−24.1	10.6	3.7	0				0			
Chiroteuthis veranyi	3	−21.6 ± 0.8	11.9 ± 1.4	3.5 ± 0.1	0				0			
Filippovia knipovitchi	3	−24.4 ± 0.9	9.6 ± 1.1	3.5 ± 0.1	1	−22.2	9.3	3.4	4	−24.9 ± 0.7	8.9 ± 0.6	3.4 ± 0.2
Galiteuthis glacialis	0				0				4	−25.5 ± 1.5	9.5 ± 0.6	3.4 ± 0.2
Mesonychoteuthis hamiltoni	0				0				4	−24.5 ± 0.2	11.2 ± 0.7	3.5 ± 0.2
Moroteuthopsis longimana	4	−24.1 ± 0.8	7.1 ± 1.1	3.3 ± 0.1	2	−25.9 ± 0.6	10.1 ± 0.1	3.0 ± 0.0	14	−25.8 ± 1.3	9.0 ± 0.1	3.3 ± 0.1
Pareledone turqueti	4	−20.8 ± 0.4	11.1 ± 0.4	3.5 ± 0.1	0				0			
Psychroteuthis glacialis	1	−23.5	11.1	3.4	0				1	−25.2	9.6	3.2
Slozarczykovia circumantarctica	7	−24.9 ± 1.9	9.1 ± 1.7	3.8 ± 0.3	0				0			
Stauroteuthis gilchristi	6	−22.6 ± 1.4	9.7 ± 1.6	3.4 ± 0.3	0				0			
Taonius notalia	1	−23.4	8.3	3.4	0				0			

Table 1. continued

Species	South Georgia				South Sandwich Islands—North				South Sandwich Islands—South			
	n	δ^{13}C (‰)	δ^{15}N (‰)	C/N mass ratio	n	δ^{13}C (‰)	δ^{15}N (‰)	C/N mass ratio	n	δ^{13}C (‰)	δ^{15}N (‰)	C/N mass ratio
Crustacea												
Euphausiid	4	−22.7 ± 2.0	7.8 ± 1.4	3.3 ± 0.2	1	−23.3	6.5	3.6	5	−25.7 ± 0.6	6.0 ± 1.4	3.5 ± 0.1
Gammarid	3	−23.0 ± 0.8	9.3 ± 1.0	3.6 ± 0.5	0				0			
Gnathophausia	1	−22.4	10.1	3.3	0				0			
Isopod	3	−20.8 ± 0.9	11.0 ± 1.2	3.9 ± 0.4	0				0			
Nematocarcinus sp.	11	−22.8 ± 1.0	9.8 ± 1.0	3.4 ± 0.1	0				6	−25.6 ± 0.5	8.8 ± 0.4	3.4 ± 0.3
Paralomis sp.	3	−20.6 ± 2.0	12.6 ± 0.7	3.5 ± 0.0	2	−22.2 ± 0.1	12.5 ± 0.6	3.6 ± 0.0	0			
Pasiphae sp.	6	−22.6 ± 0.4	9.9 ± 0.9	3.4 ± 0.1	0				2	−25.4 ± 1.2	10.0 ± 0.9	3.3 ± 0.0
Thymops sp.	3	−22.4 ± 0.9	9.9 ± 0.4	3.5 ± 0.2	0				0			
Unidentified	1	−23.1	9.3	3.3	0				0			
Other												
Asteroidea	1	−22.6	10.4	3.4	0				0			
Antipatharia	1	−19.5	12.2	3.8	0				0			
Holothuria	1	−19.9	11.3	3.2	0				2	−24.1 ± 0.1	10.9 ± 0.2	3.5 ± 0.5
Pygoscelis antarctica	0				0				1	−24.5	7.5	3.5

Values are mean ± standard deviation

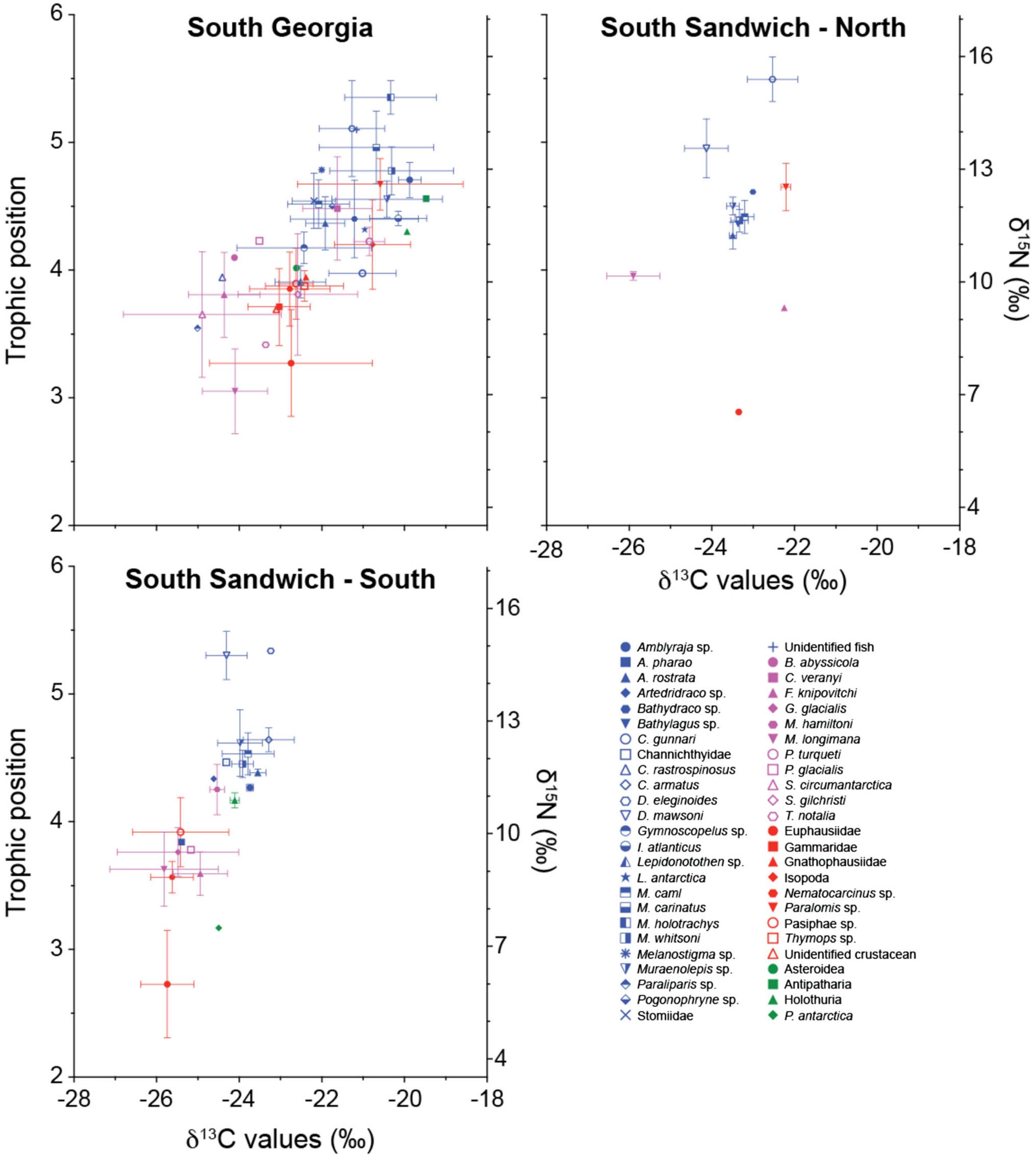

Figure 2. Trophic position, δ^{15}N and δ^{13}C values for the three studied areas. Colours define the taxonomic groups: blue—fish; pink—cephalopods; red—crustaceans; green—others. Values are mean ± standard deviation. Each plot can be seen in detail in the Online appendix A

function *simper* from *vegan* package (Oksanen and others 2022). A Principal Component Analysis (PCA) was performed for divisions with significant differences in PERMANOVA. PCA was performed using the function *prcomp* (scaled and centred) and plotted (including ellipses) using the function *fviz_pca_biplot* from *factoextra* package (Kassambara and Mundt 2020).

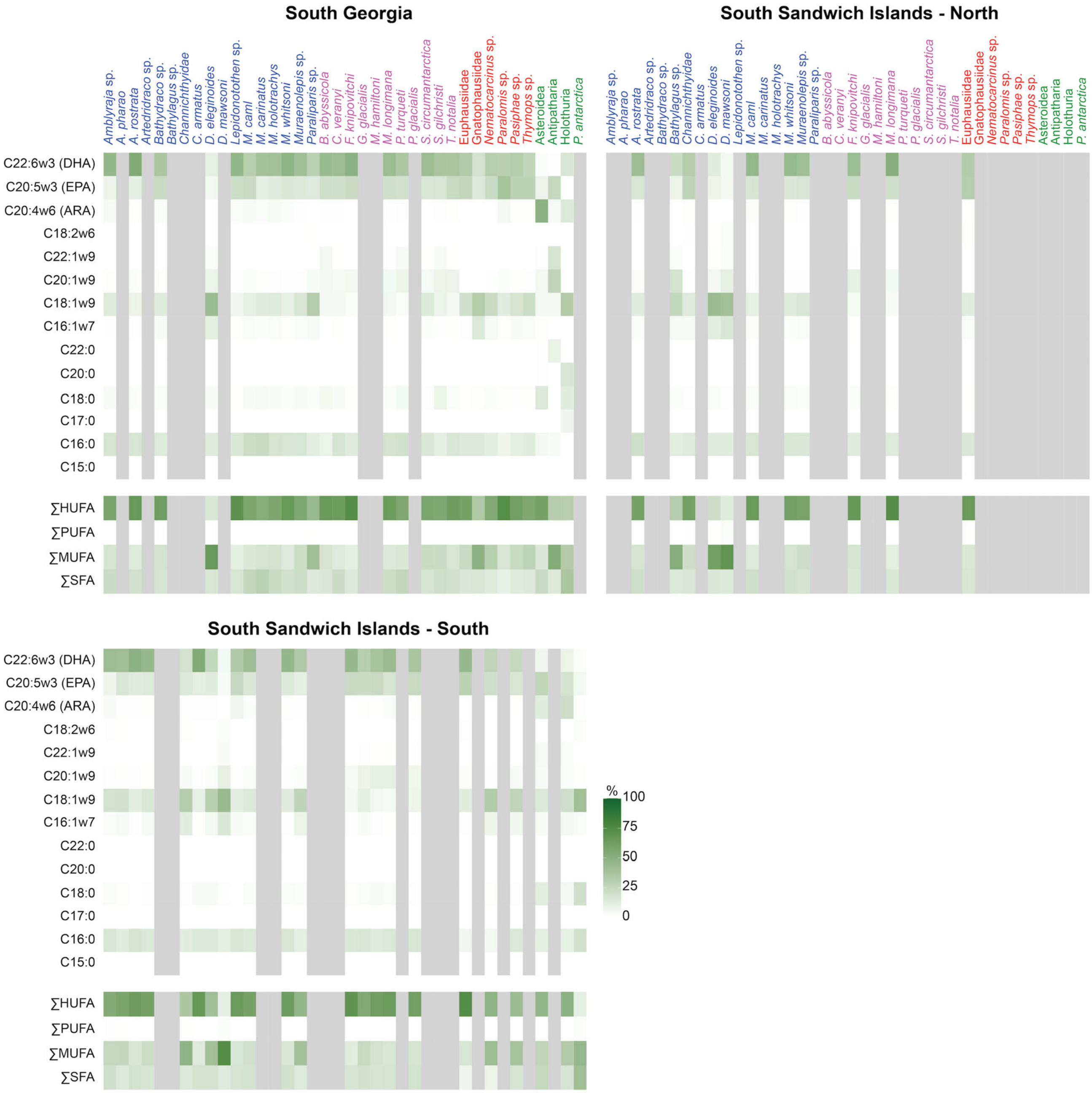

Figure 3. Heatmaps with the % of the different fatty acids in the muscle (except Asteroidea, Antipatharia and Holothurian) for the three studied areas. Colours in the name define the taxonomic groups: blue—fish; pink—cephalopods; red—crustaceans; green—others. Grey columns mean no sample of the species was analysed in this specific area. Each heatmap can be seen in detail in the Online appendix A

To evaluate the feeding strategy and the source of primary production we calculated the following ratios as indicators of carnivory/herbivory: EPA/DHA (EPA = Eicosapentaenoic Acid, C20:5ω3; DHA = Docosahexaenoic Acid, C22:6ω3), Σ(PUFA + HUFA)/ΣSFA and C16:1ω7/C16:0 (Dalsgaard and others 2003; Stowasser and others 2009b; Papadimitraki and others 2023). The ratio Σ(PUFA + HUFA)/ΣSFA is usually presented as ΣPUFA/ΣSFA but considering PUFA as the fatty acids with two or more double bounds, therefore, to accommodate the used classification we used both PUFA and HUFA (Papadimitraki and others 2023). The ratio (C16:1ω7 + EPA)/(C18:2ω6 +

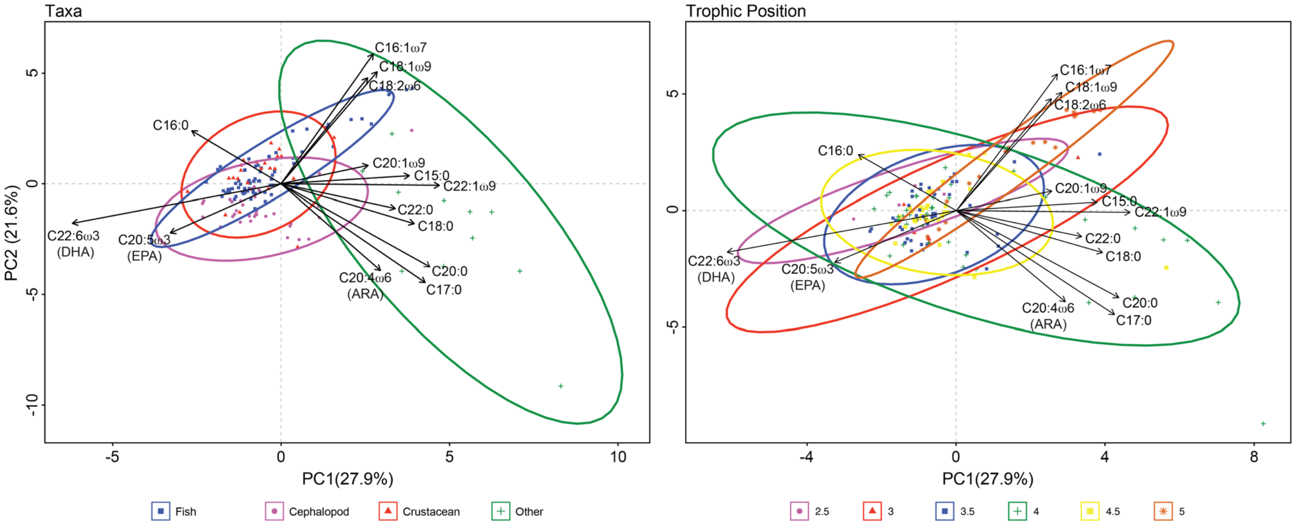

Figure 4. Principal component analysis (PCA) for the composition of fatty acids between Taxa (Left panel) and Trophic Position (right panel)

DHA) was used as an indicator of the phytoplankton community (diatom/dinoflagellate) (Dalsgaard and others 2003). The ratio C20:1ω9/DHA was used as an indicator of the copepod *Calanoides acutus* (Graeve and Greenacre 2020).

Results

Trophic Position, δ^{13}C and δ^{15}N Values at South Georgia and the South Sandwich Islands

Layman metrics varied across the three studied food webs. The smallest NR was found at SG, whereas both SSI areas had similar NR (Table 1). Contrasting, the largest CR was found at SG (δ^{13}C values ranged from −25.0 to −19.5 ‰), followed by SSI-N (δ^{13}C values between from −25.9 and −22.2 ‰) and SSI-S (δ^{13}C range from −25.8 to −23.2 ‰) with the smallest (Tables 1 and 2). Similarly, the TA decreased from SG to SSI-S, with SSI-N presenting an intermediate value though closer to SG (Table 1). The largest CD was found at SG, followed by SSI-S and with SSI-N presenting the lowest value (Table 1). Regarding the nearest neighbour distance, the highest MNND and SDNND were found at SSI-N, followed by SSI-S and SG (Table 1).

δ^{15}N values varied largely between species (Table 1), and consequently the calculated trophic position (mean ± standard deviation), ranged from the giant warty squid (*Moroteuthopsis longimana*; 3.1 ± 0.3) to *M. holotrachys* (5.4 ± 0.1) at SG; from euphausiids (2.9) to *D. eleginoides* (5.5 ± 0.2) at SSI-N; and from euphausiids (2.7 ± 0.4) to *Dissostichus* species (5.5 ± 0.2) at SSI-S (Table 1, Figure 2).

Significant differences in δ^{15}N values were found for *D. eleginoides* between SG and SSI-N and for *M. longimana* and *Nematocarcinus* sp. between SG and SSI-S (Table 2). Furthermore, significant differences were found *M. whitsoni* between the three areas, with multiple comparisons showing differences between SG and both SSI areas (Table 2). No other species showed significant differences in δ^{15}N values between studied areas (Table 2). Regarding δ^{13}C values, significant differences were found for between the three areas (Kruskal–Wallis: U = 176.0, $p < 0.0001$), with multiple comparison test showing differences between all areas (all $p < 0.0001$).

Significant correlations were found between δ^{13}C and δ^{15}N values for each of the three studied areas (Spearman correlation, SG: r = 0.692, $p < 0.0001$; SSI-N: r = 0.353, $p = 0.007$; SSI-S: r = 0.621, $p < 0.0001$).

Fatty Acid Composition of Species at South Georgia and the South Sandwich Islands

HUFA was the most abundant group of fatty acids in most of the studied species (Figure 3, Online appendix A). The exceptions were *D. eleginoides* at SG and SSI-N and *D. mawsoni* at both SSI-N and SSI-S, Gnathophausia and Antipatharia at SG, the

Table 2. Statistical Test Results for the Comparison of the δ^{15}N Values Between the Different Areas for Species with at Least Four Measurements in Two Different Areas

Species	Comparison	Test	*p*-value	Test value	Multiple Comparison
A. rostrata	SG (11) *vs* SSI-N (4) *vs* SSI-S (5)	Kruskal–Wallis	0.5455	F = 0.623	
D. eleginoides	SG (10) *vs* SSI-N (11)	Mann–Whitney	**0.0048**	U = 16.00	
D. mawsoni	SSI-N (6) *vs* SSI-S (13)	*t*-test	**0.0027**	t = 3.510	
Euphausiid	SG (4) *vs* SSI-S (5)	*t*-test	0.0956	t = 1.925	
M. caml	SG (10) *vs* SSI-N (11) *vs* SSI-S (10)	ANOVA	0.2296	F = 1.552	
M. whitsoni	SG (8) *vs* SSI-N (10) *vs* SSI-S (11)	ANOVA	< **0.0001**	F = 22.36	SG ≠ SSI-N; SG ≠ SSI-S
M. longimana	SG (4) *vs* SSI-S (14)	Mann–Whitney	**0.0248**	U = 7.000	
Muraenolepis sp.	SG (9) *vs* SSI-N (8) *vs* SSI-S (17)	Kruskal–Wallis	0.2398	F = 0.940	
Nematocarcinus sp.	SG (11) *vs* SSI-S (6)	*t*-test	**0.0384**	t = 2.270	

Number of samples analysed per study area in brackets. **Bold** *shows statistically significant results*

deep-sea smelt (*Bathylagus* sp.) at SSI-N and Channichthyidae and *P. antarctica* at SSI-S which had higher percentages of MUFA (Figure 3, Online appendix A). Considering all individuals, on average DHA (34 ± 15%) was the most common fatty acid, followed by EPA (18 ± 8%), C18:1ω9 (16 ± 12%; most common in *Dissostichus* species) and C16:0 (14 ± 5%) (Figure 3, Online appendix A).

PERMANOVA analyses showed significant differences in the fatty acid signatures between taxonomic groups and trophic levels (Table 3, Figure 4). Pairwise comparisons showed differences between all pairs of taxonomic groups (Table 3). SIMPER analysis showed that differences between fish, cephalopods and crustaceans are mainly due to concentrations of C18:1ω9 and C16:1ω7, though the separation of these groups with ''others'' is mostly created by the DHA, ARA (Arachidonic Acid, C20:4ω6) and C18:0 (Table 3, Figure 4). Regarding trophic levels, significant differences existed for almost all pairs, except for 3 with 3.5, and for 4 with 4.5 (Table 3). Species on trophic level 5 had higher abundance of C16:1ω7 and C20:1ω9 and lower abundance of C18:1ω9 and DHA while species on trophic level 2 differed due to higher concentration of C18:1ω9 and lower concentration of C18:0 and C20:1ω9 (Table 3, Figure 4).

EPA/DHA at SG varied between 0.21 ± 0.06 for *A. rostrata* and 15.7 for Anthipatharia (Table 4). At SSI-N this ratio varied between 0.35 ± 0.05 for *M. whitsoni* and 0.96 for euphausiids, while at SSI-S the lowest value was found for *Amblyraja* sp. (0.18 ± 0.08) and the highest for Asteroidea (6.85 ± 7.88) (Table 4). Regarding Σ(PUFA/HUFA)/ΣSFA, the highest values at SG were for lithodid crabs (*Paralomis* sp.; 8.12 ± 2.63) and the lowest for *D. eleginoides* (1.03 ± 0.27), at SSI-N the lowest and the highest were recorded for *D. mawsoni* (1.06 ± 0.17) and *M. longimana* (5.03 ± 1.93), respectively, and at SSI-S this ratio varied from 0.97 ± 0.16 for *D. mawsoni* and 10.5 ± 2.18 for euphausiids (Table 4). The ratio C16:1ω7/C16:0 showed a variation from 0.02 ± 0.02 in Turquet's octopus (*Pareledone turqueti*) to 0.88 ± 0.05 in *D. eleginoides* at SG (Table 4). The lowest values of this ratio in both SSI areas were measured in *M. longimana* (SSI-N = 0.04 ± 0.00; SSI-S = 0.06 ± 0.02), whereas the highest values were measured for *D. mawsoni* (1.28 ± 0.12) and the shrimp *Nematocarcinus* sp. (1.56 ± 0.82) at SSI-N and SSI-S, respectively (Table 4). (C16:1ω7 + EPA)/(C18:2ω6 + DHA) varied between 0.21 ± 0.04 (*Amblyraja* sp.) and 1.88 ± 1.60 (*Paralomis* sp.) at SG, between 0.41 ± 0.07 (*M. whitsoni*) and 2.35 ± 0.14 (*D. mawsoni*) at SSI-N, and between 0.23 ± 0.04 (abyssal grenadier, *Coryphaenoides armatus*) and 6.04 ± 5.76 (Asteroidea) at SSI-S (Table 4). Lastly, the C20:1ω9/DHA at SG varied from euphausiids (0.02) to Antipatharia (17.2), at SSI-N from euphausiids (0.01) to *D. mawsoni* (1.55 ± 0.60), and at SSI-S from plunderfish (*Artedidraco* sp.; 0.02) to *D. mawsoni* (1.77 ± 0.59) (Table 4).

DISCUSSION

Using fish captured in demersal longlines in the bathyal zone of the Southern Ocean as biological samplers granted us access to a variety of species and taxa spanning trophic levels that otherwise

Table 3. Results From PERMANOVA (and Respective Pairwise) and SIMPER Analysis for the Fatty Acids Concentration Between Region (SG, SSI-N and SSI-S), Taxonomic Group (Fish, Cephalopoda, Crustacea and ''Other'') and Trophic Position (in Groups of 0.5 Trophic Levels From the Estimated Trophic Position From δ^{15}N Values)

Variable	PERMANOVA		Pairwise PERMANOVA				SIMPER					
	F	*p*	Comparison			*p*	FA	%	FA	%	FA	%
Region	1.67	0.094										
Taxonomic group	23.89	**0.001**	Fish	*vs*	Cephalopoda	**0.001**	C18:1ω9	**0.15**	C20:1ω9	**0.30**	C16:1ω7	**0.43**
			Fish	*vs*	Crustacea	**0.001**	C20:5ω3	**0.12**	C16:1ω7	0.24	C18:1ω9	0.36
			Fish	*vs*	Other	**0.001**	C22:6ω3	**0.15**	C20:4ω6	**0.28**	C18:0	**0.37**
			Cephalopoda	*vs*	Crustacea	**0.001**	C20:1ω9	**0.17**	C18:1ω9	**0.34**	C16:1ω7	**0.47**
			Cephalopoda	*vs*	Other	**0.001**	C22:6ω3	**0.15**	C20:4ω6	**0.30**	C18:0	**0.39**
			Crustacea	*vs*	Other	**0.001**	C20:4ω6	**0.15**	C22:6ω3	**0.28**	C18:0	**0.40**
Trophic position	5.82	**0.001**	5	*vs*	4.5	**0.001**	C16:1ω7	**0.15**	C22:6ω3	**0.30**	C20:1ω9	**0.42**
			5	*vs*	4	**0.001**	C16:1ω7	**0.14**	C22.6ω3	**0.26**	C18:1ω9	**0.39**
			5	*vs*	3.5	**0.001**	C16:1ω7	**0.14**	C18:1ω9	**0.28**	C22:6ω3	**0.41**
			5	*vs*	3	**0.022**	C16:1ω7	**0.17**	C18:1ω9	**0.31**	C22:6ω3	**0.45**
			5	*vs*	2.5	**0.001**	C20:5ω3	**0.14**	C18:1ω9	**0.27**	C20:1ω9	**0.52**
			4.5	*vs*	4	0.166						
			4.5	*vs*	3.5	**0.005**	C20:1ω9	0.14	C18:1ω9	0.27	C16:1ω7	0.37
			4.5	*vs*	3	0.542						
			4.5	*vs*	2.5	**0.010**	C18:0	**0.16**	C20:1ω9	0.28	C18:1ω9	0.39
			4	*vs*	3.5	**0.004**	C20:4ω6	**0.12**	C18:0	**0.23**	C20:1ω9	0.35
			4	*vs*	3	0.659						
			4	*vs*	2.5	**0.046**	C18:0	**0.15**	C20:1ω9	0.27	C20:4ω6	0.38
			3.5	*vs*	3	0.540						
			3.5	*vs*	2.5	**0.027**	C20:1ω9	**0.17**	C18:1ω9	0.30	C18:0	0.42
			3	*vs*	2.5	**0.023**	C18:0	**0.16**	C20:1ω9	**0.32**	C18:1ω9	0.43

Bold *shows statistically significant results*

would be difficult to sample, especially at the SSI (Collins and others 2022; Queirós and others 2024b). Utilising stable isotopes and fatty acids as trophic proxies enabled us to determine the structure of the Southern Ocean deep-sea food web on a latitudinal gradient from SG to SSI-S. The three food webs have several similarities, including similar trophic diversity (most notably the presence of 5 trophic levels) and high trophic redundancy with species in the studied food webs presenting similar trophic ecologies. The 5th trophic level was exclusively composed of fish, the 4th trophic level mainly occupied by fish and the 3rd trophic level mostly populated by cephalopods and crustaceans. These three trophic levels comprise most of the species studied here and represent carnivorous/omnivorous species as shown by the high percentages of DHA and C18:1ω9 (Dalsgaard and others 2003; Papadimitraki and others 2023). Euphausiids at both SSI locations were the only species on the 2nd trophic level. Benthic species like starfish (Asteroidea), sea cucumbers (Holothuria) and black corals (Antipatharia) were attributed to the 4th trophic level. Yet, fatty acids indicated that these species belong to a specific section of the food web, with higher concentrations of C18:0 suggesting Asteroidea and Holothurians as detritivores, while higher concentrations of C20:1ω9 suggest Antipatharia as suspension feeders of zooplankton (mostly copepods). Both the presence of 5 trophic levels and the benthic species in the 4th trophic level may relate to the chosen baseline, that is, *S. thompsoni* which is a species from the pelagic component of the food web and, due to the δ^{15}N enrichment of benthic pathways may be overestimating the trophic position of species from, and related, the benthic pathway (discussed below). Some differences also exist between food webs, with the SG food web presenting a higher diversity in the primary producers' community when compared to the SSI food webs, though always dependent on diatom-based detritus. Furthermore, differences exist in the trophic position of some species in the three food webs (for

Table 4. Ratios Between Different Fatty Acids for the Different Species In the Three Sampling Areas

Species	South Georgia					
	n	$\frac{EPA}{DHA}$	$\frac{\Sigma PUFA \pm \Sigma HUFA}{\Sigma SFA}$	$\frac{C16{:}1\omega7}{C16{:}0}$	$\frac{C16{:}1\omega7 \pm EPA}{C18{:}2\omega6 \pm DHA}$	$\frac{C20{:}1\omega9}{DHA}$
Fish						
Amblyraja sp.	3	0.18 ± 0.04	2.64 ± 0.13	0.08 ± 0.01	0.21 ± 0.04	0.04 ± 0.01
A. pharao	0					
A. rostrata	3	0.21 ± 0.06	3.40 ± 0.48	0.09 ± 0.01	0.23 ± 0.06	0.04 ± 0.01
Artedidaco sp.	0					
Bathydraco sp.	4	0.67 ± 0.18	3.60 ± 0.22	0.28 ± 0.14	0.76 ± 0.19	0.05 ± 0.01
Bathylagus sp.	0					
Channichthyidae	0					
C. armatus	0					
D. eleginoides	3	0.56 ± 0.11	1.03 ± 0.27	0.88 ± 0.05	1.59 ± 0.26	0.91 ± 0.46
D. mawsoni	0					
Lepidonotothen sp.	3	0.48 ± 0.04	4.27 ± 0.68	0.12 ± 0.03	0.51 ± 0.06	0.03 ± 0.01
M. caml	3	0.79 ± 0.36	2.35 ± 0.66	0.13 ± 0.03	0.87 ± 0.36	0.09 ± 0.03
M. carinatus	3	0.25 ± 0.09	2.33 ± 1.49	0.10 ± 0.02	0.32 ± 0.04	0.06 ± 0.05
M. holotrachys	3	0.34 ± 0.02	2.68 ± 0.69	0.17 ± 0.11	0.40 ± 0.03	0.05 ± 0.02
M. whitsoni	3	0.33 ± 0.07	3.34 ± 0.07	0.11 ± 0.01	0.37 ± 0.07	0.03 ± 0.01
Muraenolepis sp.	4	0.37 ± 0.07	2.72 ± 0.51	0.17 ± 0.05	0.44 ± 0.08	0.06 ± 0.05
Paraliparis sp.	1	0.47	3.21	0.36	0.59	0.14
Cephalopoda						
B. abyssicola	1	0.48	4.27	0.10	0.50	0.15
C. veranyi	1	0.49	2.86	0.08	0.52	0.12
F. knipovitchi	2	0.49 ± 0.11	4.99 ± 0.95	0.06 ± 0.06	0.50 ± 0.12	0.12 ± 0.01
G. glacialis	0					
M. hamiltoni	0					
M. longimana	3	0.48 ± 0.09	3.02 ± 0.74	0.06 ± 0.02	0.50 ± 0.09	0.14 ± 0.01
P. turqueti	2	0.62 ± 0.29	2.38 ± 1.25	0.02 ± 0.02	0.63 ± 0.29	0.25 ± 0.15
P. glacialis	0					
S. circumantarctica	4	0.50 ± 0.26	5.91 ± 4.56	0.17 ± 0.10	1.26 ± 1.68	1.35 ± 2.58
S. gilchristi	3	0.47 ± 0.07	2.74 ± 0.37	0.14 ± 0.04	0.50 ± 0.09	0.23 ± 0.10
T. notalia	1	0.66	3.17	0.09	0.70	0.22
Crustacea						
Euphausiid	1	0.79	3.93	0.14	0.83	0.02
Gnathophausia	1	0.75	2.12	1.08	1.52	0.03
Nematocarcinus sp.	3	0.76 ± 0.09	3.95 ± 0.43	0.43 ± 0.19	0.91 ± 0.10	0.06 ± 0.07
Paralomis sp.	3	1.83 ± 1.62	8.12 ± 2.63	0.20 ± 0.10	1.88 ± 1.60	0.13 ± 0.10
Pasiphaea sp.	3	0.94 ± 0.19	7.03 ± 6.54	0.35 ± 0.15	1.06 ± 0.25	0.04 ± 0.01
Thymops sp.	3	1.07 ± 0.08	4.06 ± 0.36	0.28 ± 0.11	1.17 ± 0.05	0.07 ± 0.07
Other						
Asteroidea	1	3.49	2.58	0.30	3.25	2.49
Antipatharia	1	15.7	2.19	0.21	13.7	17.2
Holothuria	1	0.00	0.85	n.f	0.00	0.00
P. antarctica	0					

Species	South Sandwich Islands—North					
	n	$\frac{\mathrm{EPA}}{\mathrm{DHA}}$	$\frac{\Sigma\mathrm{PUFA}\pm\Sigma\mathrm{HUFA}}{\Sigma\mathrm{SFA}}$	$\frac{\mathrm{C}16{:}1\omega7}{\mathrm{C}16{:}0}$	$\frac{\mathrm{C}16{:}1\omega7\pm\mathrm{EPA}}{\mathrm{C}18{:}2\omega6\pm\mathrm{DHA}}$	$\frac{\mathrm{C}20{:}1\omega9}{\mathrm{DHA}}$
Fish						
Amblyraja sp.	0					
A. pharao	0					
A. rostrata	1	0.40	2.96	0.13	0.46	0.05
Artedidaco sp.	0					
Bathydraco sp.	0					
Bathylagus sp.	1	0.37	2.19	0.40	0.56	0.83
Channichthyidae	1	0.87	3.89	0.36	0.99	0.06
C. armatus	0					
D. eleginoides	3	0.64 ± 0.02	1.49 ± 0.47	0.94 ± 0.12	1.47 ± 0.26	0.48 ± 0.13
D. mawsoni	3	0.94 ± 0.07	1.06 ± 0.17	1.28 ± 0.12	2.35 ± 0.14	1.55 ± 0.60
Lepidonotothen sp.	0					
M. caml	3	0.38 ± 0.06	3.16 ± 0.09	0.12 ± 0.03	0.42 ± 0.06	0.03 ± 0.01
M. carinatus	0					
M. holotrachys	0					
M. whitsoni	3	0.35 ± 0.05	3.16 ± 0.16	0.16 ± 0.07	0.41 ± 0.07	0.04 ± 0.03
Muraenolepis sp.	3	0.42 ± 0.08	3.20 ± 0.39	0.22 ± 0.11	0.49 ± 0.10	0.03 ± 0.02
Paraliparis sp.	0					
Cephalopoda						
B. abyssicola	0					
C. veranyi	0					
F. knipovitchi	1	0.55	4.21	0.08	0.57	0.24
G. glacialis	0					
M. hamiltoni	0					
M. longimana	2	0.41 ± 0.09	5.03 ± 1.93	0.04 ± 0.00	0.42 ± 0.09	0.11 ± 0.00
P. turqueti	0					
P. glacialis	0					
S. circumantarctica	0					
S. gilchristi	0					
T. notalia	0					
Crustacea						
Euphausiid	1	0.96	3.99	0.22	1.01	0.01
Gnathophausia	0					
Nematocarcinus sp.	0					
Paralomis sp.	0					
Pasiphaea sp.	0					
Thymops sp.	0					
Other						
Asteroidea	0					
Antipatharia	0					
Holothuria	0					
P. antarctica	0					

Species	South Sandwich Islands—South					
	n	$\frac{EPA}{DHA}$	$\frac{\Sigma PUFA \pm \Sigma HUFA}{\Sigma SFA}$	$\frac{C16:1\omega7}{C_{16:0}}$	$\frac{C16:1\omega7 \pm EPA}{C_{18:2\omega6} \pm DHA}$	$\frac{C20:1\omega9}{DHA}$
Fish						
Amblyraja sp.	2	0.18 ± 0.08	2.70 ± 0.22	0.16 ± 0.05	0.24 ± 0.11	0.05 ± 0.01
A. pharao	1	0.39	4.13	0.33	0.48	0.04
A. rostrata	3	0.27 ± 0.02	3.29 ± 0.27	0.12 ± 0.04	0.31 ± 0.03	0.05 ± 0.02
Artedidaco sp.	1	0.30 ± 0.00	3.50	0.30	0.40	0.02
Bathydraco sp.	0					
Bathylagus sp.	0					
Channichthyidae	1	0.77 ± 0.00	2.48	1.02	1.33	0.20
C. armatus	3	0.21 ± 0.04	3.58 ± 0.16	0.09 ± 0.01	0.23 ± 0.04	0.03 ± 0.01
D. eleginoides	1	0.48 ± 0.00	2.18	0.44	0.72	0.12
D. mawsoni	3	0.72 ± 0.14	0.97 ± 0.16	1.48 ± 0.39	2.47 ± 0.47	1.77 ± 0.59
Lepidonotothen sp.	1	0.74 ± 0.00	3.80	0.23	0.84	0.04
M. caml	3	0.39 ± 0.06	3.20 ± 0.12	0.18 ± 0.04	0.45 ± 0.07	0.06 ± 0.02
M. carinatus	0					
M. holotrachys	0					
M. whitsoni	3	0.32 ± 0.04	3.19 ± 0.33	0.14 ± 0.04	0.36 ± 0.04	0.03 ± 0.01
Muraenolepis sp.	3	0.31 ± 0.06	3.34 ± 0.31	0.80 ± 0.50	0.56 ± 0.19	0.08 ± 0.03
Paraliparis sp.	0					
Cephalopoda						
B. abyssicola	0					
C. veranyi	0					
F. knipovitchi	3	0.53 ± 0.07	4.01 ± 1.02	0.08 ± 0.03	0.55 ± 0.08	0.11 ± 0.05
G. glacialis	3	0.79 ± 0.26	2.84 ± 0.62	0.23 ± 0.15	0.92 ± 0.38	0.31 ± 0.21
M. hamiltoni	3	0.64 ± 0.14	3.54 ± 0.25	0.15 ± 0.03	0.69 ± 0.13	0.27 ± 0.11
M. longimana	4	0.44 ± 0.11	3.57 ± 0.81	0.06 ± 0.02	0.47 ± 0.12	0.25 ± 0.21
P. turqueti	0					
P. glacialis	1	0.65	3.21	0.12	0.70	0.19
S. circumantarctica	0					
S. gilchristi	0					
T. notalia	0					
Crustacea						
Euphausiid	3	0.69 ± 0.33	10.5 ± 2.18	0.39 ± 0.37	0.72 ± 0.31	0.06 ± 0.05
Gnathophausia	0					
Nematocarcinus sp.	4	0.75 ± 0.08	6.47 ± 2.09	1.56 ± 0.82	1.02 ± 0.13	0.05 ± 0.03
Paralomis sp.	0					
Pasiphaea sp.	2	0.69 ± 0.08	6.38 ± 7.72	0.48 ± 0.15	1.01 ± 0.46	0.14 ± 0.01
Thymops sp.	0					
Other						
Asteroidea	4	6.85 ± 7.88	2.31 ± 1.94	0.47 ± 0.23	6.04 ± 5.76	0.58 ± 0.08
Antipatharia	0					
Holothuria	3	2.74 ± 2.48	3.23 ± 2.09	0.72 ± 0.25	3.15 ± 2.21	0.27 ± 0.07
P. antarctica	1	2.52	0.32	0.17	1.87	0.57

Values are mean ± standard deviation.

Table 5. Review of the Food-Chain Lengths Recorded in Different Studies Across the Southern Ocean

Location	Food Web	FCL	Top predator	Method	References
South Sandwich Islands (North)	Benthopelagic	5.5	*Dissostichus eleginoides*	Stable isotopes	This study
South Sandwich Islands	Benthopelagic	5.5	*Dissostichus eleginoides*	Stable isotopes	(Queirós and others 2025)
Ross Sea	Pelagic/Benthopelagic	≈5.5[1]	Large demersal fish *Physeter macrocephalus* *Orcinus orca*	Modelling	(Pinkerton and Bradford-Grieve 2014)
South Georgia	Benthopelagic	5.4	*Macrourus holotrachys*	Stable isotopes	This study
Ross Sea	Coastal benthopelagic[4]	5.4[5]	*Trematomus hansoni* *Chionodraco hamatus*	Stable isotopes	(Rossi and others 2019)
South Sandwich Islands (South)	Benthopelagic	5.3	*Dissostichus mawsoni* *Dissostichus eleginoides*	Stable isotopes	This study
Pridz Bay (East Antarctica)	Pelagic	5.3	*Physeter macrocephalus*	Modelling	(McCormack and others 2020)
Kerguelen Islands	Pelagic	5.3[2]	*Talassarche melanophrys*	Stable isotopes	(Cherel and others 2010)
Scotia Sea	Pelagic	5.2	*Macronectes halli*	Stable isotopes	(Stowasser and others 2012a)
Antarctic Peninsula	Pelagic	5.0[3]	*Orcinus orca* *Hydrurga leptonyx*	Modelling	(Murphy and others 2013)
Scotia Sea	Pelagic	5.0[3]	*Orcinus orca* *Hydrurga leptonyx*	Modelling	(Murphy and others 2013)
Fildes Bay (Antarctica Peninsula)	Coastal benthopelagic	4.9	*Harpagifer antarcticus*	Stable isotopes	(Zenteno and others 2019)
Windmill Island (East Antarctica)	Coastal benthopelagic	4.9	*Notothenia corriceps*	Stable isotopes	(Gillies and others 2012)
Adélie Land (East Antarctica)	Pelagic	4.6	*Aptenodytes forsteri*	Stable isotopes	(Cherel 2008)
Weddell Sea	Pelagic	4.3	*Oceanites oceanicus*	Stable isotopes	(Rau and others 1992)
Potter Cove (Antarctic Peninsula)	Coastal benthic	4.3	*Urticinopsis antarctica*	Feeding links	(Marina and others 2018)
Rothera Point (Antarctic peninsula)	Coastal benthic	4.0[5]	*Odontaster validus*	Stable isotopes	(Cardona and others 2021)
Cierva Cove (Antarctic peninsula)	Coastal benthic	3.9[5]	*Odontaster validus*	Stable isotopes	(Cardona and others 2021)
Paradise Harbour (Antarctic peninsula)	Coastal benthic	3.9[5]	*Diplasterias brulei*	Stable isotopes	(Cardona and others 2021)
Fildes Bay (Antarctic peninsula)	Coastal benthic	3.8[5]	*Odontaster validus*	Stable isotopes	(Cardona and others 2021)
Esperanza Bay (Antarctic peninsula)	Coastal benthic	3.8[5]	*Odontaster validus*	Stable isotopes	(Cardona and others 2021)
Adélie land (East Antarctica)	Coastal benthic	3.3[5]	*Isotalia antarctica*	Stable isotopes	(Michel and others 2019)

[1] *Approximate trophic position according to the position of the node on the figure;* [2] *A trophic level of 6.1 can be estimated for Mesonychoteuthis hamiltoni though it measures de* δ^{15}*N values in the beak and converts to muscle afterwards (Cherel and others 2010);* [3] *estimated general structure model for the Antarctic Peninsula and Scotia Sea ecosystem;* [4] *whereas this study focus in a coastal area, the studied food web includes species from deeper areas of the water column, including the species that have the highest trophic position that are known to inhabit waters up to 600 m deep;* [5] *value estimated using the equation ''TP =* $(\delta^{15}$*N reported in the study—3.5)/3.4 + 2''*

Only studies analysing different species within the same food web were considered. For studies analysing stable isotopes of δ^{15}*N but did not calculate the trophic level, we used the highest* δ^{15}*N values recorded in the study and estimated the food-chain length (FCL) with the trophic position equation used in this study. Top Predator is the species with the highest trophic level in the study. Food webs are ordered by the longest to the shortest food web*

example, *M. whitsoni* and *M. longimana*), and in the top predators with *Dissostichus* spp. being in the highest trophic position in both SSI study areas, whereas at SG this position was occupied by *M. holotrachys*.

The three deep-sea food webs studied here presented a FCL ranging from 5.3 to 5.5. We must be aware that the δ^{15}N enrichment of benthic pathways and the use of *S. thompsoni* as baseline species, may overestimate these FCLs, suggesting that benthopelagic food webs in the Southern Ocean may be shorter. Yet, previous modelling studies showed large demersal fish (for example, toothfish) in the 5th trophic level (though some studies showed these species close to the 5th trophic level, but still in the 4th (McCormack and others 2020)), supporting FCLs of five trophic levels in deep-sea Southern Ocean benthopelagic food webs (Pinkerton and Bradford-Grieve 2014). Compared to coastal and pelagic food webs in the Southern Ocean, our results suggest that deep-sea food webs (including both pelagic and benthic/demersal species) have longer food chains (for example, Stowasser and others 2012a; Marina and others 2018). This pattern seems to differ from other oceans worldwide, where shelf systems appear to present longer food chains to those in open water system (Christensen and Pauly 1993). Though previous studies also found longer food webs in the Arctic Ocean deep-sea than those in the shelf areas (reviewed in Kędra and others 2015). Furthermore, studies on deep-sea communities showed that food webs can have 3 (for example, Porcupine Abyssal Plain—NE Atlantic (Iken and others 2001)), 4 (for example, Cape Flattery—NE Pacific (Boyle and others 2012) and Canada Arctic basin (Iken and others 2005)) and 5 trophic levels (for example, Azores (North Atlantic) (Morato and others 2016), HAUSGARTEN (Arctic Ocean, deep-sea observatory from Alfred Wegener Institute (Bergmann and others 2009) and Galicia Bank—NE Atlantic (Preciado and others 2017)). In contrast, a food web from the shelf of Perú and including benthopelagic coupling, that is, presence of benthic, demersal and pelagic fauna, showed a food web including 6 trophic levels (Ñacari and others 2023) and another study in the continental margin of the NW Atlantic found a food web including almost 5 trophic levels (Parzanini and others 2019). Therefore, these results may suggest differences in the food-chain length between Southern Ocean and other oceans. Though, as the length of deep-sea food webs seem to be region-dependent, it is important that further studies study benthopelagic deep-sea food webs in other regions of the Southern Ocean. Furthermore, it is important that future studies also look to food webs including the benthopelagic coupling in shelf areas to determine if these are longer than those from the deep-sea.

Knowing the food-web structure is crucial to manage toothfish fisheries following the precautionary and ecosystem-based approach (Trochta and others 2018; Belchier and others 2022), as it is important to understand the impacts of reducing the abundance of target and non-target species on the ecosystem. Our results show the position in the marine food web of the target (*D. mawsoni* and *D. eleginoides*) and main bycatch species (for example, *Macrourus* spp. and *Amblyraja* sp.) within this fishery, allowing us to better evaluate the effects of their capture and develop better predation-release scenarios resulting from these fisheries (Pinkerton and Bradford-Grieve 2014; Queirós and others 2022). For example, it is estimated that the current spawning stock biomass of *D. eleginoides* at SG is at 47% of the pre-exploitation biomass (Trathan 2023). Therefore, predation pressure on its prey, some of which are also caught as bycatch at SG such as *Muraenolepis* sp. and *Macrourus* spp., decrease, potentially leading to an increase of its biomass (unpublished data; Pilling and others 2001; Fitzcharles and others 2021). Being in the 4th trophic level, changes in the biomass of *Muraenolepis* sp. could consequently cascade through the trophic levels below, but also influence the bycatch of this species in this fishery (Pinkerton and Bradford-Grieve 2014; Queirós and others 2022).

A limitation of this study is the estimation of the trophic position using an equation that is better suitable for food webs with a single source, that is, typical pelagic food web (Post 2002b). However, benthopelagic food webs have multiple sources of energy and, consequently multiple pathways, including the benthic pathway where nutrients are recycled and it is typically enriched in ^{15}N (Iken and others 2001; Post 2002b; Preciado and others 2017; Kiljunen and others 2020). Therefore, the use of a single source equation, together with the use of a pelagic baseline (discussed above), potentially overestimates the trophic position of the species in our food webs. The 2-end member approach would be best suitable to estimate the trophic position in our food webs (Post 2002b; Bergmann and others 2009). However, this approach requires previous knowledge on the importance of each trophic pathway in the food web; or on the diet of the different species in the food webs so we could use a Bayesian approach to estimate the contribution of the pelagic- and benthic pathway to each species and, ultimately, estimate the trophic position of each species (Post 2002b; Kiljunen and others 2020). None of this information is currently available for the Southern Ocean benthopelagic food webs, nor to most species studied here. By the importance of benthopelagic ecosystems in the Southern Ocean, it is urgent that we fulfil these gaps so we can better estimate the trophic position of the different species and, ultimately, have a more detailed picture of the structure and functioning of these food webs. Future studies should use different methodologies including, but not limited to, stomach content analyses (using both visual analyses and DNA metabarcoding), compound specific stable isotopes (CSIA), sulphur stable isotopes (δ^{34}S), or build a functional trait food web to understand which is the importance of benthic and trophic pathways in the different species (yet, for this methodology a good knowledge of the biodiversity of the region and feeding ecology is needed) (Newsome and others 2007; King and others 2008; Gravel and others 2016; McMahon and Newsome 2019). Despite these limitations, our study provides the first assessment of the structure of benthopelagic food webs in the Southern Ocean across different environments (from warmer subantarctic to colder Antarctic environments) and in a region impacted by climate change such as the Scotia Sea, being a first step towards to the understanding of the structure and functioning of these ecosystems.

Deep-Sea Food-Web Structure at South Georgia and the South Sandwich Islands

This study found that, despite some variability, the structure of the food webs is similar across the study areas. Community-wide metrics showed similar vertical structure with the range of δ^{15}N values varying by only 1 ‰, suggesting a difference of ≈0.3 trophic levels between the shortest food web at SG and the longest at SSI-N (Minagawa and Wada 1984; Layman and others 2007). This difference mostly arises by different euphausiids found in both study areas, with herbivorous species at SSI and carnivorous/omnivorous species at SG which is reflected by the ^{15}N enrichment by euphausiids at SG (discussed below). Our food webs presented lower NR than coastal food webs at Esperanza Bay (NR ≈11 ‰) and Rothera Point (NR ≈9 ‰) in the Antarctic Peninsula and Terra Nova Bay (NR ≈13.5 ‰) in the Ross Sea (Rossi and others 2019; Cardona and others 2021). This difference may suggest shorter food webs in the Southern Ocean deep-sea in comparison with coastal food webs, however such difference arises from the species analysed in each study. Previous studies included phytoplankton and particulate organic matter in their food webs, thus the range of δ^{15}N values includes primary producers, whereas our study only includes consumers, that is, starting in the 2nd trophic level (Rossi and others 2019; Cardona and others 2021). This is supported by the lowest δ^{15}N values in the three studies, that is, 6.0 ‰ in our study, ≈1.5 ‰ in the Antarctic Peninsula and ≈0 ‰ in the Ross Sea, and the highest estimated trophic position for each food web (discussed below; Rossi and others 2019; Cardona and others 2021). The lower values of CD, MNND and SDNND showed that the three food webs present high trophic redundancy, suggesting that the studied species have a similar trophic ecology (Layman and others 2007). This is supported by the high concentration of fatty acids indicators of carnivory in the studied species, and by the high levels of omnivory found in the Southern Ocean oceanic food webs (Stowasser and others 2012a; de Santana and others 2013). Nonetheless, SSI-N presented higher MNND and SDNND values than the two other studied food webs. This is explained by the lower number of species included in this food web compared to SG and SSI-S, leading to a lower packing of the species (Layman and others 2007). This similarity is supported by the TA values between SG and SSI-N that suggest similar trophic diversity in both food webs. In contrast, SSI-S showed a lower TA which suggest lower trophic diversity in comparison with the other two food webs. This is explained by the lower diversity found in the base of the food web as showed by the lower CN values of this food web (discussed below).

The similarities between the studied food webs are supported by the five trophic levels and the absence of differences in fatty acids signatures. The studied food webs were dominated by carnivory with DHA and C18:1ω9 present in high concentrations in most of the studied species, as well the low ratios of EPA/DHA and C16:1ω7/C16:0, and high ratios of Σ(PUFA + HUFA)/ΣSFA (Dalsgaard and others 2003; Maar and others 2023; Papadimitraki and others 2023). The high percentages of C16:0 in the three areas suggest a degree of dependence on detritus (Papadimitraki and others 2023), which is expected for a deep-sea food web as these commonly depend on marine snow (Silver and Alldredge 1981; Glover and Smith 2003; Maar and others 2023). Low values of (C16:1ω7 + EPA)/(C18:2ω6 + DHA) suggest that this marine snow is mainly composed of diatom-based detritus (Dalsgaard and others 2003; Graeve and Greenacre 2020). Except for SSI-N, where no Asteroidea and Holothurian were sampled, the high percentage of ARA and ΣSFA in these taxa at SG and SSI-S suggest mud feeding, including free living and endosymbiotic bacteria (Howell and others 2003), suggesting a significant benthic component in these food webs (Parzanini and others 2018).

Similarities between food webs extend to the composition of the different trophic levels. In the three food webs, the 4th trophic level is mainly composed of fish, though there were a few exceptions like the long-armed squid (*Chiroteuthis veranyi*), the glacial squid (*Psychroteuthis glacialis*) (at SG), the deep-sea squid (*Bathyteuthis abyssicola*) (at SG and SSI-S), the octopod *P. turqueti* (at SG), and the crustacean *Paralomis* sp. (both SG and SSI-N). *Paralomis* sp. is the only crustacean on this trophic level. It is a known scavenger at SG (Collins 2002), with a previous study in *P. granulosa* in the Beagle Channel (South America) showing that it also feeds on benthic organisms such as echinoderms, polychaetes, and molluscs (Comoglio and Amin 1999). Except for *P. antarctica*, species included in the group ‘‘other’’ are represented in the 4th trophic level. Asteroidea, Holothuria and Antipatharia are benthic organisms, with both Asteroidea and Holothuria being mud feeders (discussed above). Antipatharia is a known suspension feeder on zooplankton (Wagner and others 2012), which is supported, in the SG samples, by the presence of fatty acids derived from copepods (C20:1ω9, C22:1ω9 and C20:1ω9/DHA ratio) (Graeve and Greenacre 2020; Maar and others 2023; Papadimitraki and others 2023). However, having a diet relying on detritus and/or copepods it was not expected to be in the 4th trophic level as suggested by δ^{15}N values. Previous studies in the North Atlantic and North Pacific oceans found that benthic pathways in benthopelagic food webs are enriched in δ^{15}N in comparison with pelagic pathways (Boyle and others 2012; Parzanini and others 2018). The high δ^{15}N values found in these organisms suggest their reliance on a benthic pathway of this food web, most probably associated with recycled particulate organic matter (Iken and others 2001; Mintenbeck and others 2007). Therefore, the high trophic level attributed to these organisms are a consequence of using *S. thompsoni*, a pelagic organism, rather than a true reflection of their trophic position (Iken and others 2001; Preciado and others 2017).

The 3rd trophic level was composed of cephalopods and crustaceans (also including some fish species). The low EPA/DHA values and the absence of C18:1ω9 in cephalopods is a typical pattern of species feeding on herbivorous prey which is expected for species at this trophic level (Stowasser and others 2009b). The presence of some C20:1ω9 also suggests a small contribution of copepods to the diet of cephalopods in these food webs (Dalsgaard and others 2003; Papadimitraki and others 2023). The absence of differences in fatty acids in species between trophic level 3 and 4.5 (some differences exist but SIMPER does not show any fatty acid significantly contributing for such differences) may suggest some similarity between these trophic levels. This similarity may be related to the high level of omnivory present in the Southern Ocean food webs with species in different trophic position, for example, *D. mawsoni*, *M. holotrachys* or *P. antarctica*, sharing the same prey such as the squid *F. knipovitchi* and euphausiids (Morley and others 2004; Ratcliffe and Trathan 2011; Roberts and others 2011; Queirós and others 2024a).

The composition of the different trophic levels is supported by differences found in fatty acid profiles by taxonomic groups. SIMPER analyses showed that fish have a higher concentration of C18:1ω9, an indicator of carnivory for higher trophic levels, and cephalopods have higher levels of C20:1ω9 which is synthesised, for example, by copepods (Dalsgaard and others 2003; Maar and others 2023; Papadimitraki and others 2023). Unfortunately, we could not identify the fatty acid C18:1ω7 because it was absent from the reference material. Its ratio with C18:1ω9 is an indicator of carnivory and less influenced by primary production which would be better to study the higher trophic levels, and thus, easier to discriminate the differences between fish on the 4th and 5th trophic levels (Dalsgaard and others 2003; Maar and others 2023; Papadimitraki and others 2023).

Despite mostly similar, several differences were found between the three Antarctic deep-sea food webs. The range of δ^{13}C values, i.e. CR, decrease from SG to SSI-S, with SG presenting a range twofold larger than at SSI-S, with SSI-N presenting an intermediate value, though closer to SSI-S. This variability is supported by the significant differences in δ^{13}C values found between areas. The CR is known to increase when multiple carbon sources are present in the food web, with different δ^{13}C values being related to the composition of primary producers (Layman and others 2007; Newsome and others 2007; Saporiti and others 2015). SG is a hotspot for phytoplankton diversity in the Southern Ocean and its communities differ from those at SSI which may explain this result (Alvain and Ovidio 2014; Liszka and others 2022). For example, *Phaeocystis* sp. exist at SG but not at the SSI, and this microalga is responsible for several blooms in the Southern Ocean (Alvain and Ovidio 2014; Bender and others 2018). Furthermore, these differences can also relate with the mixing of Weddell Sea and western Antarctic Peninsula surface waters at SG which can influence the phytoplankton community at SG (Orsi and others 1993; Murphy and others 2013). Although, C16:1ω7 concentration and (C16:1ω7 + EPA)/(C18:2ω6 + DHA) ratio do not suggest differences in the primary production between the three food webs, all being based on diatoms (Dalsgaard and others 2003; Papadimitraki and others 2023). However, we must be aware that fatty acids only allow us to differentiate between diatoms and dinoflagellates-based diet but no other phytoplankton (Dalsgaard and others 2003; Papadimitraki and others 2023). Furthermore, δ^{13}C values also decrease with latitude (DeNiro and Epstein 1978; McCutchan and others 2003; Newsome and others 2007). Poleward decreasing of δ^{13}C values can also explain these differences as our study spans a latitudinal gradient including different oceanographic conditions (Murphy and others 2013; Thorpe and Murphy 2022). Moreover, despite being considered stable, δ^{13}C values presents a stepwise enrichment of ≈0 to 1 ‰ per trophic level (DeNiro and Epstein 1978; Peterson and Fry 1987). The positive relationship between

δ^{13}C and δ^{15}N values show that δ^{13}C values are increasing due to the trophic position, and the carbon source of the three food webs is similar, supporting fatty acids results that all food webs have diatoms (or diatom detritus) as main primary producers (DeNiro and Epstein 1978; Peterson and Fry 1987; Dalsgaard and others 2003; Papadimitraki and others 2023). Variability was also found in TA across the three food webs. The SSI-S presented a TA 1.6 and 1.5-fold lower than SG and SSI-N, respectively, suggesting a lower trophic diversity within this food web. TA is usually related with both NR and CR (Layman and others 2007). Considering that NR values were similar across the three food webs, the lower trophic diversity at SSI-S is therefore related with less diversity within the primary producers rather than with the trophic niche of the consumers (discussed above).

Regarding the diversity within the food webs, *Dissostichus* species are the top predators at SSI areas, though at SG the highest trophic position belongs to *M. holotrachys*. For both *Dissostichus* species to occupy the highest trophic level is not surprising because they are top predators in the Southern Ocean feeding mainly on fish and cephalopods (Roberts and others 2011; Pinkerton and Bradford-Grieve 2014; Yoon and others 2017; Queirós and others 2022). However, identifying *M. holotrachys* as top predator at SG was unexpected. *M. holotrachys*' fatty acids profile is similar to other *Macrourus* species from the 4th trophic level. Furthermore, the presence of EPA indicates that this species should be closer to the primary producer than *D. eleginoides*. A recent study on the bathyal region off-Peru also shows *M. holotrachys* above *D. eleginoides* in the food web (Ñacari and others 2023). One hypothesis to explain the higher trophic position relates to the presence of benthic prey in its diet, for example, echinoderms and crustaceans, previously found for individuals at SG and at the South Atlantic and South Pacific oceans (Laptikhovsky and Fetisov 1999; Morley and others 2004; Ñacari and others 2022). Therefore, *M. holotrachys* may be more associated to the benthic trophic pathway than the other *Macrourus* species in this study, explaining the higher δ^{15}N values and consequently the estimated trophic position (discussed above). Moreover, this species is a scavenger which, depending on the scavenged species, can be reflected in higher δ^{15}N values (Morley and Belchier 2002; Ñacari and others 2023). However, the fatty acid profile does not support any of these hypotheses (for example, EPA suggests a position closer to the primary production; ARA concentration is lower than other *Macrourus* spp.). To better understand the higher trophic position of *M. holotrachys* at SG different analyses are needed such as δ^{34}S stable isotopes that allow a better discrimination of benthic-pelagic diet and the contribution of chemosynthesis to the food web (Newsome and others 2007).

Differences also exist in lower trophic levels. Euphausiids are in the 2nd trophic level at both SSI areas. This is not surprising as most euphausiids in the Southern Ocean are herbivorous (though carnivorous species exist) (Cuzin-Roudy and others 2014). Herbivory is supported by the high percentages of EPA and DHA, but also by the high C16:1ω7/C16:0 ratio (Dalsgaard and others 2003; Graeve and Greenacre 2020; Papadimitraki and others 2023). However, at SG, euphausiids are in the 3rd trophic level. Both stable isotopes and fatty acids support this result, suggesting a change from an herbivorous diet to some carnivory as suggested by the higher concentration of C18:1ω9 (Dalsgaard and others 2003; Maar and others 2023; Papadimitraki and others 2023). This difference could relate to a mixture of euphausiid species being sampled in both locations (Ward and others 1990; Gurney and others 2001; Cuzin-Roudy and others 2014; Liszka and others 2022); but also, to a seasonal change in the diet of euphausiids like the Antarctic krill (*Euphausia superba*). This species is an abundant herbivorous euphausiid in the Scotia Sea (Atkinson and others 2001; Mackey and others 2012; Yang and others 2022), though with an omnivorous diet between autumn and spring (Ericson and others 2018). The lowest trophic position at SG is occupied by the squid *M. longimana*, which is thought to feed on zooplankton (mainly *E. superba*) (Nemoto and others 1988; Lu and Williams 1994; Collins and Rodhouse 2006; Queirós and others 2018, 2021). However, high concentrations of DHA and low concentrations of C18:1ω9 indicate that this species (and other cephalopods) is also feeding on salps and chaetognaths (Stowasser and others 2012b). Salps are expected to increase in abundance in the Scotia Sea with rising ocean temperatures due to climate change (Atkinson and others 2004), and this result suggests that zooplanktivorous species may already be shifting their prey, potentially affecting the energy intake of higher predators (Pakhomov and others 2002; Pietzsch and others 2023). Further studies are needed to fully understand the effects on this change.

Differences in δ^{15}N values between study areas in *M. whitsoni, M. longimana* and *Nematocarcinus* sp. also suggest differences in the mid-trophic levels. Being on the same trophic level, these differences may be related to different prey species or ratios between similar prey (Bearhop and others 2004). This is expected as different communities inhabit the three areas, but also due to differences in water masses that can influence the baselines (Bearhop and others 2004; Hollyman and others 2022; Liszka and others 2022; Thorpe and Murphy 2022; Queirós and others 2024b). We must highlight that species ontogenetic changes were not considered in this study, for example, δ^{15}N values and stomach contents of smaller *D. eleginoides* from the South Georgia shelf suggest that juveniles of this species feed in lower trophic levels than adults (Collins and others 2007; Seco and others 2021), and *M. longimana* is known to increase one trophic level with ontogeny (Queirós and others 2018). Therefore, we must be aware that the structure of these food-webs may slightly change, especially the trophic level occupied by the different species, according to the life-stage of individuals. Nonetheless, smaller (or larger) individuals of species with ontogenetic changes may not be present in the bathyal zone, belonging to a different food web such as the case of juveniles of *D. eleginoides* that inhabit the shelf of South Georgia and are rarely caught in the studied depths (Collins and others 2007). Also, changes in trophic position with size are not recorded for all species in these food webs, for example, *F. knipovitchi* in the Pacific sector of the Southern Ocean (Queirós and others 2021) and *D. mawsoni* in both Ross Sea region (despite size explained some variability in δ^{15}N values, smaller individuals feed in the same trophic level of the largest adults (Queirós and others 2022)), and Antarctic Peninsula (size only influenced the number of cephalopods in the diet with all other prey species remaining similar (Pérez-Pezoa and others 2023)). Due to the species-specific life history and the current lack of knowledge, it is currently not possible to evaluate how the structure of these food webs change with the size of individuals. To overcome these challenges, more studies on ontogenetic changes in habitat and trophic level of these species are required.

In marine ecosystems the food webs are commonly size-structured, with predators mostly feeding in smaller prey and with larger predators selecting larger prey (Cohen and others 1993). Though, recent studies showed that food webs build using predator–prey size ratio oversimplifies and do not properly represent the trophic interactions in an ecosystem (García-Oliva and Wirtz 2025). Our results showed larger species in lower trophic levels than smaller sized-species, for example, *M. longimana* that can reach 110 cm mantle length is in the 3rd trophic level (at South Georgia almost 2nd trophic level) whereas *Chiroteuthis veranyi* that only grows up to 30 cm mantle length is in the 4th trophic level, and the presence of large prey species such *Mesonychoteuthis hamiltoni* (4th trophic level; mantle length up to 250 cm and body weight up to 500 kg) in the stomach of *D. mawsoni* that is in the 5th trophic level and it is a top predator of the Southern Ocean deep-sea (Roberts and others 2011; Cherel 2020; Queirós and others 2024b; see Online appendix A for species' size). Smaller species with higher δ^{15}N values was also found in other deep-sea ecosystems elsewhere, for example, Suruga Bay (Japan; Fujiwara and others (2021)) and Northwest Atlantic (Stowasser and others 2009a). Several hypotheses may explain this absence of size-structured food web in the studied food webs: the presence of scavenger species allow smaller individuals to feed in larger prey that they would not predate (for example, *D. mawsoni* feeding in *M. hamiltoni* (Remeslo and others 2015), species associated with a benthic trophic pathway that is enriched in ^{15}N in comparison with organisms associated with the pelagic pathway (for example, *M. holotrachys* feeding in benthic organisms whereas *D. eleginoides* feeds mostly on fish (Morley and others 2004; Queirós and others 2024b), or the presence of different food chains within these food webs that using stable isotopes we cannot disentangle that approximate the predator–prey ratio to the allometric rule (Cohen and others 1993).

The Southern Ocean Food Web: Differences between Regions and Zones of the Water Column

The Southern Ocean food web varies regionally and seasonally, including differences in the overall structure, species importance, and number of trophic levels (reviewed in Queirós and others 2024a). However, no studies have evaluated patterns between food webs in different zones of the Southern Ocean, that is, deep-sea benthopelagic *vs* pelagic *vs* coastal. Our food webs are among those with the highest trophic level recorded for the Southern Ocean (Table 5). The presence of both *Dissostichus* species and *M. holotrachys* in the diet of larger predators, for example, sperm whales (*Physeter macrocephalus*), killer whales (*Orcinus orca*), or southern elephant seals (*Mirounga leonina*) (Collins and others 2010; Hanchet and others 2010), suggest that these food webs may include a 6th trophic level. Besides this study, the longest food webs were those from the deep-sea that included benthopelagic coupling (Table 5). The work of Pinkerton and Bradford-Grieve (2014) for the Ross

Sea place both *P. macrocephalus*, *O. orca* and large demersal fish (includes *D. mawsoni*) at the top of the food web. This suggests that deep-sea benthopelagic food webs in the Southern Ocean, despite their location (that is, from warmer subantarctic islands to cold Antarctic seas) and species composition, are long and have a minimum of five trophic levels. Several hypotheses may explain the presence of such longer food webs in deep-sea ecosystems from the Southern Ocean such as a lower predator–prey body size ratio that allows food chain to lengthen due to the presence of predators of intermediate size (Jennings and Warr 2003); the presence of scavengers in the food web, in particular when we found these in higher trophic levels such as the case of *D. eleginoides* and *D. mawsoni* (Bergmann and others 2009; Collins and others 2010; Hanchet and others 2015; Amiraux and others 2023); due to the limited food availability in deep-sea ecosystems the nutrients are recycled, especially in the benthic component of these ecosystems, which reflects in higher trophic positions in the pelagic component of the benthopelagic food web (Iken and others 2005; Bergmann and others 2009); and larger ecosystems such as the deep-sea allow more diversity in the food web, favouring the presence of more biotic interactions and, ultimately, favouring longer food chains (Bergmann and others 2009).

Previous studies on Southern Ocean food webs analysed the structure of pelagic and coastal food webs (Table 5). The highest trophic position recorded for pelagic food webs range from 4.3 to 5.3. However, pelagic food webs with five trophic levels include large mammals such as *P. macrocephalus* and *O. orca* (Murphy and others 2013; McCormack and others 2020), or seabirds that scavenge on seals, penguins, and fish remains from fishing vessels, thus feeding on organisms from the benthopelagic food webs, for example, black browed albatross (*Thalassarche melanophris*) and giant petrel (*Macronectes* spp.) (Cherel and others 2010; Stowasser and others 2012a; Phillips and Wood 2020). When large mammals or scavenging seabirds were absent, top predators occupy the 4th trophic level, for example, emperor penguins (*Aptenodytes forsteri*) at Adélie Land and Wilson's storm petrels (*Oceanites oceanicus*) in the Weddell Sea (Rau and others 1992; Cherel 2008). Coastal food webs are the shortest in the Southern Ocean (Table 5). The higher predators of these food webs were mostly on the 4th trophic level (Table 5). The top predator's trophic level in coastal food webs relate, to some extent, with the biodiversity. Food webs including fish have four trophic levels (Gillies and others 2012; Zenteno and others 2019), while those exclusively composed by benthic organisms, for example, corals, sponges, holothurians, are almost limited to three trophic levels (Marina and others 2018; Michel and others 2019; Rossi and others 2019; Cardona and others 2021). An exception to this pattern is the benthopelagic food web from Terra Nova Bay (Ross Sea) whose top predators were found in the 5th trophic level (Rossi and others 2019). However, the top predators of this food web were *Chionodraco hamatus* and *Trematomus hansoni* which are two species known to inhabit waters as deep as 600 and 550 m, respectively (Gon and Heemstra 1990). Therefore, this unusual longer coastal food web may be explained by the presence of deep-sea species as top predators, species that may feed in deeper waters but also include benthic species in the diet that are enriched in δ^{15}N values (discussed above; Pakhomov 1998), supporting that the length of Southern Ocean coastal food webs are strictly connected to the biodiversity included in the web. It is important to note that some studies only presented the δ^{15}N values with the trophic position being estimated using the equation that we used for our food webs, including using *S. thompsoni* as baseline species, suggesting that those including a benthic component may have an overestimated FCL (discussed above; Table 5). These results suggest that the Southern Ocean coastal benthic food webs have the shortest food-chain length (for example, Cardona and others 2021), followed by pelagic open ocean food webs (for example, Stowasser and others 2012a), with deep-sea benthopelagic food webs having the longest food-chain length (this study; Queirós and others 2025). However, we must have in mind that this is variable and dependent on the analysed food chain, for example, the pelagic food web that includes primary producer—Antarctic krill—top predator (for example, blue whale *Balaenoptera musculus*) is shorter than a coastal food web including fish (Kawamura 2007; Rossi and others 2019). The stability hypothesis proposed by Pimm and Lawton (1977) may explain this increase in food-chain length from coastal to deep-sea benthopelagic food webs. Coastal and pelagic regions are more variable than deep-sea ecosystems (Glover and Smith 2003). Sea-ice, iceberg scouring, swell, stronger currents, run-off from terrestrial environments are examples of environmental factors that induce dynamism in coastal and pelagic areas but not in the deep-sea (Glover and Smith 2003; Convey and Peck 2019; Zwerschke and others 2021; Thorpe and Murphy 2022; Tarling and others 2024). However, studies including environmental variables are needed to validate this hypothesis.

These changes in the food-chain length have different ecological implications for the Southern Ocean ecosystem: it highlights that the long standing hypothesis of a short, Antarctic krill dominated food web does not apply to all the Southern Ocean (Everson 1977; Benninghoff 1987); individuals in longer food chains have higher concentrations of biomagnifying trace elements (Seco and others 2021); food webs with longer food chains are less stable, less resistant and recover slower from disturbances; and it has implications for the energy budgets and assimilation losses in the food webs, with the amount of energy reaching the top predator on the benthopelagic deep-sea being lower than to a pelagic predator, though this hypothesis was proposed studying lake food webs which is a closed system in comparison with open systems like the one studied here (Post 2002a). Indeed, the presence of longer food webs and high number of species in intermediate levels (for example, 4th trophic level includes the highest number of species in each food web, followed by the 3rd trophic level), may suggest that top predators and mesoconsumers can use different trophic pathways, making these food webs more resistant to changes (for example, local extinction of mid-trophic level consumers) (Queirós and others 2024a). Furthermore, these ecological implications are dependent on the immigration of other species to this region, including higher predators such as humpback whales (*Megaptera novaeangliae*) (Bamford and others 2022) or mid-trophic level organisms such as myctophids (Saunders and others 2017). These migrants, when entering these food webs can change the trophic structure, the energy and nutrients flow, and ultimately influencing the stability and resistance of the food web towards external stressors (Bauer and Hoye 2014). Nonetheless, this influence depends on the trophic role the migrant species occupy in the ecosystem, that is, as prey or predator (Bauer and Hoye 2014). The presence of *Gymnoscopelus* sp. in the 4th trophic level at South Georgia may suggest that this species, that can migrate northwards to Subantarctic waters (Saunders and others 2017), may have a similar trophic role to resident fish species in the archipelago. However, this is only one species and in a winter food web when most of migrant species are not on the region. Therefore, further studies are needed to understand the role of migrant species in the benthopelagic deep-sea food webs in this region, to better understand the structure and functioning of these ecosystems. This knowledge assumes a greater importance because these ecosystems are being impacted by climate change (Rogers and others 2020), toothfish fisheries operate in this zone (Agnew 2004; Brooks and others 2018), and deep-sea species already have less productive life-cycles and are more vulnerable to these stressors (Norse and others 2012; Rogers 2015; Clark and others 2016).

ACKNOWLEDGEMENTS

The authors want to thank the crew and observers in *FV Nordic Prince* for supporting JPQ during sampling collection and to Argos Froyanes for allowing JPQ to board the fishing vessel. We would also like to thank the observers in *FV San Aspiring* and *FV Argos Froyanes* for collecting extra samples. The authors also want to thank Gaël Guillou from the Plateforme Analyses Isotopiques of LIENSs laboratory for running stable isotope analyses, and to Carine Churlaud and Maud Brault from LIENSs laboratory for supporting during sample preparation. JPQ was supported by Fundação para a Ciência e Tecnologia (FCT) PhD Scholarship co-financed by FSE (SFRH/BD/144320/2019), by FCT with an Extraordinary Scholarship to Mitigate COVID-19 Impacts in Research Activities (COVID/BD/153444/2024), and by the project CEPH-BASfr supported by FCT/MCTES through national funds (PIDDAC) and Portuguese Polar Program (PROPOLAR). JPQ would like to thanks EuroMarine for the Individual Fellowship 2022 that supported his travel to La Rochelle Université. JA was supported by national funds through FCT- PhD scholarship (2020.07291.BD). PB is an honorary member of the Institut Universitaire de France (IUF). AMMG acknowledges the University of Coimbra for the contract IT057-18-7253, the strategic projects granted to Centre for Functional Ecology—Science for People and the Planet (CFE;UIDB/04004/2020; https://doi.org/10.54499/UIDB/04004/2020), financed by FCT/MCTES through national funds (PIDDAC) and Associate Laboratory TERRA (LA/P/0092/2020; https://doi.org/10.54499/LA/P/0092/2020). This work had the support of national funds through FCT, under the projects UIDB/04292/2020, UIDP/04292/2020, granted to MARE, and LA/P/0069/2020, granted to the Associate Laboratory ARNET. The Contrat de Projet Etat-Région (CPER) and Fonds Européen de Développement Régional (FEDER) are acknowledged for funding the IRMS of LIENSs laboratory.

OPEN ACCESS

FUNDING

This work was supported by: project CEPH-BASfr supported by FCT/MCTES through national funds (PIDDAC) and Portuguese Polar Program (PROPOLAR); by FCT projects granted to MARE (UIDB/04292/2020, UIDP/04292/2020), Associate Laboratory ARNET (LA/P/0069/2020), Centre for Functional Ecology—Science for People and the Planet (CFE;UIDB/04004/2020), and Associate Laboratory TERRA (LA/P/0092/2020); CPER (Contrat de Projet Etat-Région) and FEDER (Fonds Européen de Développement Régional) are acknowledged for funding the IRMS of LIENSs laboratory. Authors were supported by: JPQ was supported by FCT PhD Scholarship co-financed by FSE (SFRH/BD/144320/2019), by FCT for the Extraordinary Scholarship to Mitigate COVID-19 Impacts in Research Activities (COVID/BD/153444/2024), and by EuroMarine Individual Fellowship 2022; JA was supported by national funds through FCT- PhD scholarship (2020.07291.BD).

DATA AVAILABILITY

Data used in this work can be found in 10.5281/zenodo.15704266.

REFERENCES

Agnew D (2004) Fishing south. The history and management of South Georgia fisheries. Antarct Sci 16:585–586

Alvain S, Ovidio FD' (2014) Phytoplankton diversity in the southern ocean: a satellite view. In: De Broyer C, Koubbi P, Griffiths HJ, Raymond B, Udekem Dcoz Cd' (eds) Biogeographic atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, pp 260–265

Amiraux R, Yurkowski DJ, Archambault P, Pierrejean M, Mundy CJ. 2023. Top predator sea stars are the benthic equivalent to polar bears of the pelagic realm. Proc Natl Acad Sci U S A 120:e2216701120

Arbizu PM. 2020. Pairwise Adonis: Pairwise multilevel comparison using adonis. R package version 04.

Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432:100–103

Atkinson A, Whitehouse MJ, Priddle J, Cripps GC, Ward P, Brandon MA (2001) South Georgia, Antarctica: a productive, cold water, pelagic ecosystem. Mar Ecol Prog Ser 216:279–308

Bamford CCG, Jackson JA, Kennedy AK, Trathan PN, Staniland IJ, Andriolo A, Bedriñana-Romano L, Carroll EL, Martin S, Zerbini AN (2022) Humpback whale (*Megaptera novaeangliae*) distribution and movements in the vicinity of South Georgia and the South Sandwich Islands Marine Protected Area. Deep Sea Res Part II 198:105074

Bauer S, Hoye BJ (2014) Migratory animals couple biodiversity and ecosystem functioning worldwide. Science 1979:344

Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. J Anim Ecol 73:1007–1012

Belchier M, Collins MA, Gregory S, Hollyman P, Soeffker M (2022) From sealing to the MPA—A history of exploitation, conservation and management of marine living resources at the South Sandwich Islands. Deep Sea Res Part II 198:105056

Bender SJ, Moran DM, McIlvin MR, Zheng H, McCrow JP, Badger J, DiTullio GR, Allen AE, Saito MA (2018) Colony formation in *Phaeocystis antarctica* connecting molecular mechanisms with iron biogeochemistry. Biogeosciences 15:4923–4942

Benninghoff WS (1987) The Antarctic ecosystem. Environ Int 13:9–14

Bergmann M, Dannheim J, Bauerfeind E, Klages M (2009) Trophic relationships along a bathymetric gradient at the deep-sea observatory HAUSGARTEN. Deep Sea Res Part I 56:408–424

Boyle MD, Ebert DA, Cailliet GM (2012) Stable-isotope analysis of a deep-sea benthic-fish assemblage: evidence of an enriched benthic food web. J Fish Biol 80:1485–1507

Brooks CM, Ainley DG, Abrams PA, Dayton PK, Hofman RJ, Jacquet J, Siniff DB (2018) Antarctic fisheries: factor climate change into their management. Nature 558:177–180

Brooks CM, Chown SL, Douglass LL, Raymond BP, Shaw JD, Sylvester ZT, Torrens CL (2020) Progress towards a representative network of Southern Ocean protected areas. PLoS ONE 15:e0231361

CAMLR. 1980. The Convention for the Conservation of Antarctic Marine Living Resources.

Cardona L, Lloret-Lloret E, Moles J, Avila C (2021) Latitudinal changes in the trophic structure of benthic coastal food webs along the Antarctic Peninsula. Mar Environ Res 167:105290

Cherel Y (2008) Isotopic niches of emperor and Adélie penguins in Adélie Land, Antarctica. Mar Biol 154:813–821

Cherel Y (2020) A review of southern ocean squids using nets and beaks. Mar Biodivers 50:98

Cherel Y, Ducatez S, Fontaine C, Richard P, Guinet C (2008) Stable isotopes reveal the trophic position and mesopelagic fish diet of female southern elephant seals breeding on the Kerguelen Islands. Mar Ecol Prog Ser 370:239–247

Cherel Y, Fontaine C, Richard P, Labat JP (2010) Isotopic niches and trophic levels of myctophid fishes and their predators in the Southern Ocean. Limnol Oceanogr 55:324–332

Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. Mar Ecol Prog Ser 329:281–287

Chouvelon T, Spitz J, Cherel Y, Caurant F, Sirmel R, Mèndez-Fernandez P, Bustamante P (2011) Inter-specific and ontogenic differences in δ^{13}C and δ^{15}N values and Hg and Cd concentrations in cephalopods. Mar Ecol Prog Ser 433:107–120

Choy CA, Haddock SHD, Robison BH (2017) Deep pelagic food web structure as revealed by in situ feeding observations. Proc Biol Sci 284:20172116

Christensen V, Pauly D. 1993. Trophic models of aquatic ecosystems. Manila, Philippines: international center for living aquatic resources management

Clark MR, Althaus F, Schlacher TA, Williams A, Bowden DA, Rowden AA (2016) The impacts of deep-sea fisheries on benthic communities: a review. ICES J Mar Sci 73:51–69

Cohen JE, Pimm SL, Yodzis P, Saldaña J (1993) Body sizes of animal predators and animal prey in food webs. J Anim Ecol 62:67–78

Collins MA, Yau C, Guillfoyle F, Bagley P, Everson I, Priede IG, Agnew D (2002)Assessment of stone crab (Lithodidae) density on the South Georgia slope usingbaited video cameras. ICES J Mar Sci59:370–379

Collins MA, Brickle P, Brown J, Belchier M (2010) The Patagonian toothfish: biology, ecology and fishery. Adv Mar Biol 58:227–300

Collins MA, Hart T, Hogg OT, Hollyman PR, Liszka CM, Stewart HA, Trathan PN (2022) South sandwich islands—an understudied isolated Southern Ocean archipelago. Deep Sea Res Part II 201:105121

Collins MA, Rodhouse PGK (2006) Southern ocean cephalopods. Adv Mar Biol 50:191–265

Collins MA, Ross KA, Belchier M, Reid K (2007) Distribution and diet of juvenile Patagonian toothfish on the South Georgia and Shag Rocks shelves (Southern Ocean). Mar Biol 152:135–147

Comoglio LI, Amin OA. 1999. Feeding habits of the false southern king crab *Paralomis granulosa* (Lithodidae) in the Beagle Channel, Tierra del Fuego, Argentina. Sci Mar 63:361–6.

Constable AJ, Melbourne-Thomas J, Muelbert MMC, McCormack S, Braiser M, Caccavo JA, Cavanagh RA, Grant SM, Griffiths HJ, Gutt J, Henley SF, Höfer J, Hollowed AB, Johnston NM, Morley SA, Murphy EJ, Pinkerton MH, Schloss IR, Swadling KM, Van de Putte AP. 2023. Marine Ecosystem Assessment for the Southern Ocean: summary for policymakers. Integrated climate and ecosystem dynamics in the southern ocean, scientific Committee on Antarctic research, scientific committee on oceanic research, integrated marine biosphere research.

Convey P, Peck LS (2019) Antarctic environmental change and biological responses. Sci Adv 5:eaaz0888

Couturier LIE, Michel LN, Amaro T, Budge SM, da Costa E, De Troch M, Di Dato V, Fink P, Giraldo C, Le Grand F, Loaiza I, Mathieu-Resuge M, Nichols PD, Parrish CC, Sardenne F, Vagner M, Pernet F, Soudant P (2020) State of art and best practices for fatty acid analysis in aquatic sciences. ICES J Mar Sci 77:2375–2395

Cuzin-Roudy J, Irisson J-O, Penot F, Kawaguchi S, Vallet C. 2014. Southern Ocean Euphausiids. In: De Broyer C, Koubbi P, Griffiths H, Raymond B, D'Acoz CU, Van de Putte A, Danis B, David B, Grant S, Gutt J, Held C, Hosie G, Huettmann F, Post A, Ropert-Coudert Y, editors. Biogeographic atlas of the Southern Ocean. Cambridge, UK: The Scientific Committee on Antarctic Research. pp 309–20.

Dalsgaard J, John MS, Kattner G, Müller-Navarra D, Hagen W (2003) Fatty acid trophic marker in the pelagic marine environment. Adv Mar Biol 43:225–340

de Santana CN, Rozenfeld AF, Marquet PA, Duarte CM (2013) Topological properties of polar food webs. Mar Ecol Prog Ser 474:15–26

DeNiro MJ, Epstein S (1977) Mechanism of carbon isotope fractionation associated with lipid synthesis. Science 1979(197):261–263

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochim Cosmochim Acta 42:495–506

Deppeler SL, Davidson AT (2017) Southern Ocean phytoplankton in a changing climate. Front Mar Sci 4:40

Downie AL, Vieira RP, Hogg OT, Darby C (2021) Distribution of vulnerable marine ecosystems at the South Sandwich Islands: results from the blue belt discovery expedition 99 deep-water camera surveys. Front Mar Sci 8:662285

Drazen JC, Sutton TT (2017) Dining in the deep: The feeding ecology of deep-sea fishes. Ann Rev Mar Sci 9:337–366

Dunne JA, Williams RJ, Martinez ND (2002) Food-web structure and network theory: The role of connectance and size. Proc Natl Acad Sci U S A 99:12917–12922

Ericson JA, Hellessey N, Nichols PD, Kawaguchi S, Nicol S, Hoem N, Virtue P (2018) Seasonal and interannual variations in the fatty acid composition of adult *Euphausia superba* Dana, 1850 (Euphausiacea) samples derived from the Scotia Sea krill fishery. J Crust Biol 38:662–672

Everson I (1977) The living resources of the Southern Ocean: Southern Ocean fisheries survey programme. FAO, Rome

Fabri-Ruiz S, Danis B, Navarro N, Koubbi P, Laffont R, Saucede T (2020) Benthic ecoregionalization based on echinoid fauna of the Southern Ocean supports current proposals of Antarctic Marine Protected Areas under IPCC scenarios of climate change. Glob Chang Biol 26:2161–2180

Fenaughty JM. 2008. The autoline system - an updated descriptive review of the method with recommendations to clarify CCAMLR conservation measures regulating longline fisheries within the convention area. Document WG-FSA-08/60 CCAMLR, Hobart, Australia: 27.

Fitzcharles E, Hollyman PR, Goodall-Copestake WP, Maclaine JS, Collins MA (2021) The taxonomic identity and distribution of the eel cod *Muraenolepis* (Gadiformes: Muraenolepididae) around South Georgia and the South Sandwich Islands. Polar Biol 44:637–651

Fujiwara Y, Kawato M, Poulsen JY, Ida H, Chikaraishi Y, Ohkouchi N, Oguri K, Gotoh S, Ozawa G, Tanaka S, Miya M, Sado T, Kimoto K, Toyofuku T, Tsuchida S (2021) Discovery of a colossal slickhead (Alepocephaliformes: Alepocephalidae): an active-swimming top predator in the deep waters of Suruga Bay. Japan Sci Rep 11:2490

GSGSSI. 2023a. Fisheries overview. https://gov.gs/overview/

GSGSSI. 2023b. Marine Protected Area. https://www.gov.gs/environment/marine-protected-area/

García-Oliva O, Wirtz K (2025) The complex structure of aquatic food webs emerges from a few assembly rules. Nat Ecol Evol 9:576–588

Gaston KJ (2009) Geographic range limits: achieving synthesis. P Roy Soc Lond B Bio 276:1395–1406

Gillies CL, Stark JS, Johnstone GJ, Smith SDA (2012) Carbon flow and trophic structure of an Antarctic coastal benthic community as determined by δ^{13}C and δ^{15}N. Estuar Coast Shelf Sci 97:44–57

Glover AG, Smith CR (2003) The deep-sea floor ecosystem: current status and prospects of anthropogenic change by the year 2025. Environ Conserv 30:219–241

Gon O, Heemstra PC. 1990. Fishes of the Southern Ocean. (Heemstra PC, editor.). Grahamstown: J. L. B. Smith Institute of Icthyology

Gonçalves AMM, Azeiteiro UM, Pardal MA, De Troch M (2012) Fatty acid profiling reveals seasonal and spatial shifts in zooplankton diet in a temperate estuary. Estuar Coast Shelf Sci 109:70–80

Goodall-Copestake WP, Perez-Espona S, Hollyman P, Belchier M. 2018. Genetic analysis of skates (*Amblyraja* spp.) caught as by-catch around South Georgia and the South Sandwich Islands. Document WG-FSA-18/73 CCAMLR, Hobart, Australia: 8.

Graeve M, Greenacre MJ (2020) The selection and analysis of fatty acid ratios: a new approach for the univariate and multivariate analysis of fatty acid trophic markers in marine pelagic organisms. Limnol Oceanogr Methods 18:196–210

Gravel D, Albouy C, Thuiller W. 2016. The meaning of functional trait composition of food webs for ecosystem functioning. Philos Trans R Soc Lond B Biol Sci 371:20150268

Gurney L, Froneman P, Pakhomov E, McQuaid C (2001) Trophic positions of three euphausiid species from the Prince Edward Islands (Southern Ocean): implications for the pelagic food web structure. Mar Ecol Prog Ser 217:167–174

Hanchet S, Dunn A, Parker S, Horn P, Stevens D, Mormede S (2015) The Antarctic toothfish (*Dissostichus mawsoni*): biology, ecology, and life history in the Ross Sea region. Hydrobiologia 761:397–414

Hanchet SM, Mormede S, Dunn A (2010) Distribution and relative abundance of Antarctic toothfish (*Dissostichus mawsoni*) on the Ross Sea shelf. CCAMLR Science 17:33–51

Hette-Tronquart N, Roussel J-M, Dumont B, Archaimbault V, Pont D, Oberdorff T, Belliard J (2013) Variability of water temperature may influence food-chain length in temperate streams. Hydrobiologia 718:159–172

Hogg OT, Downie A-L, Vieira RP, Darby C (2021) Macrobenthic assessment of the South Sandwich Islands reveals a biogeographically distinct polar archipelago. Front Mar Sci 8:650241

Hollyman PR, Hill SL, Laptikhovsky VV, Belchier M, Gregory S, Clement A, Collins MA (2021) A long road to recovery: dynamics and ecology of the marbled rockcod (*Notothenia rossii*, family: Nototheniidae) at South Georgia, 50 years after overexploitation. Godo OR, editor. ICES J Mar Sci 78:2745–2756

Hollyman PR, Soeffker M, Roberts J, Hogg OT, Laptikhovsky VV, Queirós JP, Darby C, Belchier M, Collins MA (2022) Bioregionalization of the South Sandwich Islands through community analysis of bathyal fish and invertebrate assemblages using fishery-derived data. Deep Sea Res Part II 198:105054

Horswill C, Jackson JA, Medeiros R, Nowell RW, Trathan PN, O'Connell TC (2018) Minimising the limitations of using dietary analysis to assess foodweb changes by combining multiple techniques. Ecol Indic 94:218–225

Howell KL, Pond DW, Billet DSM, Tyler P (2003) Feeding ecology of deep-sea seastars (Echinodermata: Asteroidea): a fatty-acid biomarker approach. Mar Ecol Prog Ser 255:193–206

Iken K, Bluhm BA, Gradinger R (2005) Food web structure in the high arctic Canada basin: evidence from δ^{13}C and δ^{15}N analysis. Polar Biol 28:238–249

Iken K, Brey T, Wand U, Voigt J, Junghans P (2001) Food web structure of the benthic community at the porcupine abyssal Plain (NE Atlantic): a stable isotope analysis. Prog Oceanogr 50:383–405

Jackson A, Parnell A (2023) SIBER: stable isotope Bayesian ellipses in R. R Package Version 2(1):9

Jennings S, Warr KJ (2003) Smaller predator-prey body size ratios in longer food chains. Proc Biol Sci 270:1413–1417

Kassambara A, Mundt F. 2020. *factoextra*: Extract and visualize the results of multivariate data analyses. R package version 107.

Kawamura A (2007) A review of food of balaenopterid whales. Sci Reports Whales Res Inst 32:155–197

Kelly JR, Scheibling RE (2012) Fatty acids as dietary tracers in benthic food webs. Mar Ecol Prog Ser 446:1–22

Kiljunen M, Peltonen H, Lehtiniemi M, Uusitalo L, Sinisalo T, Norkko J, Kunnasranta M, Torniainen J, Rissanen AJ, Karjalainen J (2020) Benthic-pelagic coupling and trophic relationships in northern Baltic Sea food webs. Limnol Oceanogr 65:1706–1722

King RA, Read DS, Traugott M, Symondson WO (2008) Molecular analysis of predation: a review of best practice for DNA-based approaches. Mol Ecol 17:947–963

Kolasinski J, Rogers K, Frouin P (2008) Effects of acidification on carbon and nitrogen stable isotopes of benthic macrofauna from a tropical coral reef. Rapid Commun Mass Sp 22:2955–2960

Kruse S, Pakhomov E, Hunt B, Chikaraishi Y, Ogawa N, Bathmann U (2015) Uncovering the trophic relationship between *Themisto gaudichaudii* and *Salpa thompsoni* in the Antarctic Polar Frontal Zone. Mar Ecol Prog Ser 529:63–74

Kędra M, Moritz C, Choy ES, David C, Degen R, Duerksen S, Ellingsen I, Górska B, Grebmeier JM, Kirievskaya D, van Oevelen D, Piwosz K, Samuelsen A, Węsławski JM (2015) Status and trends in the structure of Arctic benthic food webs. Polar Res 34:23775

Laptikhovsky V, Fetisov A (1999) Scavenging by fish of discards from the Patagonian squid fishery. Fish Res 41:93–97

Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88:42–48

Li Q, England MH, Hogg AM, Rintoul SR, Morrison AK (2023) Abyssal ocean overturning slowdown and warming driven by Antarctic meltwater. Nature 615:841–847

Liszka CM, Thorpe SE, Wootton M, Fielding S, Murphy EJ, Tarling GA (2022) Plankton and nekton community structure in the vicinity of the South Sandwich Islands (Southern

Ocean) and the influence of environmental factors. Deep Sea Res Part II 198:105073

Lu CC, Williams R (1994) *Kondakovia longimana* Filippova, 1972 (Cephalopoda: Onychoteuthidae) from the Indian Ocean sector of the Southern Ocean. Antarct Sci 6:231–234

López-López L, Genner MJ, Tarling GA, Saunders RA, O'Gorman EJ (2022) Ecological networks in the Scotia Sea: Structural changes across latitude and depth. Ecosystems 25:457–470

Maar K, Papadimitraki M, Hernández Ruiz L, Broughton R, Jónasdóttir S (2023) Lipids in meso-and bathypelagic fishes from the North Atlantic Ocean: dietary inputs suggested from fatty acid trophic markers. Mar Ecol Prog Ser 717:127–141

Mackey AP, Atkinson A, Hill SL, Ward P, Cunningham NJ, Johnston NM, Murphy EJ (2012) Antarctic macrozooplankton of the southwest Atlantic sector and Bellingshausen Sea: Baseline historical distributions (Discovery Investigations, 1928–1935) related to temperature and food, with projections for subsequent ocean warming. Deep Sea Res Part II 59–60:130–146

Marina TI, Salinas V, Cordone G, Campana G, Moreira E, Deregibus D, Torre L, Sahade R, Tatián M, Oro EB, De Troch M, Doyle S, Quartino ML, Saravia LA, Momo FR (2018) The food web of potter Cove (Antarctica): complexity, structure and function. Estuar Coast Shelf Sci 200:141–151

McCormack SA, Melbourne-Thomas J, Trebilco R, Blanchard JL, Constable A (2020) Alternative energy pathways in Southern Ocean food webs: insights from a balanced model of Prydz Bay. Antarctica Deep Sea Res Part II 174:104613

McCutchan JH, Lewis WM, Kendall C, McGrath CC (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102:378–390

McMahon KW, Newsome SD. 2019. Amino Acid Isotope Analysis. In: tracking animal migration with stable isotopes. Elsevier. pp 173–190.

Michel LN, Danis B, Dubois P, Eleaume M, Fournier J, Gallut C, Jane P, Lepoint G (2019) Increased sea ice cover alters food web structure in East Antarctica. Sci Rep 9:8062

Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between δ^{15}N and animal age. Geochim Cosmochim Acta 48:1135–1140

Mintenbeck K, Jacob U, Knust R, Arntz WE, Brey T (2007) Depth-dependence in stable isotope ratio δ^{15}N of benthic POM consumers: the role of particle dynamics and organism trophic guild. Deep Sea Res Part I 54:1015–1023

Morato T, Lemey E, Menezes G, Pham CK, Brito J, Soszynski A, Pitcher TJ, Heymans JJ (2016) Food-Web and ecosystem structure of the open-ocean and deep-sea environments of the Azores. NE Atlantic Front Mar Sci 3:00245

Morley S, Belchier M (2002) Otolith and body size relationships in bigeye grenadier (*Macrourus holotrachys*) in CCAMLR subarea 48.3. CCAMLR Science 9:133–143

Morley SA, Mulvey T, Dickson J, Belchier M (2004) The biology of the bigeye grenadier at South Georgia. J Fish Biol 64:1514–1529

Murphy EJ, Hofmann EE, Watkins JL, Johnston NM, Piñones A, Ballerini T, Hill SL, Trathan PN, Tarling GA, Cavanagh RA, Young EF, Thorpe SE, Fretwell P (2013) Comparison of the structure and function of southern ocean regional ecosystems: the Antarctic peninsula and South Georgia. J Mar Syst 109–110:22–42

Ñacari LA, Escribano R, Harrod C, Oliva ME (2023) Combined use of carbon, nitrogen and sulfur stable isotopes reveal trophic structure and connections in deep-sea mesopelagic and demersal fish communities from the Southeastern Pacific Ocean. Deep Sea Res Part I 197:104069

Ñacari LA, Escribano R, Oliva ME (2022) Endoparasites and diet of the ''bigeye grenadier'' *Macrourus holotrachys* Günther, 1878 from the deep sea in the Southeastern Pacific Ocean. Deep Sea Res Part I 190:103903

Nemoto T, Okiyama M, Iwasaki N, Kikuchi T (1988) Squid as predators on krill (*Euphausia superba*) and prey for sperm whales in the Southern Ocean. In: Sahrhage D (ed) Antarctic Ocean and resources variability. Springer-Verlag, Berlin Heidelberg, pp 292–296

Newsome SD, del Rios CM, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. Front Ecol Environ 5:429–436

Norse EA, Brooke S, Cheung WWL, Clark MR, Ekeland I, Froese R, Gjerde KM, Haedrich RL, Heppell SS, Morato T, Morgan LE, Pauly D, Sumaila R, Watson R (2012) Sustainability of deep-sea fisheries. Mar Policy 36:307–320

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Braak C, Weedon J. 2022. *Vegan*: community ecology package. R package version 2.6–4.

Orsi AH, Nowlin WD, Whitworth T (1993) On the circulation and stratification of the Weddell Gyre. Deep Sea Res Part I 40:169–203

Pakhomov EA (1998) Feeding plasticity of the Antarctic fish *Trematomus hansoni* Boulenger, 1902 (Pisces: Nototheniidae): the influence of fishery waste on the diet. Polar Biol 19:289–292

Pakhomov EA, Froneman PW, Perissinotto R (2002) Salp/krill interactions in the Southern Ocean: spatial segregation and implications for the carbon flux. Deep Sea Res Part II 49:1881–1907

Pakhomov EA, Henschke N, Hunt BPV, Stowasser G, Cherel Y (2019) Utility of salps as a baseline proxy for food web studies. J Plankton Res 41:3–11

Papadimitraki M, Maar K, Jónasdóttir SH (2023) Meso- and bathypelagic fish feeding ecology: a meta-analysis on fatty acids and stable isotope trophic studies. Deep Sea Res Part I 198:104083

Parzanini C, Parrish CC, Hamel J-F, Mercier A (2018) Trophic relationships of deep-sea benthic invertebrates on a continental margin in the NW Atlantic inferred by stable isotope, elemental, and fatty acid composition. Prog Oceanogr 168:279–295

Parzanini C, Parrish CC, Hamel JF, Mercier A (2019) Reviews and syntheses: Insights into deep-sea food webs and global environmental gradients revealed by stable isotope (δ^{15}N, δ^{13}C) and fatty acid trophic biomarkers. Biogeosciences 16:2837–2856

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18:293–320

Phillips RA, Wood AG (2020) Variation in live-capture rates of albatrosses and petrels in fisheries, post-release survival and implications for management. Biol Conserv 247:108641

Pietzsch BW, Schmidt A, Groeneveld J, Bahlburg D, Meyer B, Berger U (2023) The impact of salps (*Salpa thompsoni*) on the Antarctic krill population (*Euphausia superba*): an individual-based modelling study. Ecol Process 12:50

Pilling GM, Purves MG, Daw TM, Agnew DA, Xavier JC (2001) The stomach contents of Patagonian toothfish around South Georgia (South Atlantic). J Fish Biol 59:1370–1384

Pimm SL, Lawton JH (1977) Number of trophic levels in ecological communities. Nature 268:329–331

Pinkerton MH, Bradford-Grieve JM (2014) Characterizing foodweb structure to identify potential ecosystem effects of fishing in the Ross Sea, Antarctica. ICES J Mar Sci 71:1542–1553

Pinsky ML, Selden RL, Kitchel ZJ (2020) Climate-driven shifts in marine species ranges: scaling from organisms to communities. Ann Rev Mar Sci 12:153–179

Post DM (2002a) The long and short of food-chain length. Trends Ecol Evol 17:269–277

Post DM (2002b) Using stable isotopes to estimate trophic position: models, methods and assumptions. Ecology 83:703–718

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179–189

Preciado I, Cartes JE, Punzón A, Frutos I, López-López L, Serrano A (2017) Food web functioning of the benthopelagic community in a deep-sea seamount based on diet and stable isotope analyses. Deep Sea Res Part II 137:56–68

Pérez-Pezoa K, Cárdenas CA, González-Aravena M, Gallardo P, Rivero A, Arriagada V, Demianenko K, Zabroda P, Santa CF (2023) Trophodynamics of the Antarctic toothfish (*Dissostichus mawsoni*) in the Antarctic peninsula: ontogenetic changes in diet composition and prey fatty acid profiles. PLoS ONE 18:e0287376

Queirós JP, Borras-Chavez R, Friscourt N, Groß J, Lewis CB, Mergard G, O'Brien K (2024a) Southern Ocean food-webs and climate change: A short review and future directions. PLOS Climate 3:e0000358

Queirós JP, Cherel Y, Ceia FR, Hilário A, Roberts J, Xavier JC (2018) Ontogenic changes in habitat and trophic ecology in the Antarctic squid *Kondakovia longimana* derived from isotopic analysis on beaks. Polar Biol 41:2409–2421

Queirós JP, Hilário A, Thompson DR, Ceia FR, Elliott G, Walker K, Cherel Y, Xavier JC (2021) From warm to cold waters: new insights into the habitat and trophic ecology of Southern Ocean squids throughout their life cycle. Mar Ecol Prog Ser 659:113–126

Queirós JP, Hollyman PR, Bustamante P, Vaz D, Belchier M, Xavier JC (2025) Deep-sea food-web structure at South Sandwich Islands (Southern Ocean): net primary production as a main driver for interannual changes. Ecography 2025:e07263

Queirós JP, Stevens DW, Pinkerton MH, Rosa R, Duarte B, Baeta A, Ramos JA, Xavier JC (2022) Feeding and trophic ecology of Antarctic toothfish *Dissostichus mawsoni* in the Amundsen and Dumont D'Urville Seas (Antarctica). Hydrobiologia 849:2317–2333

Queirós JP, Xavier JC, Abreu J, Collins MA, Belchier M, Hollyman PR (2024b) What inhabits the South Sandwich Islands deep-sea? Biodiversity and biogeography of bathyal communities using predators as biological samplers. Deep Sea Res Part I 205:104260

R core team. 2022. R: A language and environment for statistical computing. https://www.r-project.org/

Ratcliffe N, Trathan P (2011) A review of the diet and at-sea distribution of penguins breeding within the CAMLR convention area. CCAMLR Sci 18:75–114

Rau GH, Ainley DG, Bengtson JL, Torres JJ, Hopkins TL (1992) $^{15}N/^{14}N$ and $^{13}C/^{12}C$ in Weddell Sea birds, seals, and fish: implications for diet and trophic structure. Mar Ecol Prog Ser 84:1–8

Reid K. 1996. A guide to the use of otoliths in the study of predators at South Georgia. Cambridge, UK: British Antarctic Survey, Natural Environmental Research Council

Remeslo AV, Yakushev MR, Laptikhovsky V (2015) Alien vs. Predator: interactions between the colossal squid (*Mesonychoteuthis hamiltoni*) and the Antarctic toothfish (*Dissostichus mawsoni*). J Nat Hist 49:2483–2491

Rintoul SR (2018) The global influence of localized dynamics in the Southern Ocean. Nature 558:209–218

Roberts J, Xavier JC, Agnew DJ (2011) The diet of toothfish species *Dissostichus eleginoides* and *Dissostichus mawsoni* with overlapping distributions. J Fish Biol 79:138–154

Roberts JO. 2012. Ecology and management of range edge populations: the case of toothfish species at the South Sandwich Islands. Division of Ecology and Evolution Doctoral.

Rogers AD (2015) Environmental change in the deep ocean. Annu Rev Environ Resour 40:1–38

Rogers AD, Frinault BAV, Barnes DKA, Bindoff NL, Downie R, Ducklow HW, Friedlaender AS, Hart T, Hill SL, Hofmann EE, Linse K, McMahon CR, Murphy EJ, Pakhomov EA, Reygondeau G, Staniland IJ, Wolf-Gladrow DA, Wright RM (2020) Antarctic futures: an assessment of climate-driven changes in ecosystem, structure, function, and service provisioning in the Southern Ocean. Ann Rev Mar Sci 12:87–120

Rossi L, Sporta Caputi S, Calizza E, Careddu G, Oliverio M, Schiaparelli S, Costantini ML (2019) Antarctic food web architecture under varying dynamics of sea ice cover. Sci Rep 9:12454

Saporiti F, Bearhop S, Vales DG, Silva L, Zenteno L, Tavares M, Crespo EA, Cardona L (2015) Latitudinal changes in the structure of marine food webs in the Southwestern Atlantic Ocean. Mar Ecol Prog Ser 538:23–34

Saunders RA, Collins MA, Stowasser G, Tarling GA (2017) Southern Ocean mesopelagic fish communities in the Scotia Sea are sustained by mass immigration. Mar Ecol Prog Ser 569:173–185

Seco J, Aparício S, Brierley AS, Bustamante P, Ceia FR, Coelho JP, Philips RA, Saunders RA, Fielding S, Gregory S, Matias R, Pardal MA, Pereira E, Stowasser G, Tarling GA, Xavier JC (2021) Mercury biomagnification in a Southern Ocean food web. Environ Pollut 275:116620

Seco J, Roberts J, Ceia FR, Baeta A, Ramos JA, Paiva VH, Xavier JC (2016) Distribution, habitat and trophic ecology of Antarctic squid *Kondakovia longimana* and *Moroteuthis knipovitchi*: inferences from predators and stable isotopes. Polar Biol 39:167–175

Sexton JP, McIntyre PJ, Angert AL, Rice KJ (2009) Evolution and ecology of species range limits. Annu Rev Ecol Evol Syst 40:415–436

Silver MW, Alldredge AL (1981) Bathypelagic marine snow: Deep-sea algal and detrital community. J Mar Res 39:501–530

Soeffker M, Hollyman PR, Collins MA, Hogg OT, Riley A, Laptikhovsky V, Earl T, Roberts J, MacLeod E, Belchier M, Darby

C (2022) Contrasting life-history traits of two toothfish (*Dissostichus*) species at their range edge around the South Sandwich Islands. Deep Sea Res Part II. 201:105098

Sokolov S, Rintoul SR (2007) On the relationship between fronts of the Antarctic circumpolar current and surface chlorophyll concentrations in the Southern Ocean. J Geophys Res 112:C07030

Stowasser G, Atkinson A, McGill RAR, Phillips RA, Collins MA, Pond DW (2012a) Food web dynamics in the Scotia Sea in summer: a stable isotope study. Deep Sea Res Part II 59–60:208–221

Stowasser G, McAllen R, Pierce GJ, Collins MA, Moffat CF, Priede IG, Pond DW (2009a) Trophic position of deep-sea fish—assessment through fatty acid and stable isotope analyses. Deep Sea Res Part I 56:812–826

Stowasser G, Pond DW, Collins MA (2009b) Using fatty acid analysis to elucidate the feeding habits of Southern Ocean mesopelagic fish. Mar Biol 156:2289–2302

Stowasser G, Pond DW, Collins MA (2012b) Fatty acid trophic markers elucidate resource partitioning within the demersal fish community of South Georgia and Shag Rocks (Southern Ocean). Mar Biol 159:2299–2310

Tarling GA, Thorpe SE, Henley SF, Burson A, Liszka CM, Manno C, Lucas NS, Ward F, Hendry KR, Malcolm S, Woodward E, Wootton M, Povl AE (2024) Collapse of a giant iceberg in a dynamic southern ocean marine ecosystem: in situ observations of A-68A at South Georgia. Prog Oceanogr 226:103297

Thorpe SE, Murphy EJ (2022) Spatial and temporal variability and connectivity of the marine environment of the South Sandwich Islands, Southern Ocean. Deep Sea Res Part II 198:105057

Trathan PN, Collins MA, Grant SM, Belchier M, Barnes DK, Brown J, Staniland IJ (2014) The South Georgia and the South Sandwich Islands MPA: protecting a biodiverse oceanic island chain situated in the flow of the Antarctic Circumpolar Current. Adv Mar Biol 69:15–78

Trathan PN. 2023. The future of the South Georgia and South Sandwich Islands marine protected area in a changing environment: the choice between industrial fisheries, or ecosystem protection. Mar Policy 155.

Trochta JT, Pons M, Rudd MB, Krigbaum M, Tanz A, Hilborn R (2018) Ecosystem-based fisheries management: perception on definitions, implementations, and aspirations. PLoS ONE 13:e0190467

Vanderklift MA, Ponsard S (2003) Sources of variation in consumer-diet δ^{15}N enrichment: a meta-analysis. Oecologia 136:169–182

Wagner D, Luck DG, Toonen RJ (2012) The biology and ecology of black corals (Cnidaria: Anthozoa: Hexacorallia: Antipatharia). Adv Mar Biol 63:67–132

Ward P, Atkinson A, Peck JM, Wood AG (1990) Euphausiid life cycles and distribution around South Georgia. Antarct Sci 2:43–52

Whitehouse MJ, Meredith MP, Rothery P, Atkinson A, Ward P, Korb RE (2008) Rapid warming of the ocean around South Georgia, Southern Ocean, during the 20th century: Forcings, characteristics and implications for lower trophic levels. Deep Sea Res Part I 55:1218–1228

Xavier JC, Cherel Y (2021) Cephalopod beak guide for the Southern Ocean: an update on taxonomy. British Antarctic Survey, Cambridge

Xavier JC, Cherel Y, Boxshall G, Brandt A, Coffer T, Forman J, Havermans C, Jazdzewska AM, Kouwenberg J, Schiaparelli S, Schnabel K, Siegel V, Tarling GA, Thatje S, Ward P, Gutt J (2020) Crustacean guide for predator studies in the Southern Ocean. Scientific Committee on Antarctic Research, UK, Cambridge

Xavier JC, Phillips RA, Takahashi A (2022) Antarctic Seabirds as indicators of climate change. In: Ramos JA, Pereira L (eds) Seabird Biodiversity and Human Activities. CRC Press, Boca Raton, pp 189–210

Yang G, Atkinson A, Pakhomov EA, Hill SL, Racault M (2022) Massive circumpolar biomass of Southern Ocean zooplankton: Implications for food web structure, carbon export, and marine spatial planning. Limnol Oceanogr 67:2516–2530

Yoon T-H, Kang H-E, Lee SR, Lee J-B, Baeck GW, Park H, Kim H-W (2017) Metabarcoding analysis of the stomach contents of the Antarctic Toothfish (*Dissostichus mawsoni*) collected in the Antarctic Ocean. PeerJ 5:e3977

Zenteno L, Cárdenas L, Valdivia N, Gómez I, Höfer J, Garrido I, Pardo LM (2019) Unraveling the multiple bottom-up supplies of an Antarctic nearshore benthic community. Prog Oceanogr 174:55–63

Zwerschke N, Morley SA, Peck LS, Barnes DKA (2021) Can Antarctica's shallow zoobenthos 'bounce back' from iceberg scouring impacts driven by climate change? Glob Chang Biol 27:3157–3165

Terms and Conditions

Springer Nature journal content, brought to you courtesy of Springer Nature Customer Service Center GmbH (“Springer Nature”).

Springer Nature supports a reasonable amount of sharing of research papers by authors, subscribers and authorised users (“Users”), for small-scale personal, non-commercial use provided that all copyright, trade and service marks and other proprietary notices are maintained. By accessing, sharing, receiving or otherwise using the Springer Nature journal content you agree to these terms of use (“Terms”). For these purposes, Springer Nature considers academic use (by researchers and students) to be non-commercial.

These Terms are supplementary and will apply in addition to any applicable website terms and conditions, a relevant site licence or a personal subscription. These Terms will prevail over any conflict or ambiguity with regards to the relevant terms, a site licence or a personal subscription (to the extent of the conflict or ambiguity only). For Creative Commons-licensed articles, the terms of the Creative Commons license used will apply.

We collect and use personal data to provide access to the Springer Nature journal content. We may also use these personal data internally within ResearchGate and Springer Nature and as agreed share it, in an anonymised way, for purposes of tracking, analysis and reporting. We will not otherwise disclose your personal data outside the ResearchGate or the Springer Nature group of companies unless we have your permission as detailed in the Privacy Policy.

While Users may use the Springer Nature journal content for small scale, personal non-commercial use, it is important to note that Users may not:

1. use such content for the purpose of providing other users with access on a regular or large scale basis or as a means to circumvent access control;
2. use such content where to do so would be considered a criminal or statutory offence in any jurisdiction, or gives rise to civil liability, or is otherwise unlawful;
3. falsely or misleadingly imply or suggest endorsement, approval , sponsorship, or association unless explicitly agreed to by Springer Nature in writing;
4. use bots or other automated methods to access the content or redirect messages
5. override any security feature or exclusionary protocol; or
6. share the content in order to create substitute for Springer Nature products or services or a systematic database of Springer Nature journal content.

In line with the restriction against commercial use, Springer Nature does not permit the creation of a product or service that creates revenue, royalties, rent or income from our content or its inclusion as part of a paid for service or for other commercial gain. Springer Nature journal content cannot be used for inter-library loans and librarians may not upload Springer Nature journal content on a large scale into their, or any other, institutional repository.

These terms of use are reviewed regularly and may be amended at any time. Springer Nature is not obligated to publish any information or content on this website and may remove it or features or functionality at our sole discretion, at any time with or without notice. Springer Nature may revoke this licence to you at any time and remove access to any copies of the Springer Nature journal content which have been saved.

To the fullest extent permitted by law, Springer Nature makes no warranties, representations or guarantees to Users, either express or implied with respect to the Springer nature journal content and all parties disclaim and waive any implied warranties or warranties imposed by law, including merchantability or fitness for any particular purpose.

Please note that these rights do not automatically extend to content, data or other material published by Springer Nature that may be licensed from third parties.

If you would like to use or distribute our Springer Nature journal content to a wider audience or on a regular basis or in any other manner not expressly permitted by these Terms, please contact Springer Nature at

onlineservice@springernature.com