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Research article

Deep-sea food-web structure at South Sandwich Islands (Southern Ocean): net primary production as a main driver for interannual changes

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Food-webs are a major component of ecosystems and determinant for their functioning and structure. The food chain length (FCL) is a key feature of food-webs and it is crucial for the resistance of the community to external stressors. The Southern Ocean (SO) food-web is known for being short and dominated by an Antarctic krill *Euphausia superba* surplus, though recent studies proved the existence of different pathways. However, previous studies focused on the pelagic realm, with the deep-sea and benthopelagic coupling remaining poorly understood. Using stable isotopes of δ^{13}C and δ^{15}N in muscle from individuals collected during toothfish fishing seasons 2020, 2021 and 2022, we 1) studied the bathyal food-web structure at South Sandwich Islands; 2) evaluated the interannual variability of FCL; and 3) tested which FCL hypothesis better explains the variability at the SO deep-sea. Our results show that this food-web is composed of five trophic levels with both Patagonian *Dissostichus eleginoides* and Antarctic *Dissostichus mawsoni* toothfish as top predators. The 4th and 5th trophic levels are mostly composed of fish, while in the 3rd trophic level we mainly found cephalopods and crustaceans. The benthopelagic coupling occurs at different trophic levels, though mostly between the 3rd and 4th trophic level. The FCL varied between years, being in 2022 0.30 trophic levels shorter than in 2020. Our results suggest that food-webs including a benthic component are longer than pelagic and coastal SO food-webs. The FCL is positively related with net primary productivity, supporting that the productivity hypothesis explains the variability in FCL in SO bathyal food-webs in slope and seamount areas. With climate change, the productivity in the SO is expected to increase which will increase the length of the food-web. This change will

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affect the structure of the ecosystem, increasing assimilation losses, exposure to biomagnifying contaminants and changing nutrient cycles.

Keywords: Antarctica, bathyal, benthopelagic coupling, food chain length, predator–prey interaction.

Introduction

Food-webs represent predator–prey interactions within an ecosystem (Dunne et al. 2002). Food-web structure gives information on, for example, energy and nutrients fluxes, but also how communities respond to external stressors like climate change or fisheries (Pimm et al. 1991, Post 2002a, Hette-Tronquart et al. 2013, Pinsky et al. 2020). The food chain length (FCL) is a key feature of food-webs that largely influence the structure and processes in an ecosystem, and how communities respond to such stressors (Post 2002a, Hette-Tronquart et al. 2013). The FCL can be determined either by the number of links connecting the primary producer to the top predator, or by the trophic position of the top predator (Post 2002a). Several hypotheses have been proposed to explain FCL variation across ecosystems, e.g.: productivity hypothesis which states that more productive systems have longer food-chains (Elton 1927); ecosystem size hypothesis where larger, three-dimensional (i.e. including both horizontal – latitude and longitude – and vertical – depth – dimensions), ecosystems support longer food-chains (Schoener 1989); and dynamic-stability hypothesis proposing that disturbed systems have shorter food-chains (Pimm and Lawton 1977). Hette-Tronquart et al. (2013) showed that in marine environments the dynamic-stability hypothesis can be tested by using the variability of water temperature as a proxy for the disturbance of the system, i.e. the more variability in the water temperature the more disturbed is the system and consequently the shorter is the FCL. Several studies have analysed the structure and the FCL of marine food-webs worldwide (Hette-Tronquart et al. 2013, Saporiti et al. 2015, Vinagre et al. 2015, Kortsch et al. 2019). However, studies in the Southern Ocean remain scarce.

The Southern Ocean food-webs are characterised by a high number of basal species (de Santana et al. 2013, Marina et al. 2018, Caputi et al. 2020, McCormack et al. 2020). A long-standing theory suggests a short food-web with Antarctic Krill *Euphausia superba* assuming a major role connecting primary producers to top predators (Everson 1977, Benninghoff 1987). However, recent studies proved the existence of several distinct, but equally important, pathways where other krill species, fish and cephalopods assume a major role of connecting the base of the food-web with the higher predators (La Mesa et al. 2004, Murphy et al. 2007, McCormack et al. 2020). These studies also showed regional differences in the food-webs (McCormack et al. 2020, Hill et al. 2021). The Southern Ocean food-webs are controlled by both top–down (i.e. predators control consumer populations) and bottom–up (i.e. environment influences the food-web) effects (Schaafsma et al. 2018, Atkinson et al. 2019). Therefore, these food-webs are vulnerable to environmental variability and climate change (de Santana et al. 2013, Chown et al. 2015). This is of particular concern because the Southern Ocean is one of the regions most affected by climate change (Constable et al. 2014, IPCC 2018, Rintoul et al. 2018, Rogers et al. 2020). Such a threat highlights the necessity to understand which environmental variables influence food-web structure, including the FCL. Moreover, with few exceptions that included demersal and benthic components in the high seas (Pinkerton and Bradford-Grieve 2014), most studies in the Southern Ocean focused on the shelf, including benthic food-webs, and pelagic realm (Stowasser et al. 2012, Murphy et al. 2013, Ortiz et al. 2016, Rossi et al. 2019, Caputi et al. 2020, McCormack et al. 2021). Consequently, a gap of knowledge persists regarding the deep-sea Southern Ocean food-webs.

The lack of studies regarding deep-sea food-webs result from the impossibility of visual observation of predator–prey interactions (Choy et al. 2017). In addition, several challenges are associated with the study of deep-sea ecosystems that preclude a better knowledge of the trophic interactions in this ecosystem, e.g. high logistical cost to sample the deep-sea, need for specific equipment to sample at large depths, and longer field seasons to properly sample the deep-sea biodiversity, some of which patchily distributed (Kaiser and Barnes 2008, Ramirez-Llodra et al. 2010, Danovaro et al. 2014). In the Southern Ocean, these barriers are even more evident by the high logistical costs to operate in the region (Griffiths 2010). Furthermore, deep-sea organisms tend to regurgitate when pulled to the surface, which frequently precludes the study of stomach contents and demands a large number of samples to obtain a good description of the diet (Kelly and Scheibling 2012, Drazen and Sutton 2017). The use of trophic proxies such as stable isotopes can overcome these barriers (Drazen and Sutton 2017). Stable isotopic analyses, especially of carbon-13 ($\delta^{13}C$) and nitrogen-15 ($\delta^{15}N$), have been widely used to study marine food-webs worldwide (Stowasser et al. 2012, Saporiti et al. 2015, Vinagre et al. 2015). $\delta^{13}C$ values are relatively stable through the trophic levels and are used to determine the carbon source in the food-web (Peterson and Fry 1987, Newsome et al. 2007). In contrast, $\delta^{15}N$ values increase along the food-web and are used to determine the trophic level of organisms (Minagawa and Wada 1984, Vanderklift and Ponsard 2003, Bearhop et al. 2004). Therefore, measuring $\delta^{15}N$ values in top predators allows to determine the FCL of an ecosystem (Post 2002b).

In this study, we used stable isotopes of $\delta^{13}C$ and $\delta^{15}N$ to study the deep-sea food-web in the South Sandwich Islands archipelago in three different years (i.e. 2020, 2021 and 2022). Our aims are to 1) characterise the structure (i.e.

species composition of trophic levels, FCL and benthopelagic coupling) of the bathyal food-web at South Sandwich Islands; 2) evaluate how the structure and FCL change between years; and 3) test which FCL hypothesis better explains differences in the FCL during the study period. For that, we sampled fish captured during toothfish *Dissostichus* sp. fishing operations at South Sandwich Islands, using the target species (*Dissostichus eleginoides* and *D. mawsoni*, Patagonian and Antarctic toothfishes, respectively) and, at lower extent, non-target species as biological samplers for the lower trophic levels, as well as sampling directly target and non-target species caught in the longlines. Since both toothfish species are generalist feeders and deep-sea top predators in the Southern Ocean, they provide reliable information to test the mentioned FCL hypotheses (Pilling et al. 2001, Roberts et al. 2011, Queirós et al. 2022). Furthermore, the South Sandwich Islands present interannual variability in the environmental conditions (Thorpe and Murphy 2022) make this archipelago an ideal location to study the interannual variability in the deep-sea food-web structure and to test FCL hypotheses.

Material and methods

Study area

This study was conducted at South Sandwich Islands in the Atlantic sector of the Southern Ocean (Fig. 1). The South Sandwich Islands is an archipelago comprising a north-south arc of 11 islands situated in the eastern side of the Scotia Sea (Hart and Convey 2018, Collins et al. 2022). It is located within the South Georgia and South Sandwich Islands Marine Protected Area (SGSSI MPA), which aims to preserve the biodiversity and ecosystem function whilst maintaining a sustainable and highly regulated fisheries in the area (Trathan et al. 2014, Belchier et al. 2022). Three fisheries are licensed within the MPA targeting *D. eleginoides* and *D. mawsoni* (toothfish fishery), *E. superba* (krill fishery) and mackerel icefish (*Champsocephalus gunnari*, icefish fishery) (Trathan et al. 2014, Belchier et al. 2022). These fisheries are managed by the Government of SGSSI following the conservation measures agreed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), which adopts a precautionary and ecosystem-based management (CAMLR 1980, Wendebourg 2020, Goldsworthy and Brennan 2021). The ecosystem-based management demands that ecosystems connections, e.g. predator–prey, are maintained (Trochta et al. 2018). Toothfish fisheries at South Sandwich Islands have a total coverage of scientific observers under the CCAMLR Scheme of International Scientific Observation (SISO), which provide essential data to assess the impact of the fishery on the ecosystem (Sabourenkov and Appleyard 2005). Also, it allows a consistent sampling throughout the archipelago and the collection of sufficient number of samples to study several trophic levels and taxa.

Oceanographically, the South Sandwich Islands are located south of the Southern Boundary of the Antarctic Circumpolar Current, though with influence of the Antarctic Circumpolar Current in the northern area, and within the

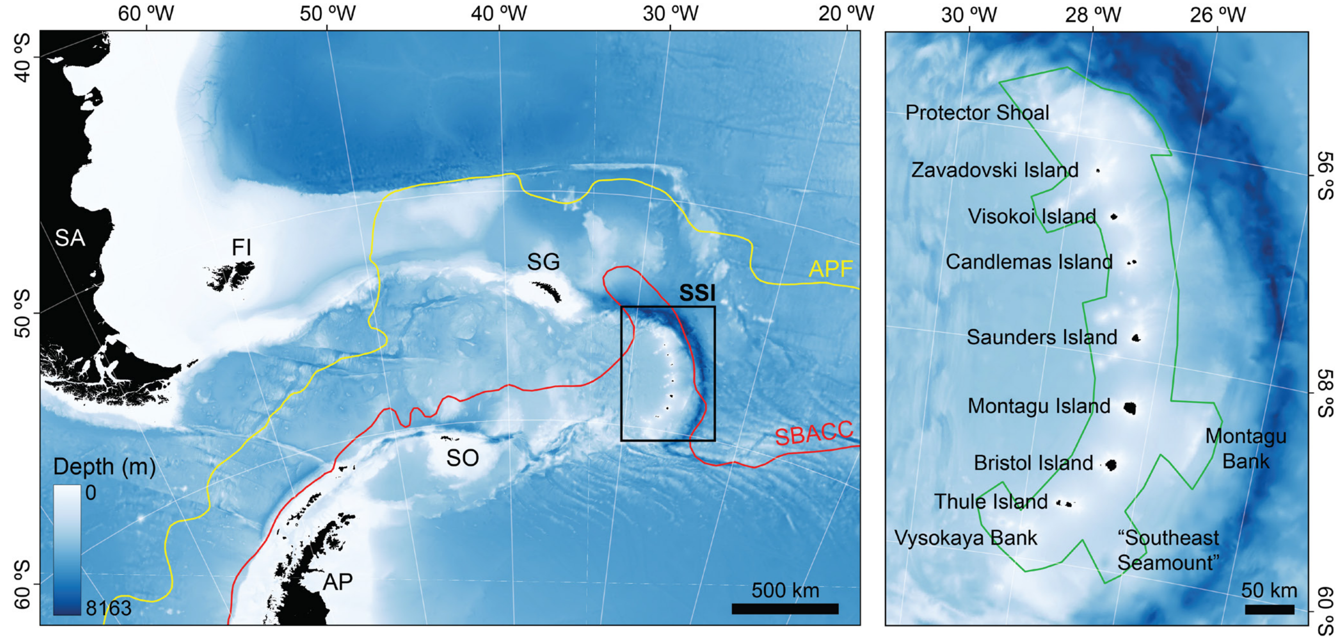

Figure 1. South Sandwich Islands (SSI) archipelago and its location in the Atlantic sector of the Southern Ocean. The green line shows the limit of the study area. APF (yellow line): Antarctic Polar Front; SBACC (red line): Southern Boundary of the Antarctic Circumpolar Current; SA: South America; FI: Falklands Islands; SG: South Georgia; SO: South Orkneys; AP: Antarctic Peninsula. Names in the right panel refer to islands, banks and seamounts in the SSI archipelago. Bathymetry retrieved from GEBCO (www.gebco.net).

influence zone of the Weddell Gyre in the southern area (Thorpe and Murphy 2022). This creates an environmental gradient with warmer waters to the north and cold Antarctic waters to the south of the archipelago (Thorpe and Murphy 2022). Such a gradient is reflected in the species inhabiting the archipelago with typical sub-Antarctic and Antarctic species in the north and south areas respectively (Downie et al. 2021, Hogg et al. 2021, Hollyman et al. 2022, Soeffker et al. 2022, Queirós et al. 2024a). The South Sandwich Islands also present strong interannual variability in temperature, sea ice extent, productivity, and chlorophyll a bloom (Hart and Convey 2018, Thorpe and Murphy 2022).

Sample collection

The samples were collected between 55°–60°S and 25°–29°W on board industrial demersal longliners operating in CCAMLR Small Scale Research Unit (SSRU) 48.4 during the toothfish fishing seasons 2020 (March and April), 2021 (March and April) and 2022 (April and May) (Fig. 1). Muscle samples of approximately 20 g of several target (*D. eleginoides* and *D. mawsoni*) and non-target (Antarctic starry skate *Amblyraja* sp., blue antimora *Antimora rostrata*, caml grenadier *Macrourus caml,* Whitson's grenadier *Macrourus whitsoni* and eel cods *Muraenolepis* sp.) species were collected from individuals caught on the longline. Occasionally, individuals from other species (e.g. Antarctic dragonfishes *Bathydraco* sp.) were also sampled from the longline. Muscle from both toothfish species was extracted from the posterior area of the fish's head, while for the other species it was extracted from the lateral region of the body. An exception was *Amblyraja* sp. whose muscle was extracted from the wing.

Muscle of other species was sampled from fresh specimens identified in the stomachs of predators (i.e. both target and non-target species in the longlines). Stomachs of *D. mawsoni* (n = 248)*, D. eleginoides* (n = 209)*, Macrourus* spp. (n = 50), *Amblyraja* sp. (n = 30), *Muraenolepis* sp. (n = 15), rockcods *Lepidonotothen* sp. (n = 3), giant warty squid *Moroteuthopsis longimana* (n = 2), and *A. rostrata*, barbeled plunderfish *Artedridraco* sp., *Bathydraco* sp., abyssal grenadier *Coryphaenoides armatus* and smooth hooked squid *Filippovia knipovitchi* (n = 1) were sampled from individuals captured on the longlines and from fresh individuals found in the stomachs of both *Dissostichus* species. Stomachs collected aboard were individually bagged and frozen until further analyses in the laboratory. Stomachs were processed both at the British Antarctic Survey (United Kingdom) and King Edward Point (South Georgia). Stomach contents were identified to the lowest possible taxonomic resolution using published identification guides (Williams and McEldowney 1990, Reid 1996, Xavier et al. 2020, Xavier and Cherel 2021) and reference collections in both laboratories. In prey species, muscle (approximately 10 g, when possible) was sampled from the lateral region of the body (fish), buccal mass (cephalopods), and body and legs (crustaceans). Pectoral muscle of chinstrap penguin *Pygoscelis antarcticus* was collected from individuals found in stomachs of *D. mawsoni*. Holothurian samples were obtained from the body wall. All samples were kept frozen at −20°C until stable isotopic analyses.

Stable isotopic analyses

In the laboratory, a subsample (approximately 2 g) of the frozen muscle fillet was transferred to a microtube and freeze-dried for 36 h. The dried samples were ground to a fine powder and lipids extracted using three successive rinses of cyclohexane. Lipid extraction was necessary because lipids are enriched in ^{13}C, so variation in the lipid content between species can affect the isotopic results (Post et al. 2007). The success of lipid extraction was assured by the C/N ratios found across species. Individuals whose C/N ratio was lower than 2.6 or higher than 4.1 were excluded from the study. After lipid extraction, the samples were dried overnight in an oven at 45°C. Between 0.2 and 0.4 mg of sample was weighted in a tin capsule using a Mettler Toledo microbalance. Carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope ratios were measured by a continuous flow mass spectrometer (Thermo Scientific Delta V Plus – Isotope Ratio Mass Spectrometer) coupled to an elemental analyser (Thermo Scientific Flash 2000). The results are presented following the δ-notation in ‰ (per mille) and were normalised using the Vienna Pee Dee Belemnite (VPDB) and atmospheric nitrogen (Air-N_2) for carbon and nitrogen respectively. Values were normalised using USGS-61 and USGS-63 (Caffeine, United States Geological Survey) as reference materials. Replicate measurements of reference materials throughout the analyses showed an uncertainty < 0.10‰ for δ^{13}C and < 0.14‰ for δ^{15}N for all sample runs. Stable isotopic analyses were performed at the Littoral, Environment and Societies (LIENSs) laboratory at the University of La Rochelle, France.

Environmental data

Monthly and daily (only for temperature) values for sea surface temperature (SST in °C), temperature at sea floor (TSF in °C), sea ice thickness (SIT in m), chlorophyll a concentration (Chl in mg m^{-3}) and net primary productivity (NPP in mg m^{-3} day^{-1}) were downloaded from the EU Copernicus Marine Service Information (https://marine.copernicus.eu). SST, TSF and SIT were extracted from Global Ocean Physics Reanalysis (2020) and Global Ocean Physics Analysis and Forecast (2021 and 2022) at a grid of 0.083°. Chl and NPP were extracted from Global Ocean Biochemistry Hindcast (2020) and Global Ocean Biochemistry Analysis and Forecast (2021 and 2002) at a resolution of 0.25°.

In QGIS 3.20 Odense, the mean and standard deviation per year of each pixel e.g. 2020 value is the mean of monthly values of March and April, were calculated using the *Raster analysis – cell statistics* function using a polygon limiting the study area (Fig. 1). The variance of daily SST (σ^2SST) and TSF (σ^2TSF) during the two months in each pixel was calculated using the same function. Mean and standard deviation of variables for the study area were calculated with the *Raster analysis – zonal statistics* function for a polygon that comprised all fishing lines deployed during the study period (Fig. 1).

Data analyses

We estimated the trophic position (TP) of each individual using the following equation:

$$TP = \frac{\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{primary consumer}}}{3.4} + \lambda$$

where $\delta^{15}N_{\text{consumer}}$ is the $\delta^{15}N$ value of the individual; $\delta^{15}N_{\text{primary consumer}}$ is the $\delta^{15}N$ value of a species with known TP; 3.4 is the trophic enrichment most commonly used in marine ecosystems (Minagawa and Wada 1984, Post 2002b, Vander Zanden and Fetzer 2007, Stowasser et al. 2012, Vinagre et al. 2015); and λ is the known TP of the primary consumer. Following Stowasser et al. (2012) and Cherel et al. (2010), we considered the salp *Salpa thompsoni* as a primary consumer and used it as baseline to estimate the TP of the studied species. This species is a known filter feeding grazer that feeds on phytoplankton, thus with a known trophic level of 2, and abundant in the Southern Ocean (Perissinotto and Pakhomov 1998, Pakhomov et al. 2006). As we did not analyse *S. thompsoni*, we calculated an average value from the two most recent $\delta^{15}N$ values for the Scotia Sea, i.e. 3.5 (Stowasser et al. 2012, Seco et al. 2021). However, we must be aware that recent evidence suggests that this species may not be the best baseline, but copepods, as *S. thompsoni* may select its food and not entirely reflect the baseline of the system (Pakhomov et al. 2019). Nonetheless, the use of *S. thompsoni* allows for the comparison with previous studies. The FCL was considered as the highest TP measured in the food chain. To test differences in the FCL between the three study years, a Kruskal–Wallis test followed by a Dunn's multiple comparison test was performed considering the estimated TP of all individuals of *D. eleginoides* (the species with highest TP) in the three studied years.

To test if $\delta^{13}C$ values increased with TP a Spearman correlation was performed for the three years and considering all species together. To evaluate changes in species TP between the three studied years, significant differences in $\delta^{15}N$ values were tested for species with at least four values measured per year. An ANOVA followed by a Tukey's multiple comparison test (parametric data) was performed for *D. mawsoni, M. whitsoni* and *Muraenolepis* sp., while a Kruskal–Wallis followed by a Dunn's multiple comparison test (non-parametric data) was used for *A. rostrata, D. eleginoides, M. caml, M. longimana* and the shrimp *Nematocarcinus* sp. Exceptions were *Amblyraja* sp. (2021 and 2022) and *F. knipovitchi* (2020 and 2022) whose differences were tested with a Mann–Whitney test due to the low number of samples collected in one of the three study years (i.e. four samples were only collected in two of the three studied years). These tests were preceded by a Shapiro–Wilk normality test and a Bartlett's test for homogeneity of variances.

To evaluate the influence of environmental variables on the FCL of the food-web, we performed a linear regression between the FCL and SST, TSF, SIT, Chl, NPP, σ^2SST and σ^2TSF.

All statistical tests were performed in GraphPad Prism ver. 9.5.1 considering an $\alpha = 5\%$. Plots were prepared in Adobe Illustrator ver. 26.4.1.

Results

Dissostichus eleginoides was the species with highest $\delta^{15}N$ values, and consequently TP, for the three studied years, followed by *D. mawsoni* (Table 1, Fig. 2). In 2020, the Euphausiids were the taxa with the lowest $\delta^{15}N$ values, though in 2021 and 2022 the lowest values were recorded for *P. antarcticus* (Table 1, Fig. 2). The range of $\delta^{13}C$ values varied across years, with 2020 having a wider range, i.e. from −27.07‰ to −20.45‰ (range = 6.62‰), contrasting with 2022 when $\delta^{13}C$ range was of 4.67‰ (Table 1, Fig. 2). Significant correlations were found between the $\delta^{13}C$ values and TP in the three study years (Spearman correlation: 2020, $p < 0.001$, $r = 0.431$; 2021, $p < 0.001$, $r = 0.326$; 2022, $p < 0.001$, $r = 0.368$).

The longest food chain in this study was recorded in 2020 (FCL = 5.48), followed by 2021 (FCL = 5.37) and 2022 with the shortest (FCL = 5.17) (Fig. 2). Significant differences in FCL were found for the three studied years (Kruskal–Wallis: $p = 0.011$, $H = 8.952$), with the main differences being between 2020 and 2022. Significant differences in $\delta^{15}N$ values between the three study years were found for *A. rostrata, D. eleginoides, D. mawsoni* and *Muraenolepis* sp. (Table 2).

Environmental conditions varied across the three-year period (Fig. 3). 2020 presented the highest SST (1.22 ± 0.42°C) and 2022 the highest TSF (0.12 ± 0.29°C). In contrast, 2021 had the lowest SST (0.39 ± 0.40°C) and TSF (−0.03 ± 0.16°C). 2020 was the only year with the presence of sea ice (0.008 ± 0.006 m). Regarding concentrations of Chl and NPP, 2020 and 2021 were the years with higher concentrations of Chl (0.35 ± 0.01 and 0.33 ± 0.02 mg m^{-3} respectively), with 2020 having the highest NPP (2.92 ± 0.14 mg m^{-3} day^{-1}). 2022 had the lowest Chl (0.25 ± 0.02 mg m^{-3}) and NPP (0.99 ± 0.18 mg m^{-3} day^{-1}). 2020 was the year with highest σ^2SST (0.36 ± 0.12°C) while 2021 and 2022 had similar values (0.15 ± 0.05 and 0.15 ± 0.06°C respectively). Similarly, σ^2TSF was highest at 2020 (0.005 ± 0.010°C), followed by 2021 (0.003 ± 0.009°C) and 2022 (0.003 ± 0.004°C).

A significant linear relationship was found between the FCL and the NPP ($p = 0.022$; $r^2 = 0.999$; FCL = 0.16 ± 0.01 (NPP) + 5.01 ± 0.01) (Fig. 4). No other variable, i.e. SST, TSF, SIT, σ^2SST or σ^2TSF, showed a significant relation with FCL.

Discussion

Combining the use of predators as biological samplers for lower trophic levels with stable isotopic analyses we were able to study the structure of the deep-sea food-web at South Sandwich Islands in three different years. This combination of methodologies appears as an important approach to study

Table 1. Isotope values of δ^{13}C and δ^{15}N for the studied species during the sampling period (2020–2022). n: number of individuals analysed; C/N: carbon/nitrogen mass ratio. Values are mean ± standard deviation.

Species	2020				2021				2022			
	n	δ^{13}C (‰)	δ^{15}N (‰)	C/N	n	δ^{13}C (‰)	δ^{15}N (‰)	C/N	n	δ^{13}C (‰)	δ^{5}N (‰)	C/N
Elasmobranchii												
Amblyraja sp.	2	−23.7 ± 0.1	11.2 ± 0.1	3.0 ± 0.2	12	−22.8 ± 0.3	10.9 ± 0.65	2.8 ± 0.1	18	−23.2 ± 0.5	10.7 ± 0.4	2.7 ± 0.1
Teleostei												
Anotopterus pharao	1	−25.4	9.8	3.4	0				0			
Antimora rostrata	9	−23.5 ± 0.2	11.4 ± 0.3	3.3 ± 0.0	19	−23.6 ± 0.4	11.3 ± 0.4	3.2 ± 0.0	22	−24.0 ± 0.4	10.9 ± 0.3	3.2 ± 0.0
Artedidraco sp.	1	−24.6	11.5	3.4	0				0			
Bathydraco sp.	1	−23.0	13.4	3.3	1	−23.6	11.2	3.2	5	−23.4 ± 0.4	12.4 ± 0.6	3.2 ± 0.1
Bathylagus gracilis	1	−23.4	11.5	3.3	0				0			
Channichthyidae	1	−24.3	11.9	3.2	1	−24.9	11.2	3.2	2	−24.0 ± 0.4	12.6 ± 0.4	3.2 ± 0.1
Coryphaenoides sp.	10	−23.3 ± 0.6	12.5 ± 0.3	3.2 ± 0.0	1	−25.6	13.2	3.8	0			
Dissostichus eleginoides	12	−22.6 ± 0.6	15.3 ± 0.6	3.3 ± 0.1	15	−22.7 ± 0.4	15.0 ± 0.6	3.3 ± 0.0	17	−22.9 ± 0.4	14.3 ± 1.4	3.2 ± 0.1
Dissostichus mawsoni	19	−24.3 ± 0.5	14.4 ± 0.9	3.3 ± 0.1	20	−24.4 ± 0.5	13.8 ± 0.7	3.3 ± 0.1	15	−24.7 ± 0.5	13.2 ± 0.7	3.2 ± 0.1
Gymnoscopelus sp.	0				0				1	−23.2	10.8	3.3
Icichthys australis	0				0				1	−25.0	9.2	3.4
Lepidonotothen sp.	0				0				13	−24.0 ± 0.7	11.7 ± 0.5	3.3 ± 0.2
Macrourus caml	21	−23.5 ± 0.5	11.9 ± 0.5	3.25 ± 0.1	16	−23.8 ± 0.8	11.7 ± 0.4	3.2 ± 0.0	21	−23.8 ± 0.6	11.6 ± 0.7	3.2 ± 0.1
Macrourus whitsoni	21	−23.6 ± 0.4	11.7 ± 0.4	3.24 ± 0.1	20	−23.9 ± 0.5	11.7 ± 0.4	3.2 ± 0.1	21	−23.8 ± 0.5	11.6 ± 0.6	3.2 ± 0.0
Muraenolepis sp.	25	−23.8 ± 0.5	12.3 ± 0.8	3.34 ± 0.1	20	−23.9 ± 0.5	11.7 ± 0.4	3.3 ± 0.0	20	−24.1 ± 0.5	12.0 ± 0.5	3.3 ± 0.1
Nansenia antarctica	0				0				1	−25.3	10.2	3.7
Notothenia coriiceps	0				0				1	−24.9	11.1	3.3
Racovitzia glacialis	0				0				1	−24.9	11.9	3.3
Stomiidae	0				0				2	−22.1 ± 1.2	11.3 ± 0.8	3.2 ± 0.1
Trematomus sp.	0				1	−24.9	10.6	3.3	0			
Unidentified	0				1	−22.7	12.4	3.2	0			
Cephalopoda												
Alluroteuthis antarcticus	0				1	−24.3	10.4	3.4	2	−25.3 ± 0.4	11.3 ± 0.2	3.3 ± 0.4
Filippovia knipovitchi	5	−24.4 ± 1.3	9.0 ± 0.5	3.6 ± 0.3	2	−25.0 ± 0.2	10.0 ± 0.2	3.4 ± 0.0	6	−25.8 ± 1.0	9.3 ± 0.5	3.4 ± 0.1
Galiteuthis glacialis	4	−25.5 ± 1.5	9.5 ± 0.6	3.4 ± 0.2	0				0			
Mesonychoteuthis hamiltoni	4	−24.5 ± 0.2	11.2 ± 0.7	3.5 ± 0.2	3	−23.5 ± 0.8	12.6 ± 0.6	3.4 ± 0.2	1	−22.6	11.7	3.2
Moroteuthopsis longimana	16	−25.8 ± 1.2	9.2 ± 1.0	3.2 ± 0.2	12	−25.1 ± 1.3	8.6 ± 0.7	3.2 ± 0.2	12	−26.2 ± 0.9	8.6 ± 0.6	3.3 ± 0.2
Psychroteuthis glacialis	1	−25.2	9.6	3.2	0				0			
Crustacea												
Decapoda	0				0				1	−24.7	9.7	3.3
Euphausiidae	6	−25.3 ± 1.1	6.1 ± 1.3	3.6 ± 0.1	2	−26.3 ± 0.9	8.0 ± 1.2	3.6 ± 0.2	1	−25.4	9.4	3.6
Nematocarcinus sp.	6	−25.6 ± 0.5	8.8 ± 0.4	3.6 ± 0.1	4	−25.0 ± 0.4	9.0 ± 0.3	3.3 ± 0.0	6	−24.8 ± 0.9	9.7 ± 1.0	3.3 ± 0.1
Paralomis sp.	2	−22.1 ± 0.2	12.5 ± 0.6	3.6 ± 0.0	0				0			
Pasiphae sp.	2	−25.4 ± 1.2	10.0 ± 0.9	3.3 ± 0.0	0				0			
Other												
Holothurian	2	−24.1 ± 0.1	10.9 ± 0.2	3.5 ± 0.0	0				1	−23.8	11.3	3.6
Pygoscelis antarcticus	1	−24.5	7.5	3.5	1	−25.1	7.8	3.4	1	−26.0	6.9	3.6

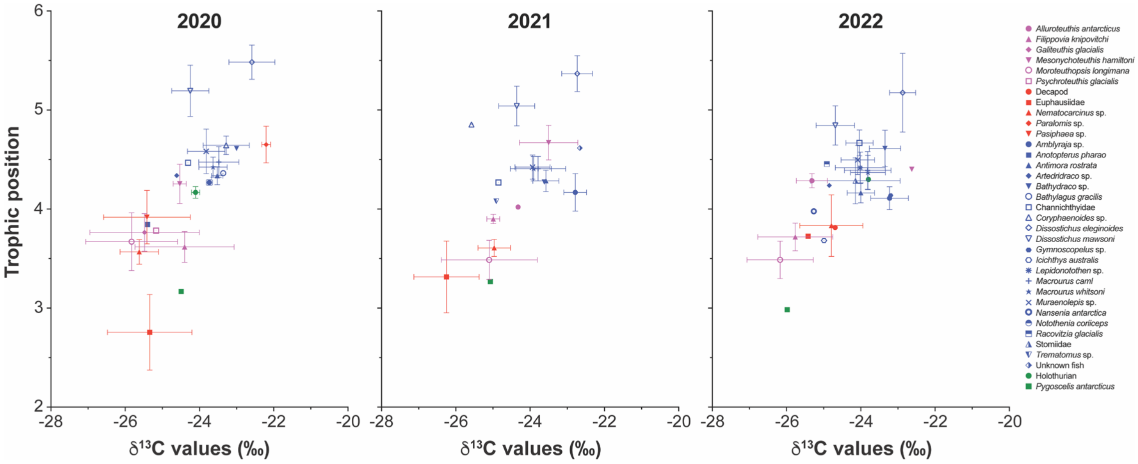

Figure 2. Trophic position and $\delta^{13}C$ values for the three studied years (2020, 2021 and 2022). All samples analysed were muscle, except for holothurian whose analyses were done in the body wall. Colours represent different functional groups, i.e. purple: cephalopods, red: crustaceans; blue: fish, green: others (holothurian and seabirds). Values are mean ± standard deviation.

deep-sea food-webs in remote locations rarely visited by research expeditions and where the deployment of scientific demersal gear is challenging due to the morphology of the seabed (Leat et al. 2016, Downie et al. 2021, Collins et al. 2022).

Our results showed that the deep-sea food-web at South Sandwich Islands is composed by five trophic levels, although the presence of toothfish in the diet of toothed whales and seals indicate a probable 6th trophic level (Collins et al. 2010, Hanchet et al. 2015). The benthopelagic coupling mainly occurs between the 3rd and 4th trophic levels, with the 3rd trophic level being mostly composed of pelagic squid and crustaceans (including euphausiids) and the 4th trophic level mostly including demersal fish such as the grenadiers *Macrourus* spp. or *A. rostrata*. Stomach content analyses of *Macrourus* spp. elsewhere in the Southern Ocean found squid and crustaceans supporting this pelagic–demersal transition between these trophic levels (Morley et al. 2004, Laptikhovsky 2005, Pinkerton et al. 2012, Queirós et al. 2024a). The FCL varied across the three years of study. The variation of FCL is explained by the productivity hypothesis, meaning that years with a higher primary production have longer food-webs (Elton 1927). Therefore, the increasing productivity in the Southern Ocean with climate change will lengthening the deep-sea bathyal food-webs in slope and seamounts areas (Constable et al. 2023). Further studies are needed to confirm that the FCL of other deep-sea Southern Ocean food-webs, e.g. fjords in the Antarctic Peninsula, deep trenches such as the South Sandwich Trench or deep-sea plains in the middle of the Southern Ocean basins, are also explained by the productivity hypothesis to confirm if the impact of climate change is similar across the Southern Ocean deep-sea.

Food-web and food chain length at South Sandwich Islands

Using stable isotopes, we were able to gain insights into the structure of the deep-sea food-web at South Sandwich Islands. Our results show that bathyal food-webs at the South Sandwich Islands have both toothfish species as the top predators and occupying the 5th trophic level. Previous studies

Table 2. $\delta^{15}N$ differences between the three study years (2020, 2021 and 2022). Post hoc test for ANOVA was the Tukey's multiple comparison test and for Kruskal–Wallis was the Dunn's multiple comparison test. [a]2021 × 2022; [b]2020 × 2022. Bold values indicate significant differences, i.e. $p < 0.05$.

Species	Test	p-value	Test value	Post hoc
Amblyraja sp.[a]	Mann–Whitney	0.4395	U = 89.00	
Antimora rostrata	Kruskal–Wallis	**0.0003**	H = 15.96	2020 × 2022 2021 × 2022
Dissostichus eleginoides	Kruskal–Wallis	**0.0114**	H = 8.950	2020 × 2022
Dissostichus mawsoni	ANOVA	**0.0002**	F = 10.27	2020 × 2022 2021 × 2022
Macrourus caml	Kruskal–Wallis	0.3954	H = 1.856	
Macrourus whitsoni	ANOVA	0.4323	F = 0.851	
***Muraenolepis* sp.**	ANOVA	**0.0142**	F = 4.557	2020 × 2021
Filippovia knipovitchi[b]	Mann–Whitney	0.2468	U = 8.00	
Moroteuthopsis longimana	Kruskal–Wallis	0.1279	H = 4.113	
Nematocarcinus sp.	Kruskal–Wallis	0.1132	H = 4.322	

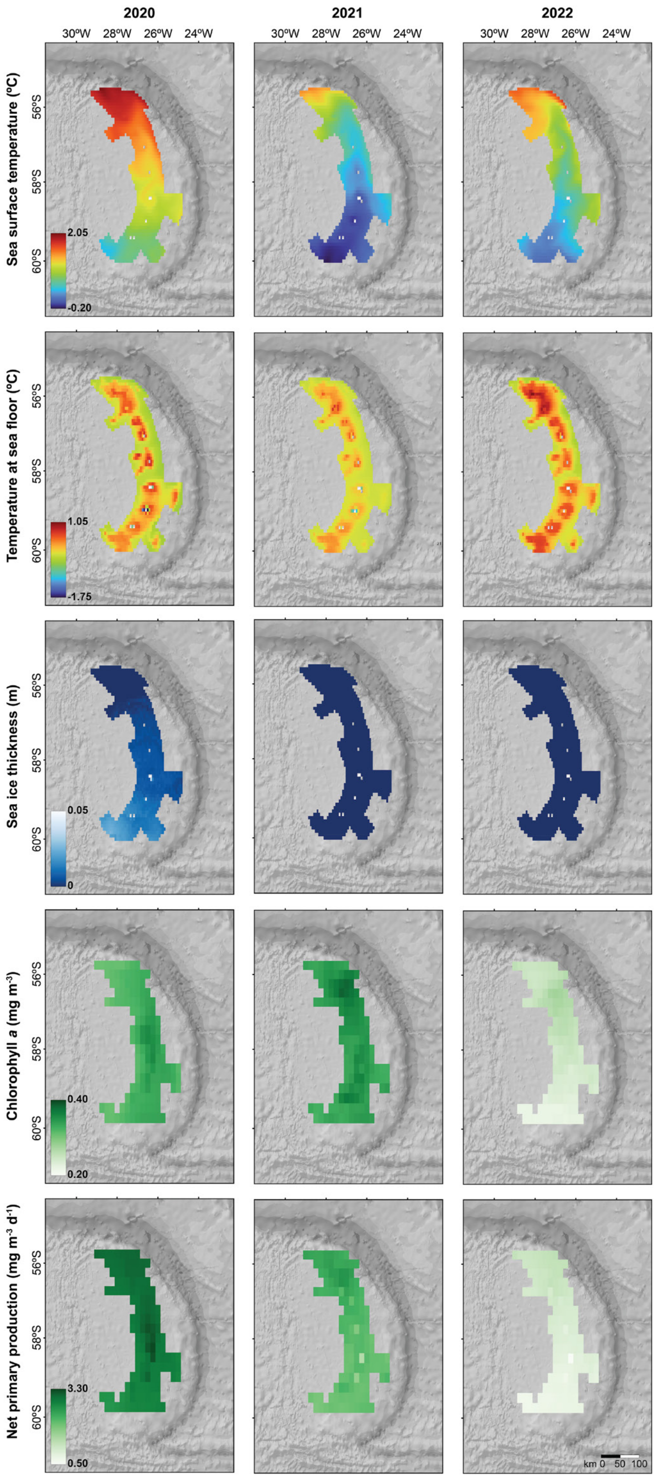

Figure 3. Environmental variables at South Sandwich Islands throughout the study period. Values are mean values for the months when fishery occurred.

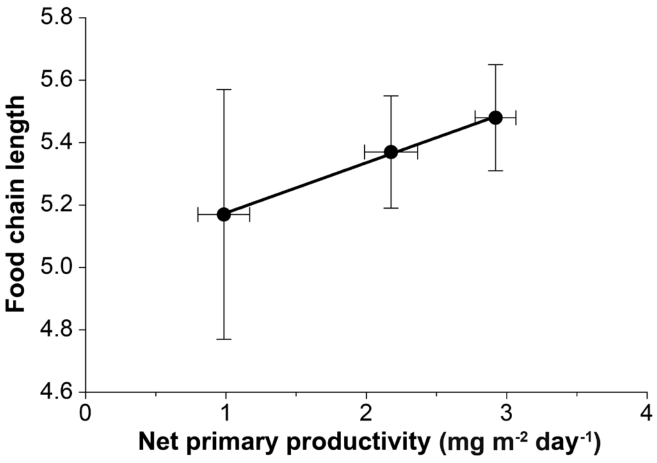

Figure 4. Simple linear regression between the food chain length (FCL) and the net primary productivity (NPP). FCL values are the mean ± standard deviation for the top predator (Patagonian toothfish *Dissostichus eleginoides*). NPP values are the mean ± standard deviation for the South Sandwich Islands.

found toothfish in the diet of Weddell seals *Leptonychotes weddellii*, southern elephant seals *Mirounga leonina*, sperm whales *Physeter macrocephalus* and killer whales *Orcinus orca* (Collins et al. 2010, Hanchet et al. 2015). Consequently, this food-web can be one trophic level longer than the values obtained in this study. Crustaceans and cephalopods dominate the 3rd trophic level while fishes dominate the 4th and above (with some exceptions like the colossal squid *Mesonychoteuthis hamiltoni*). These results support previous studies regarding the important role of fish and cephalopods in Southern Ocean food-webs (Barrera-Oro 2002, La Mesa et al. 2004, Queirós et al. 2021a). Furthermore, our results support the existence of alternative pathways to the long-standing phytoplankton – Antarctic krill *E. superba* – top predator food-web (Bocher et al. 2001, Murphy et al. 2007, McCormack et al. 2020, 2021). This is important because *E. superba* is a susceptible species to environmental changes (Atkinson et al. 2004, 2019), and the existence of these alternative pathways provide some resistance to these food-webs against climate change (McCormack et al. 2020).

The connection between the benthic/demersal and pelagic components of the food-web, i.e. benthopelagic coupling, is a key process for the functioning of ecosystems, but usually overlooked (Griffiths et al. 2017). Our results suggest that benthopelagic coupling in the South Sandwich Islands deep-sea might happen in several trophic levels, and not only with the deposition of organic matter from the surface to the seafloor (Suess 1980, Smith et al. 2006). The 3rd trophic level is mostly composed by pelagic crustaceans and squid. Most of these species perform daily vertical migrations, being an important flux of nutrients from the surface to the deep-sea (Collins and Rodhouse 2006, Smith et al. 2006, Cuzin-Roudy et al. 2014). Others, like *E. superba* perform diel vertical migrations though some populations are deep-water residents (Schmidt et al. 2011). The presence of these species in the diet of demersal predators such as *Dissostichus* spp. and *Macrourus* spp. confirm they are a major connection between the pelagic and benthic/demersal food-webs (Queirós et al. 2024a). The demersal component of this food-web only appears at the 4th trophic level with fish species (e.g. *Macrourus* spp.) and some benthic organisms (e.g. Holothurian), though some pelagic species are present (e.g. *M. hamiltoni*). The 5th trophic level is the only trophic level exclusively composed by demersal species, i.e. both toothfishes. The presence of toothfish in the diet of toothed-whales and seals shows an upward flux towards the pelagic component, suggesting that this food-web is composed by pelagic species in a potential 6th trophic level (Collins et al. 2010, Hanchet et al. 2015). This suggests both a downward and upward flux of energy in the benthopelagic coupling at the South Sandwich Islands deep-sea, with major exchanges between the benthic/demersal and pelagic components occurring in the transition from the 3rd to the 4th trophic level and between the 5th and 6th trophic levels (Fig. 5). The presence of both pelagic and demersal species in the 4th trophic level suggests an exchange between both components from the 4th to the 5th trophic levels, but less important (Fig. 5).

Interannual variability on the Southern Ocean deep-sea food-web

Our results showed that the FCL varied across years. In 2022, the food-web was approximately 0.30 shorter than in 2020. Though this difference is not of a trophic level, it suggests that the deep-sea food-web at the South Sandwich Islands is not static and changes across years. This is supported by the differences found for the TP of *A. rostrata, D. eleginoides, D. mawsoni* and *Muraenolepis* sp. Differences in mid-trophic level species such as *A. rostrata* and *Muraenolepis* sp., showed that changes are not restricted to the top predators. Besides we were only able to test differences in some species, several species presented distinct TP between years. For example, we recorded an important increase in euphausiid TP between 2020 (≈ 2.75) and 2023 (≈ 3.75). This trophic level increase proposes a change from an herbivorous (e.g. *E. superba*) to carnivorous (e.g. spiny krill *Euphausia tricantha*) euphausiids in the community (Cuzin-Roudy et al. 2014). Indeed, $\delta^{15}N$ values in euphausiids from the Scotia Sea showed that differences between herbivorous and carnivorous species can reach ≈ 3.8 ‰ which is more than one trophic level (Stowasser et al. 2012, Seco et al. 2021). Regarding top predators, *D. eleginoides* presented the highest TP in the three years of study, followed by *D. mawsoni*. Both *Dissostichus* species in the top of this food-web was expected as both are known top predators in the Southern Ocean (Pilling et al. 2001, Roberts et al. 2011, Queirós et al. 2022). Yet, the higher TP of the *D. eleginoides* was surprising because

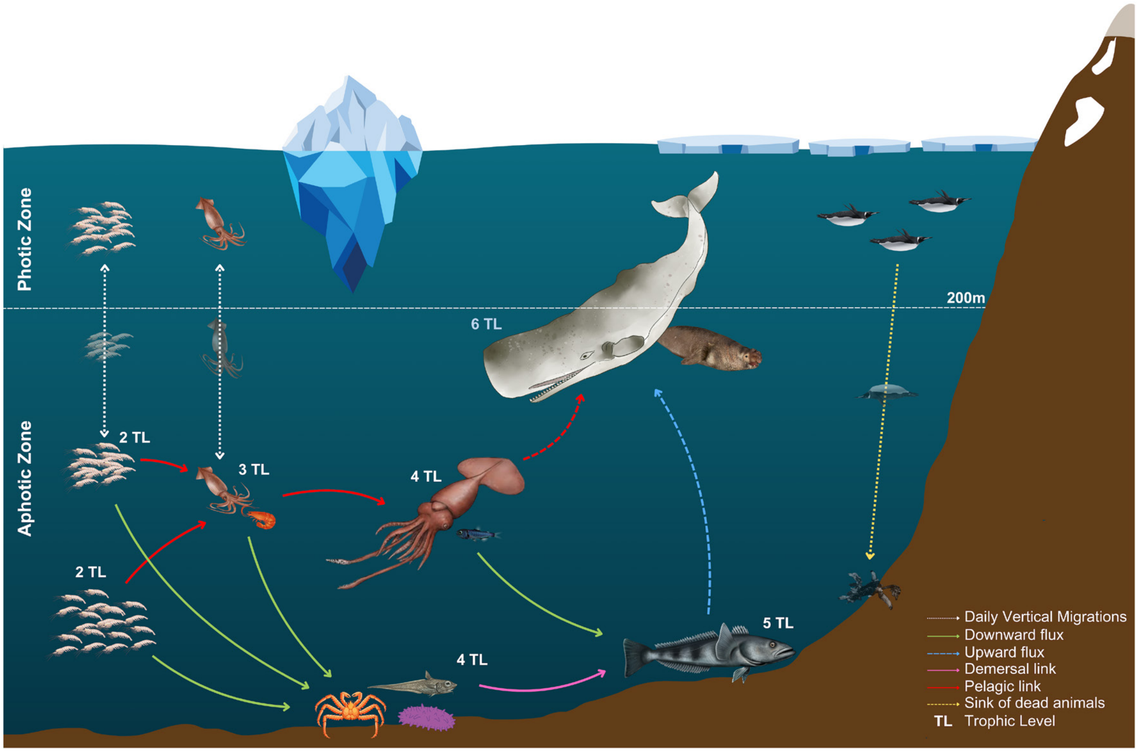

Figure 5. Illustration of the Southern Ocean deep-sea food-web with focus on the benthopelagic coupling. White dashed arrows show the vertical migration of euphausiids and other pelagic species; the yellow dashed arrow shows the sinking of dead pelagic species to the bottom of the ocean; green arrows show the downward flux; the pink arrow shows a demersal transition; red arrows show a pelagic transition; the blue dashed arrow shows the potential upward connection from the toothfish to other predators; the red dashed arrow shows the predation of colossal squids *Mesonychoteuthis hamiltoni* by sperm whales *Physeter macrocephalus*. TL indicates the approximate trophic level for each component of the food-web. Myctophid (4 TL) and toothfish (5 TL) were drawn by Tom Langbehn – BAS. References used: (Everson 2000, Collins and Rodhouse 2006, Collins et al. 2010, Hanchet et al. 2015, Cherel 2021).

this species usually feeds on smaller prey than *D. mawsoni* at this archipelago (Roberts et al. 2011). Such difference might be related with the higher proportion of fish (mostly in 4th trophic level) in the diet of *D. eleginoides* in contrast to the *D. mawsoni* that presents a high percentage of cephalopods (mostly in 3rd trophic level) in the diet (Pilling et al. 2001, Roberts et al. 2011, Stevens et al. 2014, Queirós et al. 2022). Here it is noteworthy to say that we used the same baseline for the entire archipelago, which could mask dissimilarities given by the different main distribution of both toothfish species (*D. eleginoides* to the north and *D. mawsoni* to the south) and the environmental and biological differences between north and south of the archipelago (Hollyman et al. 2022, Soeffker et al. 2022, Thorpe and Murphy 2022).

Our results show that the food-web at South Sandwich Islands is longer than others in the Southern Ocean, such as that in Adélie Land, Kerguelen Islands, Potter Cove (Antarctic Peninsula), North Scotia Sea and Weddell Sea. In the Weddell Sea and Adélie Land, a FCL of 4.3 and 4.6 was estimated (Rau et al. 1992, Cherel 2008). Similarly, a coastal food-web in Potter Cove (King George Island, Antarctic Peninsula) presented a shorter FCL (4.3 – Marina et al. 2018). Other studies estimated the TP, and consequently the FCL, using $\delta^{15}N$ values in the sub-Antarctic islands of South Georgia ($TP = 5.2$ for northern giant petrel *Macronectes halli* – Stowasser et al. 2012) and Kerguelen ($TP = 5.3$ for black-browed albatross *Thalassarche melanophrys* – reviewed by Cherel et al. 2010). Both food-webs are slightly shorter than what we have estimated for the South Sandwich Islands ($FCL = 5.5$ in 2020). On the other hand, these trophic levels were recorded for seabirds with scavenging behaviour, including following toothfish longliners and eating deep-sea fish that drop from the hooks and are not usually accessible to them (Xavier et al. 2004, Phillips and Wood 2020). In Kerguelen Islands a TP of 6.1 was estimated for the *M. hamiltoni* (Cherel et al. 2008), which places them approximately 1.4 trophic levels above those sampled here. However, such $\delta^{15}N$ values were measured in the beaks and posteriorly estimated for the muscle (Cherel et al. 2008). In the Ross Sea, higher $\delta^{15}N$ values were also measured for this species, still lower than those for Kerguelen Islands, suggesting that the *M. hamiltoni* has a lower TP in the South Sandwich Islands ($TP = 4.7$) than elsewhere in the Southern Ocean (Thompson et al. 2012). Pinkerton and Bradford-Grieve (2014) modelled a similar FCL for the Ross Sea region. However, such food-web model included toothfish's predators and, in contrast to other studies that exclusively considered the pelagic component, we considered the benthic/demersal component of the ecosystem (Pinkerton and Bradford-Grieve 2014). This may suggest that the Southern Ocean deep-sea food-webs, especially those with a benthic/demersal component, are longer than pelagic and coastal food-webs. This is supported not only by comparing previous studies (Cherel et al. 2008, Stowasser et al. 2012, Marina et al. 2018) with this and Pinkerton and Bradford-Grieve (2014), but also by the low TP estimated for the *P. antarcticus,* which is known to feed on *E. superba*, following the short phytoplankton – Antarctic krill *E. superba* – top predator food-web (Ratcliffe and Trathan 2011). The dynamic-stability hypothesis may explain the difference between pelagic and deep-sea food-webs because the deep-sea is more stable than the surface. This is supported by the higher variability of temperature observed in our study period in the surface compared to the bottom (30× more variance in SST than TSF), thus sustaining a longer food-web (Pimm and Lawton 1977).

However, differences to other food-webs are not restricted to the FCL. Besides the *M. hamiltoni*, the squids *Galiteuthis glacialis, F. knipovitchi* and *M. longimana* had a lower TP at the South Sandwich Islands than in Kerguelen Islands (Cherel et al. 2008), and some species also have a lower trophic level when compared to the northern area of the Scotia Sea (Anderson et al. 2009). In contrast, *G. glacialis,* glacial squid *Psychroteuthis glacialis* and *M. longimana* had higher TPs in our study area than in the Ross Sea (Thompson et al. 2012). Similarly, the trophic level of fish at South Sandwich Islands differ from other regions, e.g. lanternfish *Gymnoscopelus* spp. have a higher TP than those in Kerguelen Islands, Adélie Land, and elsewhere in the Scotia Sea (Cherel et al. 2008, Stowasser et al. 2012, Seco et al. 2021); *Trematomus* sp. in the Ross Sea and both *Lepidonotothen* sp. and *A. rostrata* in the Scotia Sea had higher values than those measured here (Ceia et al. 2012, Jo et al. 2013). We must be aware that most of these taxa were not identified to species level so differences might also be related to the fact that they were different species, though within the same genera. Nonetheless, these differences support a regional variability in the deep-sea food-web structure of the Southern Ocean, as observed in the pelagic realm (McCormack et al. 2020, Hill et al. 2021).

As shown for $\delta^{15}N$, the range of $\delta^{13}C$ also changed throughout the study period. The range of $\delta^{13}C$ values indicates variability in the base of the food-web (Saporiti et al. 2015). The widest range in 2020 may suggest more diversity on primary producers. 2020 was the year with highest Chl and NPP, and the only with sea ice. Phytoplankton blooms at South Sandwich Islands seems to be highly related with the retreat of the sea ice both in time and intensity due to the higher availability of nutrients and light (Thorpe and Murphy 2022). Furthermore, the sea ice also influences the phytoplankton community composition in the Southern Ocean such as the presence of sympagic phytoplankton (Lizotte 2001, Mendes et al. 2018). A study in the Antarctic peninsula tip (near Clarence Island) showed that the phytoplankton community in years with sea ice is more diverse, e.g. presence of cryptophytes, small dinoflagellates and *Phaeocystis antarctica*, when compared to years without sea ice where diatoms dominate (Mendes et al. 2018). Similarly, the presence of sea ice in 2020 and not in 2021 and 2022 may be inducing a difference in the phytoplankton community at South Sandwich Islands and, consequently, a wider variability in the base of our food-webs reflected in the $\delta^{13}C$ range. The correlation between $\delta^{13}C$ and TP indicates an expected trophic enrichment in $\delta^{13}C$ (despite consider stable, $\delta^{13}C$ values increase approximately 1‰ per trophic level, DeNiro and Epstein 1981) and a single carbon-source of the food-web

(Drazen and Sutton 2017). Thus, although a more diverse phytoplankton community was likely present in 2020, the source of the carbon to the food-web is similar across years.

Environmental influence on the Southern Ocean deep-sea food-chain length

The differences found in the environmental conditions across the three study years were expected due to the known inter-annual variability of the region (Thorpe and Murphy 2022). This supports that our sampling period is adequate to test the influence of environmental variability in the food-web structure. Furthermore, with different Chl and NPP values we were able to test the FCL productivity hypothesis (Elton 1927). Similarly, changes in the variance of SST and TSF between years, allowed us to test the dynamic-stability hypothesis (Pimm and Lawton 1977, Hette-Tronquart et al. 2013).

The significant positive relationship between the FCL and the NPP suggests that the productivity hypothesis explains the variation in FCL in the Southern Ocean deep-sea food-web (Elton 1927). Despite the dynamic-stability hypothesis possibly explaining the difference between pelagic and deep-sea food-webs (discussed above), the absence of a relationship between the FCL and the σ^2SST and σ^2TSF suggests an absence of a linear relationship between these variables, which is used as a proxy for the stability of the system (Hette-Tronquart et al. 2013). In addition, our results show that the higher the σ^2SST and σ^2TSF the longer is the food-chain, contrasting with the expected results to support the dynamic-stability hypothesis that suggest shorter food-webs in more disturbed (i.e. more variability) ecosystems (Pimm and Lawton 1977). Therefore, our results refute this hypothesis as determinant across deep-sea food-webs in the Southern Ocean. These differences may support that the FCL across the Southern Ocean cannot be explained by only one of the existing FCL hypotheses but by a combination of them. Unfortunately, we were not able to test different hypotheses such as the ecosystem size and diversity-richness hypotheses to better understand the variation of the FCL in the Southern Ocean deep-sea (Schoener 1989).

Being influenced by the productivity of the ecosystem, the FCL may not only vary between years but intra-annually. The productivity at South Sandwich Islands is strictly connected with sea ice melting and varies throughout the year with a peak from December to March (Thorpe and Murphy 2022), meaning that the food-web should be longer during summer. However, because of the influence of productivity, the deep-sea food-web at South Sandwich Islands is also vulnerable to climate change. Studies suggest that the reduction of sea ice, warming, iron supply and change in westerly winds can lead to an increase of primary production (Turner et al. 2013, Morley et al. 2020). At the same time, this drives changes in the phytoplankton community, with large diatoms being replaced by smaller cryptophytes which also favours the lengthening of the food-web (Hollowed et al. 2013).

Longer food-webs tend to be less stable, are more susceptible to external stressors and recover slower from disturbance (Post 2002a). Furthermore, in longer food-webs the energy assimilation loss is higher, requiring top predators to eat more for the same energy input, populations become less stable, and increase the load of biomagnifying contaminants (Post 2002a, Hollowed et al. 2013, Seco et al. 2021). Nonetheless, in case primary production does not increase the FCL it may contribute to the dilution of these contaminants (Chouvelon et al. 2018). Such changes can impact not only the studied food-web but others in the Southern Ocean because some of these species are also major prey of other predators, e.g. the squid *M. longimana* is found in the diet of albatrosses, penguins, toothed-whales and seals (Cherel and Klages 1998, Daneri et al. 2000, Xavier et al. 2018, Cherel 2021, Queirós et al. 2021b). Longer foraging trips and biomagnifying contaminants, associated with fluctuations in populations due to climate change, can increase the vulnerability of several top predators of the SGSSI MPA, some of which have a low conservation status such as the grey-headed albatross *Thalassarche chrysostoma* which is classified as endangered by the IUCN red-list (Xavier et al. 2013, Birdlife International 2018, Seco et al. 2021). Changes in the FCL will also change the nutrient cycling and atmospheric carbon exchange (Post 2002a, Hette-Tronquart et al. 2013). This is especially concerning because the Southern Ocean is the main sink for anthropogenic CO_2 in the world's oceans, up taking approximately 40% of the oceanic anthropogenic carbon (Caldeira and Duffy 2000, Mikaloff Fletcher et al. 2006).

In conclusion, this study demonstrates that the Southern Ocean bathyal deep-sea food-web in slope and seamount areas may vary inter-annually, and it is influenced by the productivity of the system. Because primary production varies around Antarctica, the deep-sea food-web may present a regional variability throughout the Southern Ocean. To fully understand the structure of deep-sea ecosystems in the Southern Ocean, further studies in different areas are needed, e.g. in deep-sea trenches, abyssal plains or deep fjords. Increasing primary production with climate change may induce a lengthening of the food-web, which may ultimately increase the loss of energy obtained by predators and the load of biomagnifying contaminants. Such changes may leave the populations of top predators more susceptible to other climate change pressures.

The SGSSI MPA aims to protect the entire ecosystem from external stressors, such as climate change and fisheries, and protect important species of the food-web (Trathan et al. 2014, Belchier et al. 2022). Knowing the structure of the food-web, and how it is influenced by environmental conditions, our study also provides useful information for a better management of the SGSSI MPA. Our results complement previous research that, despite the only fishery happening in the archipelago occurs in the deep-sea, focused on the structure of the pelagic food-web for the Scotia Sea (Stowasser et al. 2012, Seco et al. 2021, López-López et al. 2022). The structure of the food-web is crucial in determining the resistance of the community to fisheries disturbance (Hette-Tronquart et al. 2013, Pinsky et al. 2020, Funes et al.

2022). Our results show that increased productivity due to climate change may be a determinant factor in changing the structure of the food-web, but also show that other species, including those captured as bycatch in fisheries, are crucial in maintaining the functioning of the deep-sea ecosystem at South Sandwich Islands.

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Author contributions

José P. Queirós: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Philip R. Hollyman**: Conceptualization (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Paco Bustamante**: Resources (equal); Validation (lead); Writing – original draft (equal); Writing – review and editing (equal). **Diana Vaz**: Methodology (equal); Writing – original draft (equal). **Mark Belchier**: Conceptualization (equal); Supervision (equal); Writing – original draft (equal). **José C. Xavier**: Conceptualization (equal); Supervision (equal); Writing – original draft (equal).

Transparent peer review

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.8cz8w9h23 (Queirós et al. 2024b).

Supporting information

The Supporting information associated with this article is available with the online version.

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