

RESEARCH ARTICLE

Macrozooplankton community structure and trophic interactions differ across a sub-Antarctic shelf break, independent of Antarctic krill

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Abstract

The South Georgia continental shelf break is a highly productive and biodiverse region of the Southern Ocean, with abundant macrozooplankton forming the foundation of off- and on-shelf communities. Antarctic krill (*Euphausia superba*) are a major component of these communities and can dominate total biomass. In this study, we analyze a new 10-year timeseries of spatially varied net samples from summer campaigns spanning the South Georgia shelf region to examine patterns of variability in macrozooplankton species abundance on- and off-shelf in the austral summer. We found total net catch abundance was similar on- and off-shelf, with particularly high abundances when Antarctic krill were present. Overall trends showed on-shelf to be more variable in community composition, and more likely to contain high abundances of Antarctic krill. Community composition in the off-shelf environment remained consistent between sites and with time and was more species rich than the on-shelf community. Our analysis further revealed strong statistical associations in co-occurrence between certain taxa, which sometimes varied between on-shelf and off-shelf communities. In a number of instances, these associations reflect either feeding guilds (taxa with similar prey preferences) or predator-prey co-occurrence. Overall, although community composition differed between on-shelf and off-shelf environments, these compositions appeared to be relatively stable in space and time irrespective of the presence or absence of Antarctic krill. This finding, that the macrozooplankton communities appear relatively resilient to intra-decadal environmental fluctuations in abundance, has particular importance when considering the impact of rapid regional climate change and potential longer-term changes in the biomass of Antarctic krill on the wider South Georgia pelagic ecosystem.

Continental shelf systems are well known to be major areas of productivity compared to the open ocean (Springer et al. 1989). Regions surrounding these shelves, both on-shelf shallower waters and off-shelf deeper waters, support distinct species assemblages (Brandt et al. 2007; Ward et al. 2005) and thus different food-web structures. The Antarctic continental shelf in the Southern Ocean comprises around 11.4% of the world's continental shelf area (Griffiths 2010). This system

provides nutrients to support productive regions and diverse ecosystems, including charismatic mammals such as fur seals, penguins, and whales (Henley et al. 2018; Holm-Hansen 1985). These communities are dependent on macrozooplankton assemblages—defined here as larger pelagic organisms with limited swimming capabilities—and support primary producers that form the foundation of these food webs. Antarctic krill (*Euphausia superba*) which have greater than average swimming capabilities for macrozooplankton, sometimes dominate the biomass of these food-webs and are a major focus of research (Murphy et al. 2007a). This is due to their role as prey for numerous predators, their dominance as the main harvest in regional fisheries (McBride et al. 2021), and their role in sequestering carbon to the deep ocean (Manno et al. 2015; Belcher et al. 2019; Cavan et al. 2019; Cavan et al. 2024).

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Antarctic krill are active swimmers and very patchy in their distribution, but with a general tendency to reach higher levels of biomass on-shelf compared to off-shelf (Tarling et al. 2009). Despite this prominence, the extent to which Antarctic krill shape wider macrozooplankton assemblages remains unclear.

Climate fluctuations, both natural and anthropogenic, are altering the success and structure of Southern Ocean food-webs, which could have severe impacts on biodiversity (Hogg et al. 2011) and thus threaten these systems and the ecosystem services dependent on them. Much like krill, all zooplankton inhabiting these polar regions require specific conditions and form unique habitats defined by frontal systems (Johnston et al. 2022). As fronts are shifting under climate change, zooplankton are therefore vulnerable to the effects—such as increasing sea surface temperatures, ocean acidification and wind activity. Studies of Antarctic krill suggest large-scale distributional shifts and declines in recruitment (Murphy et al. 2017; Atkinson et al. 2019; Veytia et al. 2020; Atkinson et al. 2022), but limited knowledge is available as to the wider zooplankton communities and specific inter-species relationships. For instance, we know little about the broader responses of other euphausiids, hyperiid amphipods and other groups of zooplankton to the environmental drivers of climate change (Johnston et al. 2022), and a holistic, whole-ecosystem view is required to improve our understanding of these systems.

This study focusses on the sub-Antarctic island of South Georgia (54°S, 37°W). While being surrounded by iron-limited high-nutrient-low-chlorophyll zones (Martin et al. 1990), the waters around South Georgia sustain the largest and most intense phytoplankton blooms of the Scotia Sea (0.69–2.19 mg chlorophyll *a* (Chl *a*) m⁻³ growth season average) (Borrione and Schlitzer 2013), lasting for up to 6 months (Korb et al. 2012) and driving highly productive food-webs around the island (Murphy et al. 2007b; Ward et al. 2006). As well as interactions with terrestrial systems providing nutrients to nearshore waters, a continuous supply of nutrient-rich deep waters provided by the shelf system is likely to increase the availability of iron and enhance primary productivity (Korb et al. 2008; Nielsdóttir et al. 2012; Schmidt et al. 2016). Despite the comparatively low latitude of the region, a large Antarctic krill population inhabits the waters of South Georgia, far from the core population further south, in the vicinity of the Antarctic Peninsula (Siegel and Watkins 2016). Abiotic factors such as advective transport carry *E. superba* to South Georgia from this core region (Hofmann et al. 1998), and the fate of these expatriated krill are likely further impacted by the community of macrozooplankton organisms that co-habit these waters and influence the availability of food and risk from macrozooplankton predators (e.g., chaetognaths, amphipods and cnidarians) alongside other predatory threats from fish, birds and mammals.

In addition to euphausiids, previous studies focusing on sub-Antarctic zooplankton communities lead us to expect to find simple food-web structures, dominated by the well-studied *Salpa thompsoni* (Atkinson et al. 2004) and the predatory amphipod *Themisto gaudichaudii*. There is evidence to suggest that in low-density Antarctic krill years, these species replace krill as the main prey for larger predators (Murphy et al. 2007a). Chaetognaths, pteropods (*Limacina* spp., *Clione* spp.) and polychaetes (*Tomopteris* spp.) are also common in sub-Antarctic waters, and are all mid-trophic level predators within the zooplankton food web.

Here we aim to assess krill abundance variability in the context of the wider macrozooplankton community in the South Georgia region and use a more ecosystem-based approach to establish potential feeding guilds within this community, defined here as different taxa exploiting the same prey and forming a shared ecological function, as described by Root (1967). We also aim to examine temporal and spatial variation in the macrozooplankton community to identify the core composition of taxa both on- and off-shelf. The degree to which Antarctic krill contribute to and affect macrozooplankton community structure is also considered. We assess patterns of co-occurrence to establish distributional relationships between taxa and further relate this to published information on diets to identify potential feeding guilds as well as predator–prey interactions in both on- and off-shelf environments. Predator–prey interactions here will refer to dynamic relationships in which one organism (predator) consumes another (prey), thereby influencing population dynamics and ecosystem structure. In exploring feeding guilds and predator–prey relationships, this study highlights dependencies of different species on the same food source, an aspect that could amplify the impact of alterations to the food landscape as a result of regional environmental change. This further identifies those species that may be most vulnerable to such future changes.

Methods

Data collection

Sampling was conducted in the waters around the island of South Georgia (Southern Ocean) during the austral summer (November to February) between 2009 and 2020, with exact timings varying each year (cruises: JR228, JR206B, JR280, JR291, JR304, JR15002, JR16003, JR17002, DY086, JR19001; Supporting Information Table S1). Net sampling efforts took place at eight points along paired transects that are part of the Polar Ocean Ecosystem Time-series–Western Core Box (Fiedling et al. 2014) conducted by the British Antarctic Survey. The survey area (NE corner: 53°8.4', 37°44.4'; NW corner: 53°16.8', 39°37.2'; SE corner: 53°50.4', 37°30'; SW corner: 53°58.2', 39°27') spans 133 km by 80 km over the continental shelf-break northwest of South Georgia (Fig. 1), and comprises a consistent set of acoustic transects and net

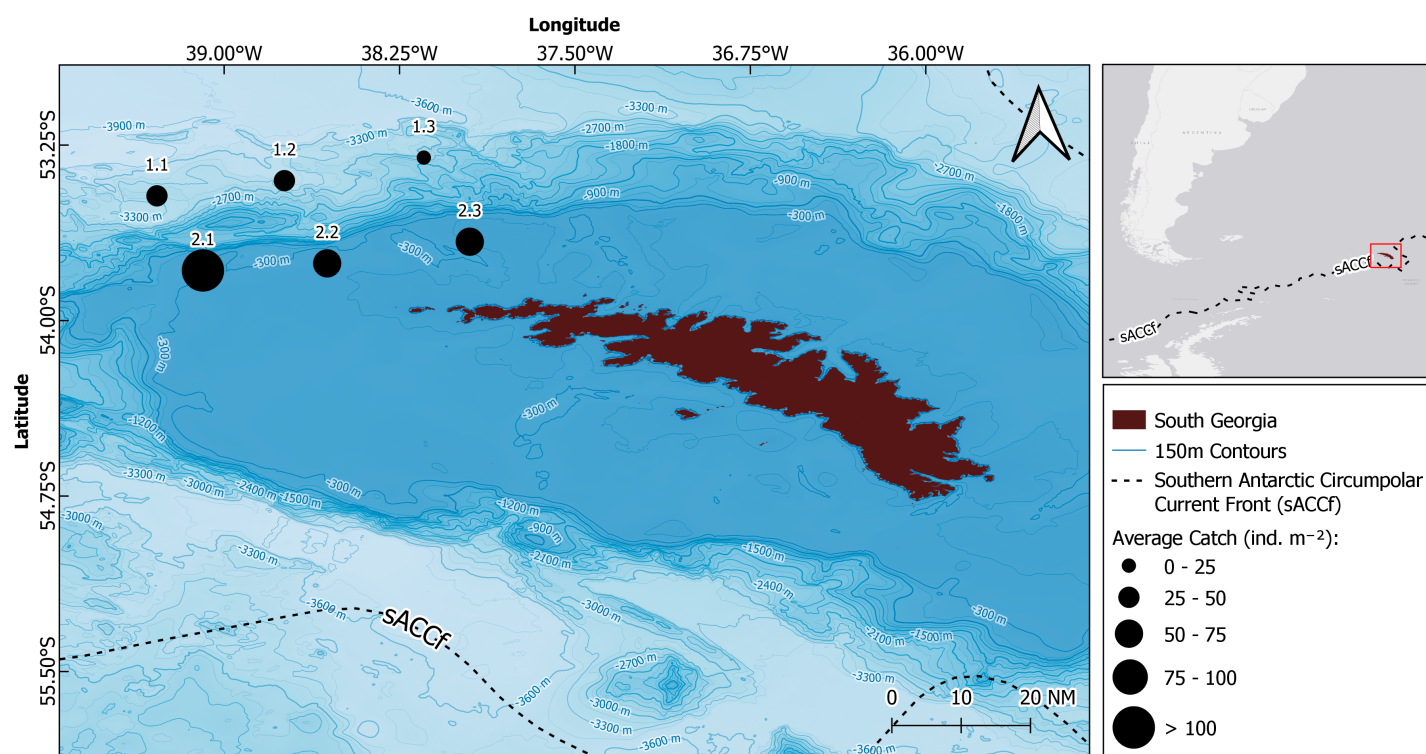


Fig. 1. Locations of Western Core Box stations to the north of South Georgia. Blue depth contours are shown every 150 m (GEBCO Bathymetric Compilation Group 2022). Radius of circles is proportional to the average catch (individuals m⁻²) for stations (labeled 1.1–2.3, NE to SW) and include all individuals of all species captured across all years. The dashed line represents the Southern Antarctic Circumpolar Current Front.

sampling stations undertaken annually. An 8-m² rectangular midwater trawler (Roe and Shale (1979)) containing two opening and closing nets with 4.5-mm mesh was deployed in double oblique fashion (Net 1: surface to maximum depth of 200 m or to within 15 m of seabed; Net 2: maximum depth to surface) at each net sampling station. Nets 1 and 2 were treated as replicate samples of the same sampling site.

Net sampling was carried out during hours of both darkness and daylight at a tow speed of 2–3 knots with each of the two nets opened for approximately 30 min per deployment. Volume filtered was estimated either by a flowmeter positioned at the mouth of the net or, when not operational, the distance covered through water multiplied by the opening area of the net (8 m²). This value was divided into the net catch abundance to derive individuals per m³ and then multiplied by the vertical distance covered by the oblique deployment to derive individuals per m² (ind. m⁻²). The wet weight of each catch were measured immediately after capture. Taxonomic identification was completed on-board, to the lowest possible taxonomic level and their respective abundance determined to obtain taxon species values of ind. m⁻². In certain instances where there was a high abundance of particular taxa, the catch was divided into fractions until a countable subset of individuals remained, small enough to be enumerated by eye. Abundance values were determined through multiplying the counted number by the inverse fraction of the subsample.

The wet weight of each enumerated taxon was then measured. These wet weight values were divided by the volume of water filtered to determine the wet weight biomass (g wet weight m⁻³).

Satellite environmental data were sourced from NASA OceanColor (MODIS-Aqua Level-3 SMI monthly, 4-km composites) for Chl *a* and sea-surface temperature. For each survey month-year, polygon means were extracted for predefined on- and off-shelf areas and linked to the corresponding tows.

Data analysis

Ninety-four taxa were identified, including six euphausiid taxa and several mesopelagic fish species. Due to differences in the level of identification between years, some species were grouped at a higher taxonomic level to ensure a higher level of confidence in analysis. Stations surveyed were grouped by position in relation to the continental shelf break, with on-shelf stations classified as those with an average depth of around 200 m and off-shelf stations, an average depth of around 2000 m (data source: GEBCO [https://www.gebco.net/] with graphical projections generated in QGIS version 3.8; QGIS Development Team 2019; Fig. 1). Data were analyzed using R and RStudio, version 4.4.1 (R Core Team 2023).

Species richness was calculated as the number of distinct taxa per net catch, and diversity using Shannon's diversity index per net catch. Non-metric multi-dimensional scaling

was used to compare community structure on- and off-shelf, with Bray–Curtis dissimilarity and scaled with a square root transformation, using the “vegan” package (Oksanen et al. 2019). Shelf region (on- or off-shelf) was used to constrain abundance data in a non-metric multi-dimensional scaling ordination analysis, with variation between centroids calculated via Adonis (permutational multivariate ANOVA). Significant differences could be caused by differences in diversity but could also relate to the spread of data between groups. Therefore, data dispersion was reviewed to establish if significant differences were indeed related to differences in communities.

Other environmental factors were considered by applying the same constrained non-metric multi-dimensional scaling and Adonis tests, though neither sea-surface temperature (Supporting Information Fig. S1a) nor Chl *a* concentration (Supporting Information Fig. S1b) was seen to influence community composition. The influence of day and night (Supporting Information Fig. S2) was also not found to be a statistically significant driver of differences in community. As previously stated, the exact timing of each survey varied between November and February, and it is acknowledged that there may be a level of seasonal variance between surveys that cannot be attributed to environmental factors alone. However, it is not possible to distinguish such a potential underlying influence within the present dataset since this requires a multidecadal timeseries (Mackas and Beau-grand 2010). Hence, the focus of the present study was on the influence of shelf region on community structure.

Further analyses were focused on selected key taxa with selection based on groups with the highest abundances overall, or consistent presence (recorded in at least 8 of the 10 survey years) (Supporting Information Fig. S3). We analyzed the absolute and relative abundance of these key taxa on- and off-shelf across all survey seasons and compared the data with and without Antarctic krill to take their impact into account. Pearson's correlation matrices were then generated via the “Hmisc” package in R (Harrell 2023) to establish any significant correlations between species abundance within on- and off-shelf regions. As abundance distributions were non-normal, significant correlations were assessed using a permutation test.

Feeding guilds were identified through combining abundance data with knowledge of feeding to estimate trophic relationships within a community (similar to approaches used by Luczkovich et al. (2002) and French et al. (2013)). Guild membership was established from published literature on the diets of taxa, determining whether they belong to a feeding guild or are predator and prey (Supporting Information Table S2). Strong and recurring patterns of co-occurrence between taxa over spatial and temporal scales were then examined using correlation matrices to establish how these diet-based relationships were expressed and differed across on- and off-shelf regions.

Results

Total abundance

Euphausiids dominated total abundances both on- and off-shelf in our 10-year survey period. The most abundant catch off-shelf was the euphausiid *Thysanoessa* spp. (55 ind. m^{-2} , 2010), and the greatest catch on-shelf was *E. superba* (925 ind. m^{-2} , 2017). For non-euphausiids, the mysid *Antarctomysis* spp. had the highest individual catch abundance on-shelf (50 ind. m^{-2} , 2014), and the amphipod *Themisto gaudichaudii* off-shelf (39 ind. m^{-2} , 2010). No significant difference was seen between shelf regions in total catches (Fig. 2a) ($p = 0.3$); however, off-shelf abundances were less variable than on-shelf when combined across all sampling years. We also carried out an analysis having excluded *E. superba* from the data matrix, which again found no significant difference in total catch abundance between shelf regions ($p = 0.4$). However, there appeared to be less variability on-shelf compared to off-shelf total catch abundance (Fig. 2b). Peak catches in both regions were also closer in abundance when *E. superba* was removed, with the off-shelf peak (107 ind. m^{-2} , 2014) only slightly lower than that of the on-shelf (111 ind. m^{-2} , 2010). Overall, this indicates similar abundances of macrozooplankton were caught in both the on-shelf and off-shelf regions of our survey area.

Community structure and distribution

We found less variation in diversity metrics off-shelf compared to on-shelf (Fig. 3). This was the case for Shannon's diversity, taxonomic richness and the standard deviation of average catch, with variation in richness between regions being the smallest. Highest variability in diversity and richness on-shelf was in 2013 and 2012, respectively, when there was a low total catch abundance, whereas off-shelf values showed no comparable extremes. Euphausiids were also dominant contributors to total catch abundance in most seasons, and biomass on-shelf (Table 1), with exceptions in abundance being salps and *T. gaudichaudii* off-shelf in 2013 and 2019, *Antarctomysis* spp. on-shelf in 2014, and *T. gaudichaudii* on-shelf in 2010. Off-shelf biomass showed more variation, and so large-bodied organisms and gelatinous zooplankton were often recorded highest (Periphylla periphylla in 2013, Myctophidae in 2015, salps in 2017, Cnidaria in 2018, and Ctenophora in 2019).

The ordination analysis of key taxa showed *Euphausia superba* and *Antarctomysis* spp. were strongly associated with the on-shelf region (Fig. 4; see Supporting Information Appendix S1 for species abbreviations). Neither was central to the on-shelf community in centroids (Supporting Information Fig. S4), consistent with their variable abundances. *Antarctomysis* spp. was recorded only seven times across the timeseries and occurred only at depths shallower than 200 m. *T. gaudichaudii* also associated more with on-shelf but sat among the main body of taxa.

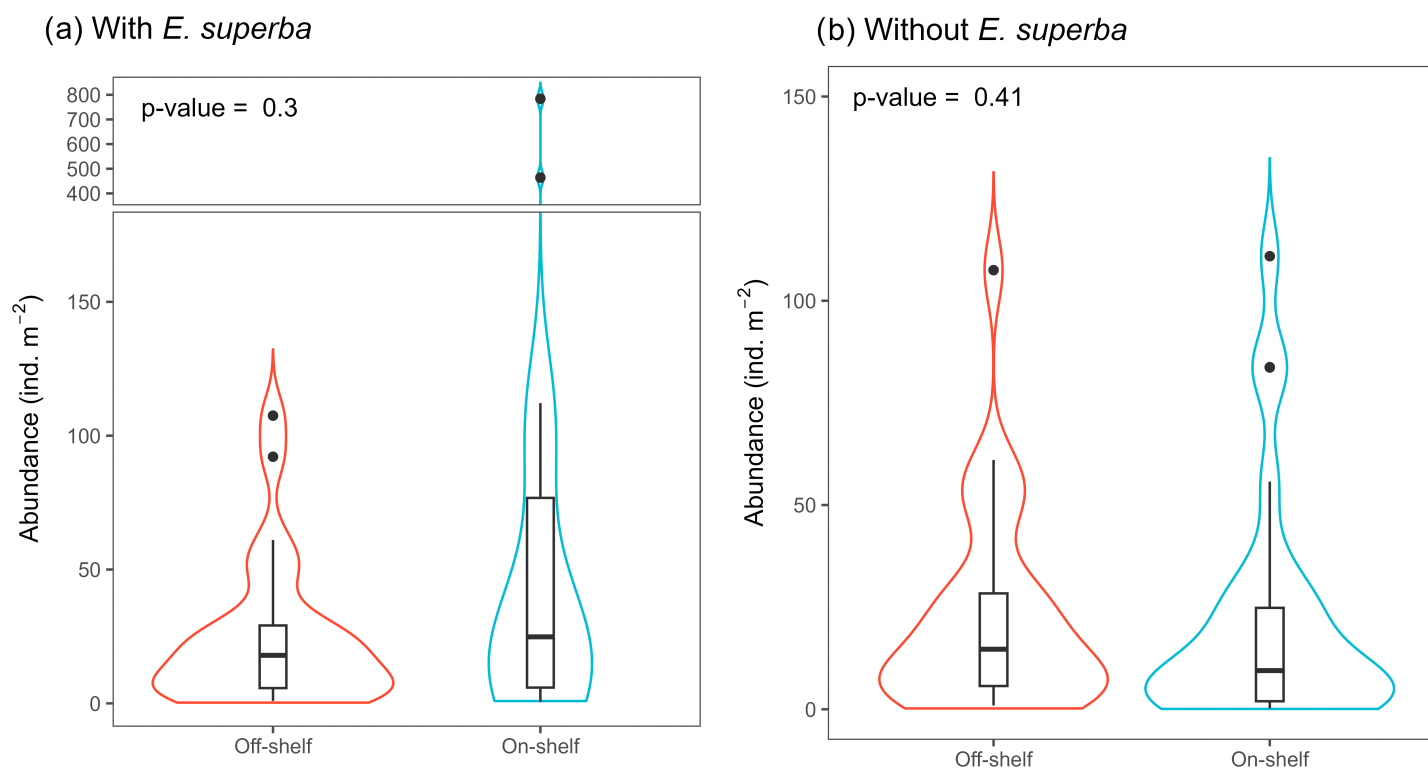


Fig. 2. Total abundance of catches per site, grouped by area, are plotted, (a) with *Euphausia superba* and (b) with *E. superba* removed as an outlying species. Width of violins indicate the number of data points with respective abundances, and boxplots indicating the interquartile range (box lengths), the median (horizontal line) and 95% confidence intervals (whiskers), with outlying data points also plotted (dots). Note the axis differs between plots, and plot (a) has an axis break.

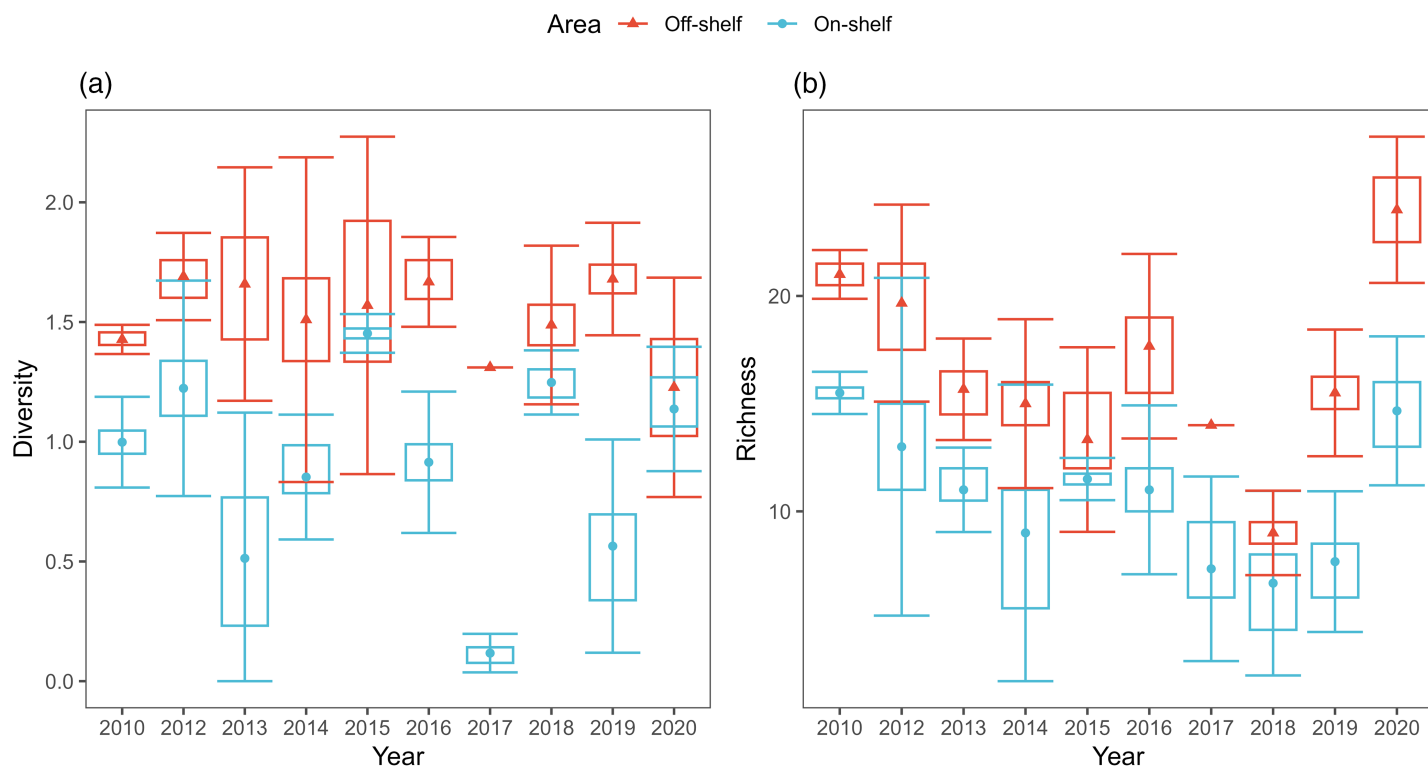


Fig. 3. Boxplots for (a) Shannon's diversity index and (b) richness, plotted with 95% confidence intervals.

Table 1. Dominant taxa by abundance and biomass on off-shelf and on-shelf areas for each survey season. For each shelf and season, the abundance and biomass columns list the dominant taxon and the seasonal total (ind. m^{-2} or g m^{-3}), with the taxon's share of the seasonal shelf total catch given alongside. Totals are sums across all tows, with sampling effort and additional cruise information provided in Supporting Information Table S1.

Survey season	Off-shelf				On-shelf			
	Abundance		Biomass		Abundance		Biomass	
	Dominant taxon	Ind. m^{-2}	Dominant taxon	g m^{-3}	Dominant taxon	Ind. m^{-2}	Dominant taxon	g m^{-3}
2010	<i>Thysanoessa</i> spp.	55 (38%)	<i>E. triacantha</i>	0.02 (24%)	<i>T. gaudichaudii</i>	66 (48%)	<i>E. superba</i>	0.04 (52%)
2012	<i>E. superba</i>	42 (30%)	<i>E. superba</i>	0.37 (76%)	<i>E. triacantha</i>	13 (43%)	<i>Thysanoessa</i> spp.	0.01 (27%)
2013	<i>Salpa</i> spp.	12 (38%)	<i>Periphylla periphylla</i>	0.54 (92%)	<i>E. superba</i>	464 (90%)	<i>E. superba</i>	2.52 (99%)
2014	<i>Thysanoessa</i> spp.	50 (44%)	<i>E. triacantha</i>	0.11 (62%)	<i>Antarctomysis</i> spp.	50 (42%)	<i>Antarctomysis</i> spp.	0.08 (57%)
2015	<i>E. triacantha</i>	6 (36%)	Myctophidae	0.14 (41%)	<i>Thysanoessa</i> spp.	4 (47%)	<i>Thysanoessa</i> spp.	0.002 (22%)
2016	<i>E. triacantha</i>	12 (29%)	<i>E. superba</i>	0.02 (31%)	<i>E. frigida</i>	29 (64%)	<i>E. frigida</i>	0.01 (45%)
2017	<i>E. triacantha</i>	21 (41%)	<i>Salpa</i> spp.	0.08 (65%)	<i>E. superba</i>	925 (99%)	<i>E. superba</i>	2.3 (99%)
2018	<i>Thysanoessa</i> spp.	2 (39%)	Cnidaria	0.003 (46%)	<i>E. triacantha</i>	3 (37%)	<i>E. triacantha</i>	0.004 (51%)
2019	<i>T. gaudichaudii</i>	4 (30%)	Ctenophora	0.002 (22%)	<i>E. superba</i>	90 (70%)	<i>E. superba</i>	0.27 (93%)
2020	<i>Thysanoessa</i> spp.	30 (44%)	<i>E. triacantha</i>	0.02 (38%)	<i>E. frigida</i>	43 (60%)	<i>E. frigida</i>	0.01 (31%)

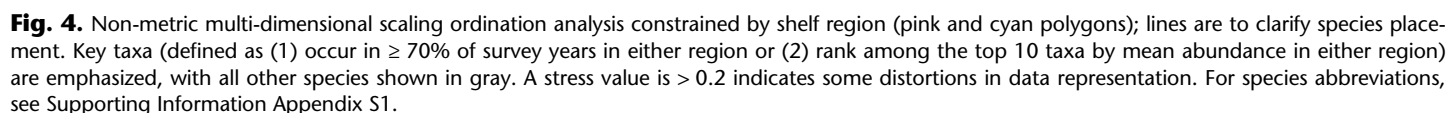
The myctophids *Gymnoscopelus fraseri*, *Gymnoscopelus braueri*, and *Electrona antarctica* were particularly associated with the off-shelf region, and also showed a marked level of co-occurrence. All other key taxa were positioned within the overlap between on-shelf and off-shelf polygons, and tended to cluster in sub-groups, with the exception of *Euphausia* spp., the wider category for unidentified euphausiids.

An Adonis test carried out on the correlation matrix showed a significant difference in centroids of groups ($p = 0.001$, $R^2 = 0.009$). This indicates a significant difference in community composition between the on-shelf and off-shelf regions. A significant beta dispersion ($p = 0.001$) also highlights the difference in community variability, with on-shelf showing much more variable community structure than the off-shelf region. Nevertheless, overlap in the polygons and a low R^2 means that a certain level of caution is required in this assessment.

We also observed large temporal differences in the abundance of key taxa within the survey region. Off-shelf, there was a consistent presence of key taxa between years, with little variation in relative contribution. The minimum key taxa abundance and biomass off-shelf was seen in 2018 (4 ind. m^{-2} , 0.007 g m^{-3}) and maximum abundances in 2010 (144 ind. m^{-2}), whereas highest biomass off-shelf was in 2013 (0.6 g m^{-3}) (Fig. 5). Off-shelf, biomass and relative abundances of taxa remained temporally similar (Fig. 5c, e), but biomass amplified the strong contribution of certain taxon, such as salps, *Antarctomysis* spp., and myctophids. Salps were highly variable in abundance, with notable peaks in 2013, 2015, and 2017 when they comprised over 25% of the total key taxa abundance. *Thysanoessa* spp. and *E. triacantha* were highly

abundant (up to 55.9 ind. m^{-2} and 40.9 ind. m^{-2} , respectively) and consistently present, often being the dominant species off-shelf. *T. gaudichaudii* also has a regular abundance, though notably lower relative abundances from 2013 to 2017. *E. frigida*, and Chaetognatha were also regularly present, again showing varying abundance within the off-shelf community.

There was more variation in key taxa catch abundance on-shelf compared to off-shelf, mostly due to the large but periodic abundances of *E. superba*. This was the result of there being substantially more krill on-shelf, apart from in 2012. Minimum catches of krill on-shelf were recorded in 2012, 2015, and 2018 all recording < 1 ind. m^{-2} , with maximum catch abundances in 2013 (515 ind. m^{-2}) and 2017 (937 ind. m^{-2}) when *E. superba* dominated overall community composition. Other euphausiid species exhibited large temporal changes in abundance (Fig. 5d, f), with the dominant species changing annually between *Thysanoessa* spp., *E. frigida* and *E. triacantha*. One driver of this variability was the particularly high abundance of *E. frigida* in 2016 and 2020 compared to other years. Large temporal variability was also true of non-euphausiid species such as *Antarctomysis* spp. which was only observed on-shelf and was very abundant in 2014 (0.08 g m^{-3}), but absent in other years. Few recordings of salps were seen on-shelf, other than in 2014 when an abundance of ~ 5 ind. m^{-2} (0.02 g m^{-3}) was observed, which was greater than that of *E. superba* on-shelf (~ 3 ind. m^{-2}) and salps off-shelf (~ 2 ind. m^{-2} , 0.006 g m^{-3}). Although of lower in abundance, *Primno macropa* and *Tomopteris* spp. were notable in being consistently present over time. Overall, compared to the off-shelf community, there was greater variability in the composition and abundance of taxa on-shelf.



Pearson's correlation analysis identified significant associations between the abundance of taxa within regions, as well

as between regions (Fig. 6). All but one association remained significant under permutation testing, confirming that non-normality does not account for these relationships. Only

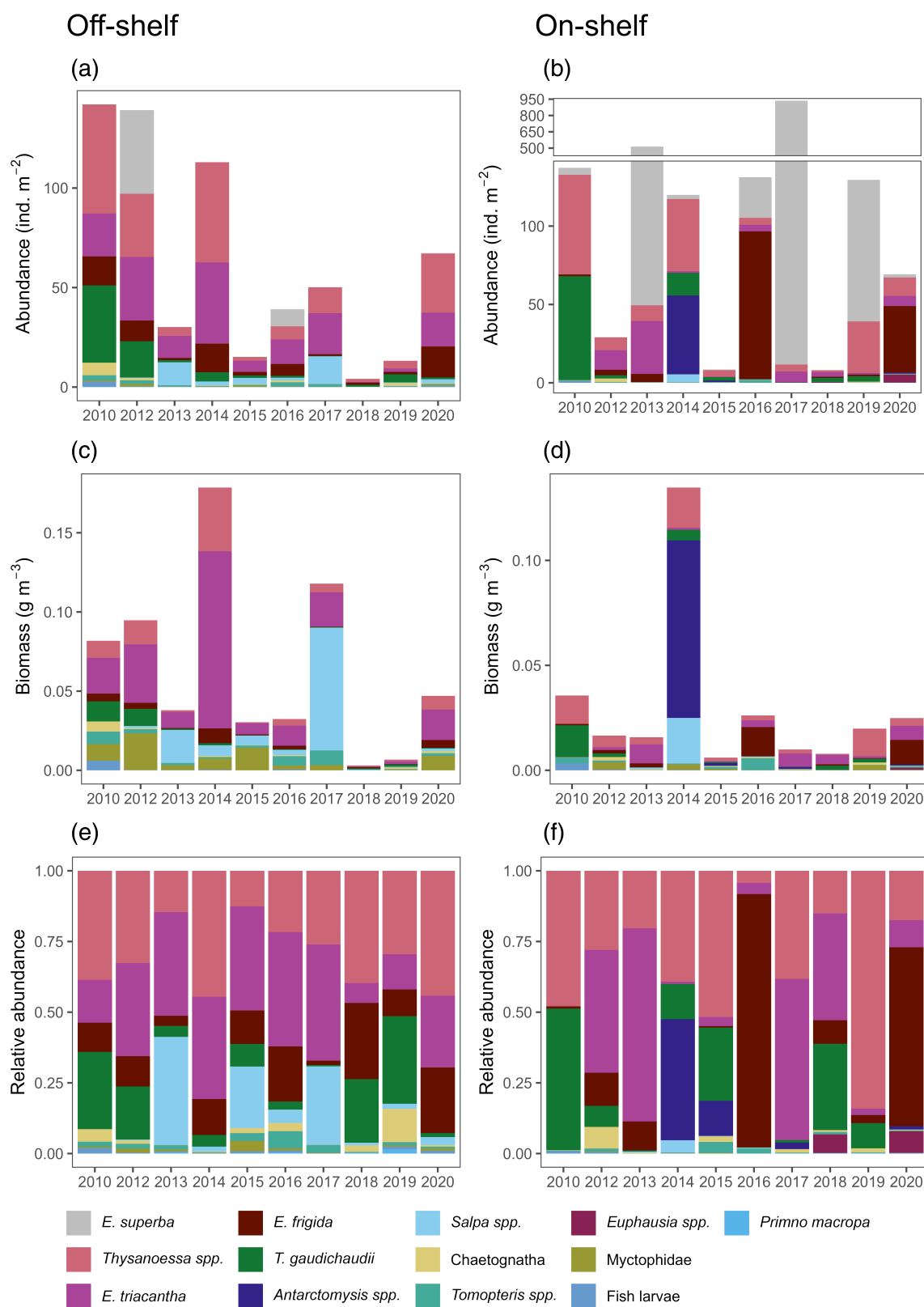


Fig. 5. Absolute abundance (ind. m⁻²) of all key taxa (a) off-shelf and (b) on-shelf stations. Broken-axis in (b) is to account for extremely high abundance of *Euphausia superba*. Biomass (g m⁻³) of key taxa, excluding *E. superba*, at (c) off-shelf and (d) on-shelf stations. Relative abundances with *E. superba* data excluded at (e) off-shelf and (f) on-shelf stations.

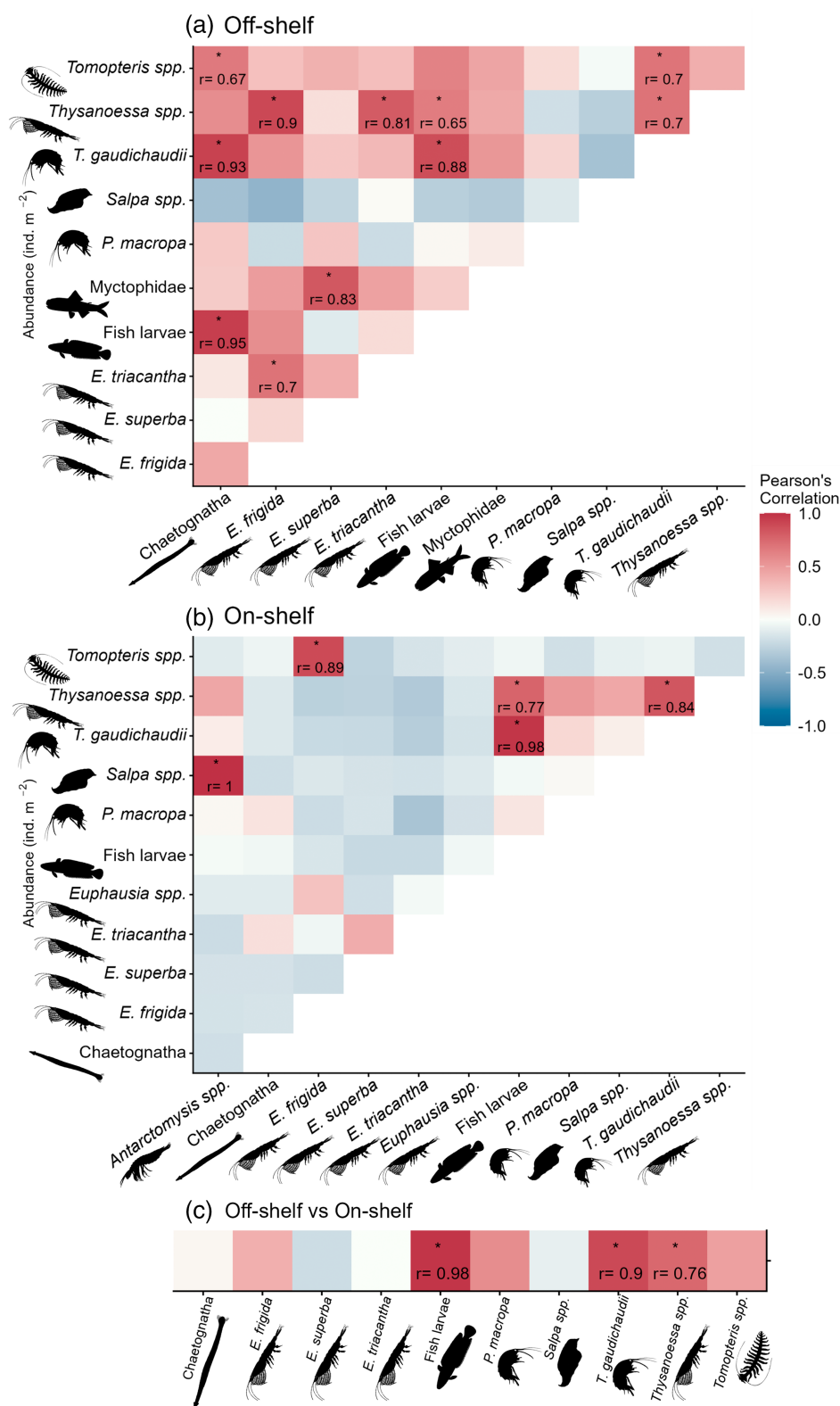


Fig. 6. Pearson's correlation matrix showing associations between total taxa (a) within off-shelf region (b) within on-shelf regions and (c) between regions, where abundance (ind. m⁻²) of taxa were correlated across both on- and off-shelf environments. All correlation coefficients are shown on a color-scale from blue (negative) to red (positive). Significant associations ($p < 0.05$) are annotated with respective r and p values.

positive correlations were found to be significant, indicating associations between taxa followed similar trends in abundance (i.e., both either increased or decreased within region). Off-shelf, 11 significant associations were seen, with *T. gaudichaudii* and *Thysanoessa* spp. both having four of those relationships (Fig. 6a). Here significant r -values ranged from 0.65 to 0.95, with the strongest relationships being between Chaetognatha and fish larvae, and between Chaetognatha and *T. gaudichaudii* ($r = 0.95$, $p < 0.001$ and $r = 0.93$, $p < 0.001$, respectively). The three non-krill euphausiids also all showed significant positive correlations with one another (*Thysanoessa* spp./*E. frigida* $r = 0.90$, $p < 0.001$. *Thysanoessa* spp./*E. triacantha* $r = 0.81$, $p = 0.005$, and *E. frigida*/*E. triacantha* $r = 0.70$, $p = 0.024$). *E. superba* showed a significant relationship with myctophids when off-shelf ($r = 0.68$, $p = 0.031$), but with no other taxa.

On-shelf, we observed five significant relationships which were all positively correlated, with r -values being much higher than off-shelf, ranging from 0.77 to 0.998, likely due to more fluctuating abundances within off-shelf catches (Fig. 6b). *Antarctomysis* spp. and salps showed a very strong relationship ($r = 0.998$, $p < 0.001$) but were both caught in high abundance on-shelf in 2014 and irregularly in all other years surveyed; this association was not confirmed by permutation testing and likely reflects an abnormal year for the on-shelf region. *Thysanoessa* spp. showed two significant relationships with fish larvae and *T. gaudichaudii* ($r = 0.77$, $p = 0.007$ and $r = 0.84$, $p < 0.001$ respectively). Similar to off-shelf, we saw a strong relationship between fish larvae and *T. gaudichaudii* on-shelf ($r = 0.98$, $p < 0.001$), and the addition of a strong relationship between *E. frigida* and *Tomopteris* spp. ($r = 0.89$, $p < 0.001$).

Between regions, we found significant positive correlations for *Thysanoessa* spp., fish larvae, and *T. gaudichaudii* ($r = 0.76$, $p = 0.010$, $r = 0.98$, $p < 0.001$, and $r = 0.90$, $p < 0.001$, respectively), suggesting that the abundance of these taxa were ubiquitous across the shelf region and that the region is not a defining factor in their distribution (Fig. 6c).

Discussion

Our analysis of South Georgian shelf macrozooplankton community structure synthesizes a decade of annual net sampling, revealing communities of similar abundances but differing structures. Off-shelf communities were more species-rich and consistent across years, whereas on-shelf communities were more variable and periodically dominated by Antarctic krill.

Off-shelf to on-shelf comparison

Overall, we found higher diversity off-shelf, with less variability in the presence and abundance of key species, consistent with greater community stability toward the open ocean and echoing findings in zooplankton diversity across shelf

systems globally (Keister and Peterson 2003; Lopes et al. 2006). As shelf regions present a gradual shift in environment moving from off-shelf to on-shelf, some species overlap is expected, though we further found a divide in shelf communities with respect to the presence and absence of certain key taxa (e.g., *E. superba*, salps, myctophids) as well as clear differences in abundances between on-shelf and off-shelf regions. These results agree with studies from other systems that suggest shelf bathymetry influences assemblage structure, for example demersal fish communities on the Brazilian Continental Shelf (Eduardo et al. 2018), zooplankton communities of oceanic and shelf regions (Springer et al. 1989), and euphausiids at the sub-Antarctic Prince Edward Islands, where reduced advection of deep water into the shelf region was responsible for a substantial difference in community structure between shelf regions (Hunt and Pakhomov 2003).

The bathymetric transition from off-shelf to on-shelf had a particular influence on Antarctic krill distribution in this region, with a number of our analyses indicating that on-shelf is the preferred habitat of the species. This aligns with historic observations of krill density at South Georgia being higher on-shelf and around the shelf break (Atkinson et al. 1999; Brierley et al. 1999; Cresswell et al. 2007; Reid et al. 1999). Antarctic krill are capable of preferential habitat distribution in large numbers, associating with on-shelf continental shelf regions (Korb et al. 2004; Tarling and Fielding 2016). High-density krill swarms are driving this high abundance seen on-shelf (Klevjer et al. 2010). This pattern of swarming behavior may be a defensive strategy against land-based predators (Cox et al. 2011; Murphy and Reid 2001; Tarling and Fielding 2016), while still maintaining feeding benefits of the on-shelf region. Cresswell et al. (2007) modeled this trade-off and predicted that optimal krill behavior alters along an on-shelf to off-shelf gradient, acting to retain a shelf-break location and swarming at densities that varied with body size, particularly on-shelf. Swarming itself generates a patchy distribution, which further explains why this species was found in large abundances when present but did not always appear to dominate the on-shelf region. The influence of this behavior on community structure is likely sporadic rather than sustained, with krill briefly competing with other grazers when present in high densities. This remains consistent with the few significant associations seen between krill and other on-shelf taxa. Our analyses did not find Chl *a* to be a significant factor in explaining patterns of abundance even though the underlying assumption in many of the above studies is that food availability is higher in on-shelf environments. This may be a result of scales of variability in Chl *a* itself do not match well with the net-based sampling resolution of the present study. Furthermore, the satellite data do not resolve sub-surface Chl *a* which may be substantial in this region (Korb et al. 2004).

Other species within our study also showed strong associations with either the on-shelf or off-shelf region. For instance, *Antarctomysis* spp. were only recorded on-shelf, in-line with

the species being considered an on-shelf mysid (Ward 1984), and similar to the observations of Lancraft et al. (2004) in the Croker Passage (Antarctic Peninsula). This species was also notable for large observed variations in abundance. For instance, *Antarctomysis* spp. was highly abundant in 2014, yet absent or present only in very low numbers in all other years. High abundances may be the result of swarming by this taxon, which may be part of its mating and fertilization behavior (Siegel and Mühlenhardt-Siegel 1988). *Antarctomysis* spp. is also a prominent vertical migrator, which may result in it avoiding certain net tows. The species was almost exclusively recorded during day tows, and 2014 was a year in which only day tows were conducted.

Off-shelf, myctophids were a key component of the community structure with abundances being significantly higher than on-shelf. The myctophid community was dominated by *Gymnoscopelus braueri*, *G. fraseri*, and *E. antarctica*, which were present in at least 8 of the 10 survey years. Off-shelf, myctophids can access mesopelagic layers with which they are more widely associated. Myctophids migrate into the surface layer to feed at night, with copepods, euphausiids, salps, and mysids being the main components of their diet (Korb et al. 2012; Shreeve et al. 2009).

Salps, fish larvae, *Themisto gaudichaudii*, and non-Antarctic krill euphausiids (e.g., *Thysanoessa* spp.) did not show a particular affinity to either on-shelf or off-shelf regions. These taxa do not have the swimming capabilities of those previously discussed and their distributions may be more reflective of the prevailing currents in this region. Accurately representing salp abundance in net surveys is difficult due to the organism's body tissue and chain-forming structure, which are often damaged during capture (Ohman and Lavaniegos 2002). Since the 1970s, studies have found an increase in salp densities and a southward expansion of their distribution, although direct competition with Antarctic krill is more difficult to diagnose (Pakhomov et al. 2002; Atkinson et al. 2004). Fish larvae showed a significant positive correlation between both on-shelf and off-shelf regions, highlighting that abundance tended to increase and decrease simultaneously across regions in any one particular survey year. *Thysanoessa* spp. and *T. gaudichaudii* were both consistently abundant and also showed a similar trend to fish larvae, with significant positive correlations in abundance across the regions. *Thysanoessa* species are widespread throughout the Southern Ocean, consisting of two species, *T. vicina* and *T. macrura*, with overlapping distributions. *T. macrura* is believed to be omnivorous, with the adults at least being major consumers of copepods (Wallis 2019), whereas *T. vicina* is less well-studied and so the dietary preferences and behavior as not as well understood. *T. gaudichaudii* has been described as highly abundant and a dominant species within the oceans surrounding South Georgia (Siegel 2016; Watts and Tarling 2012). They are aggressive predators, opportunistically feeding on a range of copepods, polychaetes, and euphausiids (McCormack

et al. 2017; Pakhomov and Perissinotto 1996; Watts and Tarling 2012), with complex parasitic or predatory relationships with gelatinous taxa (Havermans et al. 2019). Despite variability in abundance throughout this study, *T. gaudichaudii* is a key taxa in both on- and off- shelf systems. Showing associations with multiple species, they are considered to be non-selective in choice of prey and place a major predatory pressure on the local macrozooplankton community (Pakhomov and Perissinotto 1996).

Off-shelf trophic relationships

Off-shelf, we identified three prominent feeding guilds: (1) primary consumers, (2) mid-trophic level predators, and (3) myctophids (Fig. 7a). Within the primary consumer guild, fewer significant relationships were seen than expected based on literature analysis. Predatory relationships from myctophids and amphipods were not resolved, with *Thysanoessa* spp. having the most observed associations. *T. macrura* and *T. vicina* are the most prominent species of *Thysanoessa* within the Southern Ocean (Ward et al. 1990), and provide a vital link between trophic levels. It has been further suggested that *T. macrura* may be more adaptable to changes within their environment than other Southern Ocean euphausiids, and could therefore help mitigate the potential impacts of reduced densities of Antarctic krill (Johnston et al. 2022; Pinkerton et al. 2020).

The strongest associations found off-shelf were within the mid-trophic level predators feeding guild, with almost all predator-prey interactions from the mid-trophic level predators, where co-varying abundances indicate consistent and recurring interactions. Such cycles may not always be apparent within abundance data, even when a trophic relationship is present, as abundance may be offset in time, decoupled by patchy distributions, or obscured by predators feeding across a range of prey. The associations presented here are therefore likely a conservative view of interactions. We found a strong connection between *Thysanoessa* and *E. frigida* which, as well as having similar food sources, are similar in size, inhabit similar biogeographical areas and are consumed by similar predators (i.e., fish and seabirds) (Main et al. 2009; Waluda et al. 2012). The primary consumer guild predominantly feeds non-selectively. Euphausiids are possibly more selective than salps, and *Thysanoessa* spp., specifically *T. macrura*, display the most predatory behavior within the group (Hagen and Kattner 1998). The species has been described as “an omnivorous species with a strong carnivorous tendency,” allowing the species to cope with the absence of phytoplankton (Hagen and Kattner 1998). This may allow the species to persist in environments with lower primary production as is commonly found off-shelf.

Mid-trophic level predators were also seen to have strong associations with species within the same feeding guild (*T. gaudichaudii*, Chaetognaths, and *Tomopteris* spp.). Though no strong statistical associations were observed, *P. macropa* may also fit within this guild based on wider literature. This guild

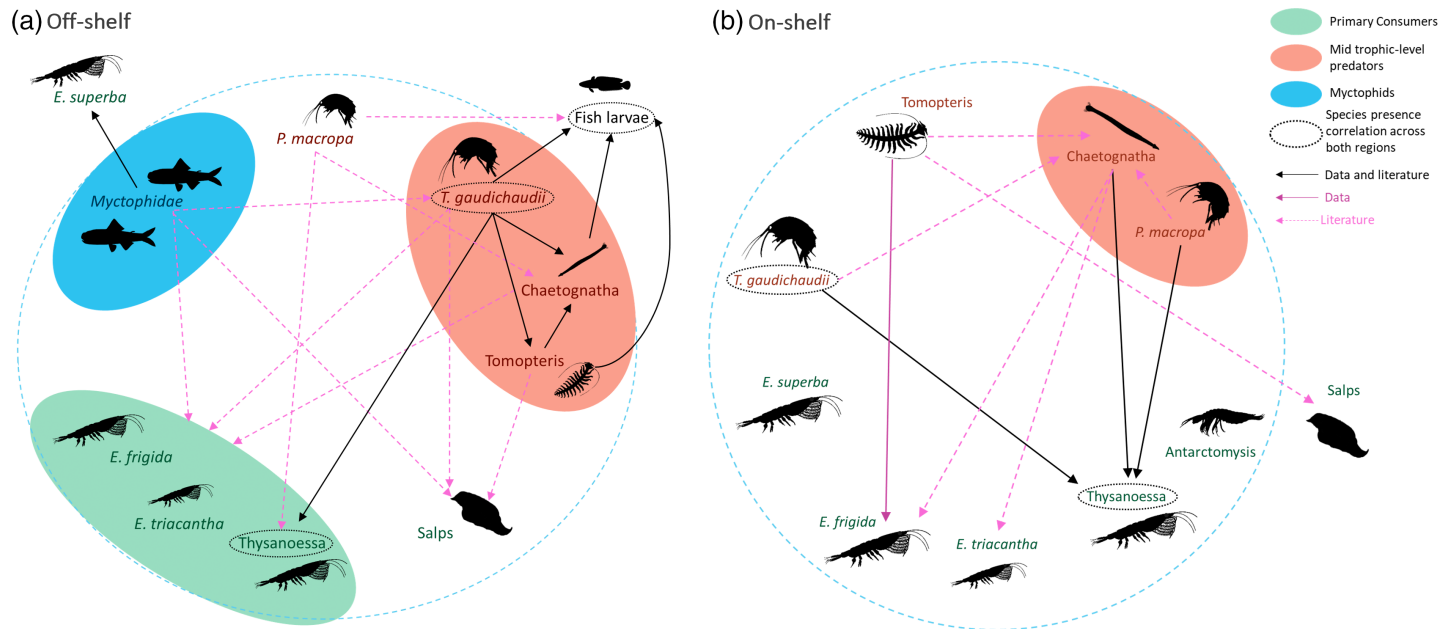


Fig. 7. Conceptualized feeding guilds for both (a) off- and (b) on-shelf regions across the South Georgia shelf basin. Relationships identified were categorized as either (1) a feeding guild (spheroids), where species fulfill a shared ecological function (Root 1967), or (2) as predator–prey interactions (arrows), where one species is known or likely to be preying on another species. For predator–prey relationships, line type reflects whether interactions were supported by our abundance data (solid purple), the diet literature (Supporting Information Table S2) (pink dashed), or both (black). Krill and salps remain outside the core shelf communities, as they appeared only intermittently and did not form part of the core community structure.

predominantly associated with and predated on fish larvae off-shelf, with predation on other predators also seen. *T. gaudichaudii* is the least selective and most predatory, with regards the number of prey types, within this feeding guild, as discussed by Watts and Tarling (2012) and McCormack et al. (2017).

Myctophids occupy the highest trophic level within our dataset and were predominantly found off-shelf. They exclusively associated with Antarctic krill, a predatory dynamic well documented in the literature, especially between *G. braueri* and *E. superba* (Kock et al. 2012). No further associations with myctophids and other species were seen, including with other known prey, such as amphipods and *Thysanoessa* spp. (Kock et al. 2012; Shreeve et al. 2009). This may reflect that our sampling methodology specifically targets macrozooplankton and not fish, so net avoidance by these higher trophic level organisms is to be expected.

On-shelf trophic relationships

Trophic relationships on-shelf appear less complex than for off-shelf (Fig. 7b). Fewer inter-specific associations were identified, and these were concentrated within a few taxa, suggesting a higher dependency on these fewer key species. Mid-trophic level predators showed the strongest links between species on-shelf, and though more primary consumers were observed, they were not as interconnected as strongly as off-shelf. *T. gaudichaudii*, Chaetognaths and

P. macropa were the only predatory species observed, and *Thysanoessa* spp. was again the most interconnected primary consumer and a core part of the on-shelf food-web.

Our analysis only showed four predator–prey interactions on-shelf, that between *T. gaudichaudii*, Chaetognaths and *P. macropa* upon *Thysanoessa* spp., and *Tomopteris* spp. and *E. frigida*. This latter interaction has not been widely reported elsewhere apart from Rakusa-Suszczewski (1968), who identified *Tomopteris* spp. feeding on young *E. frigida*. The positive correlation of *T. gaudichaudii* across both regions also indicates that mid-trophic level predators are prominent in both off- and on-shelf regions. Though the community compositions of either region are similar, far fewer associations were resolved on-shelf than off-shelf, including those expected based on literature analysis. This finding suggests that while functional diversity may be similar, the ecological and environmental conditions across the shelf region are driving differences in trophic interactions and community dynamics—which may include meandering frontal boundaries and variations in temperature and primary productivity.

We saw no statistical on-shelf connections between other species and *E. superba*. This dissociation from other species within the on-shelf communities has also been reported by Hosie et al. (2000) and again in Yang et al. (2011). This may be because Antarctic krill occurs in high abundances, which are intermittent and so do not correlate with similar trends seen in other on-shelf macrozooplankton taxa. Generally, one

can consider there to be a core on-shelf macrozooplankton community which has ephemeral interactions with intermittently abundant Antarctic krill.

We did not find a significant relationship between Antarctic krill and salps, although the correlation was broadly negative. This lack of relationship may be a product of the patchy distributions of both taxa generated by their respective tendencies to swarm. Atkinson et al. (2004, 2019, 2022) and Loeb et al. (1997) found a negative relationship between Antarctic krill and salps, with salps increasingly occupying spatial regions previously dominated by Antarctic krill. Nevertheless, the negative relationship between the taxa does not necessarily indicate competition for a shared food resource, which cannot be established from abundance data alone.

General structure of trophic relationships

Overall, the off-shelf region supported three distinct feeding guilds, a greater number of associations consistent with predator–prey interactions, and less inter-annual variability in community composition. This suggests that the off-shelf environment of the South Georgia shelf has a higher level of community stability, and changes in abundance of individual species or taxa are less likely to alter overall community structure. The on-shelf environment showed less complexity in associations within this study, with only one feeding guild emerging as a distinct grouping. This is consistent with a high dependency on the presence of a small number of species, implying that any changes to the abundance of one species will have strong ramifications on community structure and stability.

Perspective

The present study analyzes net-catch data from a spatial discrete region collected each summer for 10 years. This represents a major logistical effort in considering levels of variability in macrozooplankton community structure in a hostile sampling environment. Nevertheless, interpreting any intra- or interannual temporal trends from this data is premature since such perspectives require multidecadal timeseries (Mackas and Beaugrand 2010). Hence, our focus here was considering the data as providing repeated insights into the taxonomic structure and spatial distribution of the South Georgia macrozooplankton community. We found that this community had a comparatively stable structure that appears to remain similar whether or not Antarctic krill are present. This implies that although predictions suggest Antarctic krill may become less prevalent in range edge environments, such as South Georgia (Atkinson et al. 2022; Atkinson et al. 2004), the remainder of the macrozooplankton community appears to be relatively resilient to fluctuations and potential long-term decline in the biomass of dominant species. Our findings further indicate that trophic interactions on-shelf are focused around a few key species. Nevertheless, the overlap and gradients in species distribution highlight the complexity in

predicting potential impacts on community structure through factors such as ocean warming (Whitehouse et al. 2008). The taxa that will be most resilient to any future changes at South Georgia are likely to use a diversity of food sources and are capable of foraging both on- and off-shelf.

Author Contributions

Anona N. Griffiths, Geraint A. Tarling, and Emma L. Cavan conceptualized the study. Anona N. Griffiths led the data analysis, graphical presentation, and writing of the manuscript. Anna Belcher, Gabriele Stowasser, and Sophie Fielding all contributed greatly to the data collection and the Western Core Box project. All authors contributed to the writing and editing of the manuscript.

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Conflicts of Interest

None declared.

Data Availability Statement

The data that support the findings of this study are openly available in Stowasser, G., Fielding, S., and Tarling, G. A. (2025). The taxonomic composition, abundance and wet weight of macrozooplankton and micronekton captured by an 8-m² rectangular midwater trawler net during surveys of the Western Core Box (South Georgia), 2009–2019 (Version 1.0) [Data set]. NERC EDS UK Polar Data Centre. <https://doi.org/10.5285/967411bd-0a07-49fd-ad52-2bec65781ce7>. The code used in this study for analysis and plotting is available at <https://doi.org/10.5281/zenodo.18216623>.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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