Ecological networks in the Scotia Sea: structural changes across latitude and depth

Short title: Ecological networks in the Scotia Sea

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Abstract

The Scotia Sea is a productive pelagic ecosystem in the Southern Ocean, which is rapidly changing as a consequence of global warming. Species range shifts are particularly evident, as sub-Antarctic species expand their range from North to South, potentially rearranging the structure of this ecosystem. Thus, studies are needed to determine the current extent of variation in food web structure between these two biogeographic regions of the Scotia Sea, and to investigate whether the observed patterns are consistent among depth zones. We compiled a database of 10,888 feeding interactions among 228 pelagic taxa, underpinned by surveys and dietary studies conducted in the Scotia Sea. Network analysis indicated that the Northern Scotia Sea (NSS), relative to the Southern Scotia Sea (SSS) is more complex: with higher species richness (more nodes) and trophic interactions (more links) is more connected overall (greater connectance and linkage density). Moreover, the NSS is characterised by more groups of strongly interacting organisms (greater node clustering) than the SSS, suggesting a higher trophic specialisation of Antarctic compared to sub-Antarctic species. Depth also played a key role in structuring these networks, with higher mean trophic position and more dietary generalism in the mesopelagic and bathypelagic zones relative to the epipelagic zones. This suggests that direct access to primary producers is a key factor influencing the trophic structure of these communities. Our results suggest that under current levels of warming the SSS ecosystem will likely become more connected and less modular, resembling the current structure of the NSS.

Keywords: ecological network, food web, ecosystem structure, pelagic, Southern Ocean, Scotia Sea

Highlights

- First depiction of the topology of a depth-structured pelagic ecosystem.

- Structural differences in the Scotia Sea evident both across latitude and depth.

- Predicted shifts in species distributions threaten the structure of Scotia Sea ecosystem.

Introduction

Among the generally low primary production of the Southern Ocean, the Scotia Sea is an oasis of marine productivity (Park and others, 2010). Extensive phytoplankton blooms occur in spring, fuelling a diverse and productive pelagic ecosystem (Atkinson and others, 2001; Ward and others, 2002). The Scotia Sea has traditionally been considered a krill-dominated system, however, other functional groups such as copepods, amphipods, and myctophids comprise alternative trophic pathways from primary production to top-predators (Murphy and others, 2007; Ward and others, 2012). These alternative pathways may become increasingly important as climate-driven reorganization of the Scotia Sea fauna takes place, linked to warming of surface waters and a retreat in the extent of winter sea-ice (Mackey and others, 2012; Gutt and others, 2015; Atkinson and others, 2019; Freer and others, 2019). The latitudinal compartmentalization of the Scotia Sea into two distinct pelagic biogeographic regions, separated by the South Antarctic Circumpolar Current Front (SACCF; Ward and others, 2012), offers a useful setting to investigate the possible effects of climate change on the structure of ecological communities based on a space-for-time substitution (Pickett, 1989; Blois and others, 2013). One limitation, however, is that oceanic fronts might not be such effective barriers to the distribution of marine biota at depth (Gutt and others, 2015). Nevertheless, increasing water temperatures have been detected down to meso- and bathypelagic depths in the Southern Ocean (Armour and others, 2016; Desbruyères and others, 2017). In fact, depth is also considered a major structuring factor in pelagic ecosystems (Angel, 2003; Buckling and others, 2010; Robinson and others, 2010), but few studies have quantified trophic structuring across the depth continuum, and how warming affects the structure of communities in the meso- and bathypelagic remains an open question.

To characterise the differences in the structure of ecological communities, we first need to summarise their inherent complexity, i.e. the density of interactions within the network.

Among all possible interaction types (e.g. parasitism, mutualism, and commensalism), direct feeding links are the most easily observed and essential in terms of energy transfer. Thus, binary networks of trophic interactions have arisen as the most straightforward method for describing pathways of energy flow and the main structural features of complex ecosystems (Thompson and others, 2012). For example, greater modularity can limit the spread of perturbations through the network, increasing food web persistence (Stouffer and Bascompte, 2011). Higher connectance has been demonstrated to increase the robustness of food webs (Dunne and others, 2002a; Gilbert, 2009) and their resistance to invasions (Smith- Ramesh and others, 2017). Longer food chains indicate greater energy availability in the network (Elton, 1927). Omnivory may help to stabilise communities by mitigating top-down control and thereby reducing the probability of trophic cascades (McCann and Hastings 1997, Bascompte and Melián, 2005, Wootton 2017). Finally, generality and vulnerability measures are often related to the extent of bottom-up or top-down control (Curtsdotter and others, 2011).

Ecosystem structure is dynamic in space and time. Among all the possible abiotic drivers of these changes, temperature seems to play a principal role (Woodward and others, 2010). This is particularly true in marine ecosystems where spatial temperature gradients exert strong control over the distribution of species and the structure of communities (Tittensor and others, 2010; Boyce and others, 2015). Indeed, recent investigations of food web properties along both geographical and temporal temperature gradients have confirmed the effects of temperature on marine ecosystem complexity (Kortsch and others, 2019; Habbat and others, 2016). In Arctic and sub-Arctic marine communities, for example, there is a decrease in connectance and an increase in modularity with increasing latitude (Kortsch et el. 2019), but this pattern is currently challenged by boreal generalist species spreading toward cooler high latitude waters, with important implications for ecosystem function and

stability (Kortsch and others, 2015). Along the depth gradient, temperature and light are also the main drivers of food web structure in pelagic ecosystems (Bucklin and others, 2010). In the epipelagic zone (< 200m depth), temperature varies seasonally, and light penetrates with sufficient intensity to support primary production (Robinson and others, 2010). Below the epipelagic zone, the entire food web is sustained by epipelagic production, and consumers either feed on sinking organic matter or perform diel vertical migrations to feed in surface waters (Angel, 2003). Pelagic species commonly occupy a particular depth range, which is reasonably well described for most species in the Southern Ocean (De Broyer and others, 2014). However, there has still been no assessment of how shifting marine species assemblages could reshape trophic networks along depth gradients.

Here, we report the first investigation of the trophic network of the Scotia Sea, a pelagic polar food web, with high taxonomic resolution. We expect the food web of the Northern Scotia Sea to have a higher connectance and mean trophic level due to the higher prevalence of generalist species within this region (Murphy and others, 2007; de Broyer and others, 2014). In contrast, we expect consumers in the Southern Scotia Sea to be more specialised due to the lower temperatures, seasonal sea ice, and stable environmental conditions (Kassen, 2002, Raymond, 2011), and to display lower omnivory and higher modularity. In addition, we expect these differences to be most apparent in epipelagic waters, with greater spatial similarities in network structure in deeper ocean layers. We also expect taxa to exhibit a lower mean trophic level, linkage density, and generality in the deeper ocean, given the expected prevalence of trophic specialists below a certain depth (Ramirez-Llodra and others, 2010).

Methods

Study area

The Scotia Sea is a deep-sea basin within the Southern Ocean, delimited by the Drake Passage to the West and by the island complex of the Scotia Arc to the North, East, and South, with an approximate extension of 1.5×10^6 km^2 (Murphy and others, 2007). Its oceanography is dominated by the Antarctic Circumpolar Current, which flows west to east around the Antarctic continent and is spatially structured by frontal systems which constitute oceanographic discontinuities across physical, chemical, and biological parameters (Whitworth, 1980). In particular, the South Antarctic Circumpolar Current Front (SACCF) subdivides the Scotia Sea into two biogeographic regions: the Northern Scotia Sea (NSS) is characterised by higher and more variable temperatures, and the Southern Scotia Sea (SSS) by lower and more stable temperatures and influenced by seasonal sea ice (Raymond, 2011). Species diversity is generally higher in the NSS across different taxa (De Broyer and others, 2014), which leads to distinct structure and functioning of the pelagic ecosystems in these two areas (Ward and others, 2012). The main trophic pathway through the SSS food web is phytoplankton to krill to top predators, while other crustaceans (copepods and amphipods) and mesopelagic fish become more prominent in the NSS (Murphy and others, 2007; 2016).

Food web construction

We constructed a metaweb for the Scotia Sea, based on data gathered during the Discovery surveys performed in spring 2006, summer 2008, and autumn 2009. The surveys followed a transect from SW to NE along the Scotia Sea, from the Southern Boundary of the Antarctic Circumpolar Current near the South Orkney Islands to the Polar Front, North of South Georgia (Fig. 1), which characterised the entire pelagic community (Tarling and others, 2012a). We used several detailed quantitative dietary studies from the Discovery surveys as a starting point to build the trophic network (e.g. Saunders and others, 2014, Saunders and others, 2015a, Saunders and others, 2015b; Lourenço and others, 2016).

Subsequently, we performed literature research that identified 106 scientific articles depicting consumer-resource interactions, mainly in the Scotia Sea and Southern Ocean (Table S1). Some taxa, such as the phylum Cnidaria and Ctenophora and the class Ostracoda, were not appropriately resolved at the species level, so we complemented the node list with the most abundant species of these taxa based on recent literature for the Scotia Sea (see Table S2), guided by expert advice. The resulting metaweb comprised 228 nodes including detritus, bacteria, 31 phytoplankton taxa, 140 zooplankton taxa, 35 fish, and 18 cephalopods. In total, 74% of nodes were described at the species level and 21% at the genus level (Table S2). Marine birds and mammals were not included, as these apex predators can have strong migratory patterns, do not permanently dwell in the open ocean, and instead transit between pelagic, coastal, and terrestrial habitats. Pelagic detritus (i.e. marine snow) was included because it is a major component of pelagic networks, with several mesopelagic consumers specialized in feeding on detritus due to the absence of phytoplankton in deeper ocean layers.

We implemented a step-wise procedure based on taxonomy (i.e. species, genus and family) and geographic distribution (i.e. Scotia Sea, Southern Ocean, worldwide) for allocating interactions to each node in the network (Fig. S1; Table S1). For each node, the procedure stopped at the step at which at least one study intensively characterising the diet of the node was obtained. To this aim, only quantitative studies characterising both the diet and the interaction strengths between species were considered. Across this step-wise procedure, the taxonomic and geographic specificity of the diet decreased, and thus, we considered the dietary information obtained in earlier steps of higher quality. When we had to assume the diet from other consumer species in the same genus or family, feeding links were only included if at least two species within the genus or family were known to feed on that resource. The resources identified in stomach contents were often described to a lower taxonomic resolution than the taxa in our list of nodes. In such instances, we assumed links to

all the taxa in our list of nodes that fell within that taxonomic group (e.g. if a predator was shown to feed on the copepod genus *Clausocalanus*, we would include feeding links between that predator and all *Clausocalanus* species in our metaweb). Note that we only followed this procedure up to the class level, i.e. we did not include links to all taxa in the case of phyla such as Crustacea or Mollusca.

Food webs are frequently constructed from the literature using the protocol we have outlined above (e.g., Jacob and others, 2011, Gray and others, 2015, Laigle and others, 2018), but this approach is often criticised for overestimating the number of links in the network. To address this issue, we applied two filters to the assumed links. (1) Nodes were assigned a vertical range based on bibliographic research and characterised as strictly epipelagic (0-200 m), epi + mesopelagic (0-1000 m), strictly mesopelagic (200-1000 m), or meso + bathypelagic (200-3000 m). Only consumer-resource pairs whose vertical distribution is known to overlap were kept as links. (2) Feeding links were removed if the consumer-resource body mass ratio was unrealistically large or small. Here, each node was assigned a mean body weight from the available literature (Table S2). Consumer-resource body mass ratios are known to vary strongly among taxonomic and functional groups (Hansen and others, 1994, Conley and others, 2018, Brose and others, 2019), so we characterised these ratios for 11 consumer groups (Fig. S2), based exclusively on interactions described in the literature at the species level. We then excluded any interactions inferred from higher taxonomic levels in our database that were deemed unlikely to occur, by considering only the links whose body mass ratio fell within the range of the known distribution of body mass ratios for that consumer group (Fig. S2).

The resulting metaweb included 10,888 feeding links, depicting the main trophic interactions among the most abundant species in the Scotia Sea pelagic ecosystem (Lopez-Lopez and others, 2020). 56% of the links in the database were described from gut content

analysis of the consumer taxon described at the species level and 66% of links originated from dietary studies conducted in the Scotia Sea, with the remaining links inferred from higher taxonomic levels or other geographic regions. Based on records of presence/absence of the nodes in the NSS and the SSS, we could subset this metaweb to represent the networks of the NSS and SSS biogeographic regions. The taxonomic composition of these networks is susceptible to field sampling error, thus we tested the integrity of the networks through a series of simulations in which between 1 and 25 nodes were randomly deleted (999 permutations without replacement). This enabled us to test the sensitivity of our studied metrics to sampling error (see Fig. S3).

Topological food web properties

We compared the structure of the NSS and SSS using a broad range of metrics, calculated at both the network and node levels. While the network-level metrics described the structure of the whole NSS and SSS, the node-level metrics represented the role played by the individual nodes at each depth zone in each biogeographic region (Table 1). All the node-level properties were thus calculated for the communities found at different depth ranges, allowing us to investigate vertical changes in food web structure across the water column. We examined mean trophic level with and without primary producers included (i.e. topologically excluding them from the network). This allowed us to better compare the trophic level of consumers between depth ranges, given that primary producers only occur in the epipelagic zone. We carried out a series of simulations to determine whether the difference in network-level metrics between the NSS and SSS was greater than could occur by chance. Here, to characterise the null model, we randomly sampled the same number of nodes for each biogeographic region from the Scotia Sea metaweb 1,000 times, constructing two random networks with the same number of nodes as the NSS and SSS. Subsequently, we calculated

the difference between the network-level metrics for these randomised NSS and SSS webs in each case. We hypothesise that, if the empirical difference between the NSS and SSS for any given network-level metric was greater than 95% of the randomised differences, there was a statistically significant difference between the NSS and SSS for that particular metric. These tests were run as one-tailed tests, based on the hypothesised differences in topological structure between the NSS and the SSS. We also performed two-way ANOVAs to investigate the main and interactive effects of latitude (two levels: NSS and SSS) and depth (four levels: epipelagic, epi + mesopelagic, mesopelagic, meso + bathypelagic) on the node-level properties. Note that we considered the individual nodes as independent replicates within this analysis, though we acknowledge that metrics such as connectivity and trophic level depend to some extent on the other nodes in the network. We performed Tukey's post hoc tests to find out which of these depth levels were significantly different from each other.

Results

The number of nodes was 12% higher in the NSS (218) than in the SSS (192), with 16% of nodes from the NSS and only 5% of nodes from the SSS unique to each of these biogeographic regions. These unique nodes spanned a wide range of taxonomic groups, including ciliates, ostracods, copepods, amphipods, tunicates, euphausiids, cephalopods, and fish (Table S2). The number of trophic links was 28% higher in the NSS (10,008) than in the SSS (7,241), with 4.3% of links from the NSS and only 0.6% of links from the SSS unique to each of these regions. Both linkage density and connectance were significantly higher in the NSS (empirical differences greater than 99.0% and 99.2% of randomised differences, respectively; Fig. 2a-b). The differences in the degree of omnivory and mean trophic level between the NSS and SSS were not significantly different from the randomised food webs (empirical differences more extreme than 72.5% and 73.4% of randomised differences,

respectively; Fig. 2c-d). Both NSS and SSS food webs were clearly modular, but the difference among them was not statistically significant (both networks included four modules and the empirical difference was more extreme than 88.3% of randomised differences; Fig. 2e).

Regarding depth ranges, 19% of the nodes were strictly epipelagic (12% of which corresponded to autotrophs), 15% were epi + mesopelagic, 8% were strictly mesopelagic, 6% were meso + bathypelagic, and roughly half of the nodes (51%) were common to all depth ranges. There was no interaction between latitude and depth for any of the node-level network properties considered, i.e. linkage density, generality, vulnerability, mean trophic level, and clustering coefficient ($F_{1,1242}$ =0.339, p = 0.797; Fig. 3). The node-level properties only identified differences between the NSS and SSS for clustering coefficient, which was higher in the North ($F_{1, 1242}$ = 4.343, p = 0.037; Fig. 3f). The food webs were mostly differentiated vertically by two depth-strata: a shallower stratum (epipelagic and epi + mesopelagic), which included the nodes with permanent or regular access to the surface waters, and a deeper stratum (mesopelagic and meso + bathypelagic) which included nodes with no access to surface waters (Fig. 3). This pattern was clearly seen for generality ($F_{3, 1242}$ = 8.533, p < 0.001; Fig. 3b) and clustering coefficient ($F_{3, 1242}$ = 28.755, p < 0.001; Fig. 3f), which both increased markedly in the deeper stratum. Node-level linkage density also increased in the deeper strata ($F_{3, 1242}$ = 6.296, p < 0.001), but the post-hoc results were not as clear (Fig. 3a). Mean trophic level was also significantly higher in the deeper than the shallower stratum ($F_{3,1242}$ = 31.954, p < 0.001; Fig. 3d) and this pattern was still evident after excluding primary producers from the analyses ($F_{3,1242}$ = 6.624, p < 0.001; Fig. 3e). Vulnerability, on the other hand, showed no vertical differentiation ($F_{3,1242}$ = 0.901, p = 0.44; Fig. 3c).

Discussion

Our food web analyses substantiate the higher complexity commonly attributed to the Northern Scotia Sea (Murphy and others, 2007; Ward and others, 2012), and identify multiple pathways for energy transfer. The Northern food web displayed higher taxon richness, which was evenly distributed across taxonomic groups (Table S1), reflecting the generally higher biodiversity of sub-Antarctic versus Antarctic pelagic systems (de Broyer and others, 2014). The NSS also displayed a much higher number of links than its Southern counterpart, which resulted in a higher linkage density and connectance. The higher connectance of the NSS at the network level was associated with a higher clustering coefficient for individual taxa, suggesting a tightly knit network. Note that it is not unusual for the lower clustering coefficient in the SSS to be associated with a marginally higher modularity relative to the NSS (Fig. 2e) – this is merely indicative of a network with more modules, but with a lower density of links within the modules. The lower biodiversity and connectance of the SSS would often be associated with reduced stability, particularly lower robustness to secondary extinctions or resistance to invasions (Dunne and others, 2002a). However, the combination of lower clustering coefficient and relatively high modularity should ensure that taxa are organised into many sparsely connected groups. This configuration could isolate the impact of perturbations, preventing their propagation throughout the web, and thus increasing the overall robustness of the network (Rezende and others, 2009). The definitive implications for stability would need to be explored with a formal stability analysis, however.

Both the NSS and the SSS exhibited lower modularity than other marine polar ecosystems (Kortsch and others, 2015; Saravia and others, 2019). Oceanographic discontinuities, such as the SACCF, are the only permanent features that compartmentalise pelagic ecosystems into distinct regions. Pelagic habitats are also dynamic and often depend on ephemeral gradients with low predictability (Hyrenbach and others, 2000; Álvarez-

Berastegui and others, 2014). In contrast, shelf ecosystems are strongly structured along continuous gradients such as depth, and thus, their food web properties also change progressively across these gradients (Kortsch and others, 2019).

The mean trophic level in this work is calculated as the simple mean of the prey-averaged trophic levels of all nodes within the network, rather than being weighted by their biomasses (Table 1). Nevertheless, our estimates of mean trophic level for the Scotia Sea network agree with previous estimates in the area based on stable isotopes, size spectra theory, and food web modelling (Tarling and others, 2012b, Hill and others, 2012). The Scotia Sea networks, however, displayed higher connectance and mean trophic level than other marine Antarctic food webs (Saravia and others, 2019), even though we did not consider apex predators such as marine mammals and seabirds in our trophic networks. Benthic and demersal ecosystems are known to be both structurally and functionally more complex than open pelagic ecosystems (Reynolds, 2008), but our results challenge the simplicity traditionally associated with open pelagic food webs. The Scotia Sea food web is the only purely pelagic trophic network that has been investigated to date from a topological point of view, and these differences with other Antarctic trophic networks could partly result from the high levels of omnivory among the consumers of this pelagic ecosystem.

Depth was a stronger factor than latitude in structuring the node-level properties of the Scotia Sea food web. No interaction between depth and latitude was observed for any of the metrics considered, indicating that changes in trophic structure with depth were consistent for both the NSS and SSS. In fact, depth is typically seen as the main structuring factor in open pelagic ecosystems, covarying with light and temperature, and resulting in a layering of the ecosystem (e.g. epi-, meso-, and bathypelagic) (Angel, 2003, Robison, 2004). As the transitions between these physical layers are gradients rather than surfaces, the ecological communities overlap, making the distinctions in ecological layers somewhat fuzzy (Ramirez-

Llodra and others, 2010). In the Southern Ocean, most taxa are known to span multiple depth layers, often migrating daily between depths (e.g., Collins and others, 2008; Cisewski and others, 2010). This mixing makes it impossible to partition entire networks according to depth, but allowed us to consider the properties of the nodes that strictly occupy each layer, or that link adjacent layers. Our analyses clearly identified an increase in mean trophic level, linkage density, clustering coefficient, and generality of taxa with depth, indicating more predatory behaviour and more opportunistic feeding in the deeper layers. This difference was particularly stark for taxa that do not occupy (or migrate to) the productive epipelagic zone, which suggests that having permanent or regular access to surface waters is a key factor influencing topological changes along the depth gradient. Future studies should explore the biological traits of organisms that might help to explain this trophic structuring according to depth (e.g. Olmo Gilabert and others, 2019).

Vulnerability to a broader range of predators was the only metric considered that did not increase with depth, pointing to an asymmetry in how trophic roles change with increasing depth, i.e. prey were no less vulnerable to predation in the deeper stratum even though predators expanded their diet. This could be driven by the decreasing abundance, and thus encounter rates, of organisms from the epipelagic, through mesopelagic, to bathypelagic (Marshall, 1979). Unfortunately, the diversity and trophodynamics of deep-pelagic species is poorly known and cannot be easily estimated to compare with other ecosystems, as challenging conditions and intrinsically low abundances can strongly constrain effective sampling (Robison, 2008). Mesopelagic species, for example, commonly migrate upward during the night to feed in the more productive shallow ocean layers, and migrate downwards at night to minimise visual detection by predators (Angel, 2003). Our results challenge the paradigm of trophic specialism prevailing in the deeper ocean (Ramirez-Llodra and others, 2010) and, on the contrary, suggest that trophic generalism could be considered a strategy to

survive in these deep environments where prey are scarce. The relatively low encounter rates with potential predators could also serve as a refuge from predation for many mobile species.

Over recent decades, the Scotia Sea has experienced one of the largest levels of warming of any polar region (Whitehouse and others 2008), affecting the duration and extent of seasonal sea-ice (Arrigo and Thomas, 2004). These changes will favour the southward migration of sub-Antarctic taxa into Antarctic waters. Species thermal tolerances could be a straightforward predictor for their distributional changes (Schuetz and others, 2019), but their ability to adapt to diverse biotic environments could also be key. For example, generalist predators have been the first species showing distributional changes towards higher latitudes in the Barents Sea (Kortsch and others, 2015). The expansion of generalist predators from the NSS towards the SSS would likely increase the connectance of this Antarctic ecosystem while decreasing its modularity. This reflects opposing responses in terms of network stability, i.e. lower modularity would increase the probability of perturbations spreading through the network (Stouffer and Bascompte, 2011), but may be offset by increased connectance enhancing robustness to species loss (Dunne and others, 2002b; Dunne and others, 2004).

These broad structural changes in response to warming are likely to be underpinned by significant species turnover in the Scotia Sea. Projections of macrozooplankton distributions based on species environmental envelope models have indicated a southward shift in the Scotia Sea (Mackey and others, 2012). Empirical studies found contrasting evidence, however, with post-larval krill following the predicted shift from the North to South Scotia Sea (Atkinson and others, 2019), but the most abundant copepod species maintaining its distribution (Tarling and others, 2018). These conflicting results highlight the context-dependence of species level adaptive responses to warming. Nevertheless, food web modelling may help overcome these limitations, e.g. by helping to identify how a decrease in

krill abundances would relax both predation on copepods and their competition for food (Ward and others, 2018), as the distributional range of a species depends not only on the abiotic niche but also on biotic interactions. Indeed, one additional consequence of the predicted increase in generality and connectance of taxa in the SSS could be an increase in the number of trophic pathways and consequently the loss of transfer efficiency in the food web, which may no longer sustain large populations of top predators (i.e. seabirds and marine mammals). This emphasizes the interest in adopting a structural approach to studying the effects of climate change on marine ecosystems, complementing the large but growing body of evidence of climate effects at the species level.

Marine fauna can shift their vertical distribution in the water column to track their thermal optimum in response to warming (Poloczanska and others, 2013). Surface isotherms also migrate between 3 and 5 orders of magnitude faster vertically than horizontally, indicating that depth refugia could become a key factor in maintaining populations in a warming ocean. Thus, Southern Ocean taxa might find it easier to adapt by shifting a few metres vertically than a few kilometres horizontally (Jordá and others, 2020). Nevertheless, light penetration is a major constraint to vertical shifts in species distributions and epipelagic organisms are predicted to become compressed towards the bottom of the photic layer in such scenarios (Agusti and others, 2015, Jordá and others, 2020). This compression will affect phytoplankton diversity and generally decrease its productivity (Jordá and others, 2020), but it might also facilitate consumer-resource encounters as organisms are predicted to compress towards the deeper end of the epipelagic, possibly increasing network connectance in this depth layer and even the availability of these epipelagic resources to mesopelagic consumers. Vertical changes in species distributions could thus have profound effects on the structure of the trophic network.

While our study effectively tested our working hypothesis on the changing structure of the Scotia Sea across latitude and depth, we recognize that this static approach does not take into account dietary switching, and that considering biomasses and feeding preferences could challenge some of our conclusions, particularly regarding trophic levels (Olmo Gilabert and others, 2019; Kortsch and others, 2021) and generality (e.g. Scotti and others, 2009). In addition, our network model is likely biased in three different aspects: towards (1) the warmest seasons, (2) the upper ocean layers, and (3) the largest taxa. Due to the technical limitations of accessing and sampling the Southern Ocean during the winter months, the vast majority of the studies used for constructing the trophic network were carried out between spring and autumn. Likewise, due to technical and time constraints, the highest sampling effort commonly relies on the upper ocean, with the deepest mesopelagic and the bathypelagic domains often under-sampled. Lastly, the trophic information is primarily compiled from analyses of stomach contents, which consistently underestimate the importance of prey that lack hard morphological structures and/or digest rapidly (Arai and others, 2003). Among these under-represented taxa may be the gelatinous plankton, arguably a common group among the deep-sea fauna (Robison, 2004; Robinson and others, 2010), but also the smallest part of the marine life size spectrum, which requires equipment and taxonomic expertise not often found among trophic ecologists and is commonly underrepresented in biodiversity studies (Troudet and others, 2017). Molecular methods, such as DNA metabarcoding, are deemed as a powerful tool to bridge this knowledge gap in the structure of marine food webs, as they can identify taxa based on digestion remains or even tissue traces. These molecular techniques have revealed 3-8 times greater diversity of planktonic taxa than previously described based on morphology (de Vargas and others, 2015), holding immense potential to improve our understanding of the structure of pelagic ecosystems in the near future (D'Ambrosio and Mariani, 2021).

In spite of these limitations, our study is the first to characterise the topology of pelagic food webs at high taxonomic resolution, suggesting that the structure of pelagic ecosystems is more complex than previously thought (Reynolds, 2008). Our results confirm structural differences between the North Scotia Sea and the South Scotia Sea (Murphy and others, 2007; Ward and others, 2012; Murphy and others, 2016), but also indicate that depth might have a stronger effect than latitude in the topology of pelagic ecosystems. Well documented changes in species distributions are a major concern regarding how restructuring of the ecosystems might affect ecosystem functioning, but our work suggests that current research on pelagic ecosystems should broaden its focus to include changes in depth distributions, commonly overlooked in the literature.

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Figure 1. Map of the study area with sampling points across the region (central panel) and representation of the food web network in the North and South Scotia Sea (left and right panels, respectively). Nodes that are unique to each region are illustrated in yellow or orange. Networks were illustrated with Network 3D (Yoon and others, 2004, Williams and others, 2010).
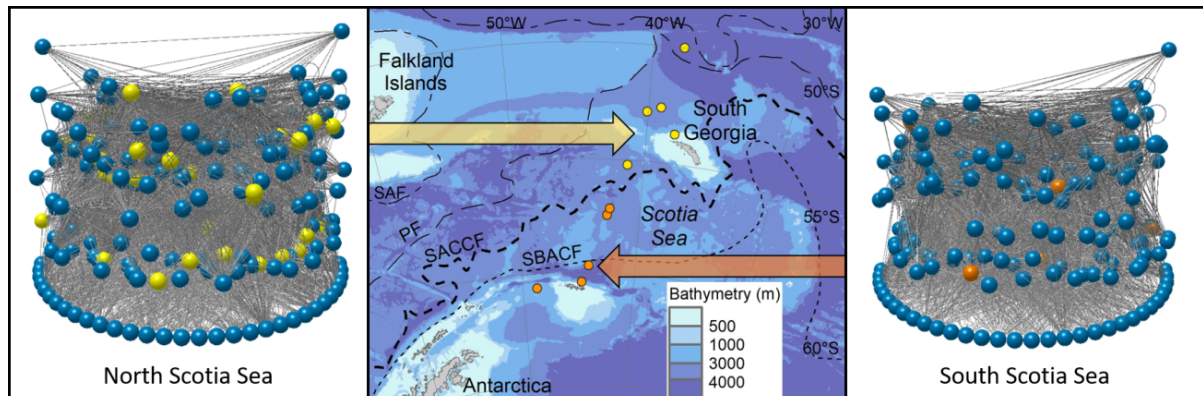
Figure 2. Differences (Δ) in network-level metrics between the Northern Scotia Sea (NSS) and Southern Scotia Sea (SSS) food webs. The vertical line corresponds to the true difference between NSS and SSS, while the grey bars indicate the frequency distribution of differences obtained from 1,000 simulations of each network containing the same number of nodes as the actual webs, but randomly sampled from the Scotia Sea metaweb. The black bars correspond to the 5% tail of the distribution, i.e. the likelihood of obtaining a more extreme difference between NSS and SSS than the true difference.
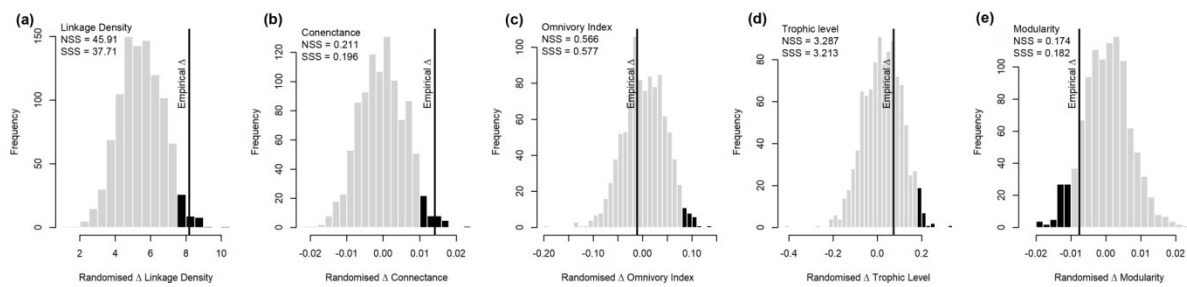
Figure 3. Node-level network metrics (mean ± SE) evaluated for each of the depth ranges considered in the North Scotia Sea (NSS, white) and South Scotia Sea (SSS, grey). Depth zones not sharing a common letter are significantly different from each other according to Tukey's post-hoc Test.
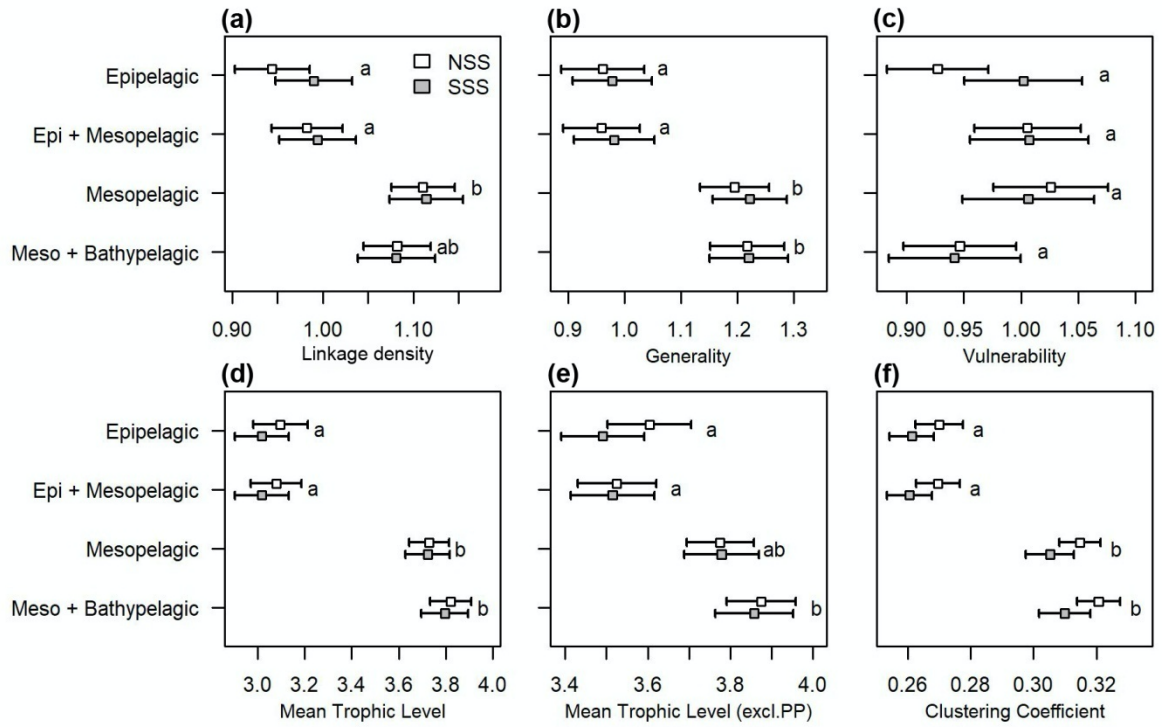
1   **Table 1.** List of metrics used, their description and their implications for network stability. Computing methods include the Cheddar, iGraph and

2   NetIndices packages in R (Hudson and others, 2020, Csardi and Nepusz, 2006, Kones and others, 2009, R Core Team, 2020) and the Network3D

3   software (Yoon and others, 2004, Williams, 2010).

Metric	Level of organisation	Description	Formula	Network implications	Reference	Computation
Node Richness	Network	Number of taxa (nodes) in the network	$Node\ richness = N$	Informs on the size of the food-web.	May, 1972	NumberOfNodes() R: Cheddar package
Number of trophic links	Network	Number of feeding interactions (links) in the network	$Number\ of\ trophic\ links = L$	Informs on the size and complexity of the food-web.	Dunne and others, 2002a	NumberOfTrophic Links() R: Cheddar package
Linkage density	Node	Number of links to a node normalized by the average number of links across the network	$LD_i = \dfrac{L_i}{\frac{\sum_{i=1}^{N} L_i}{N}}$ Where L_i is the number of links of node i.	Species with higher linkage density usually play an important role in stabilising food webs.	Dunne and others, 2002a; Strogatz, 2001	Network3D
	Network	Average number of links per node	$LD = \dfrac{L}{N}$	Informs on the complexity of the food web.		LinkageDensity() R: Cheddar package
Connectance	Network	Number of links as a fraction of all possible links in the network	$C = \dfrac{L}{N^2}$	Informs on the network robustness, depending on the randomness in the distribution of the links and their strength.	May, 1972; Dunne, 2002	DirectedConnecta nce() R: Cheddar package
Generality	Node	Number of prey of a node normalized by the average number of prey	$G_i = \dfrac{L_{Ri}}{\frac{\sum_{i=1}^{N} L_{Ri}}{N}}$ Where L_{Ri} is the number of	Relates to the vertical structure of the network and the existence of bottom-up	Bersier et al., 2002; Dunne and Williams, 2009	Network3D

		across the network	resources of node i.	controls.		
Vulnerability	Node	Number of predators of a node normalized by the average number of predators across the network	$V_i = \dfrac{L_{Ci}}{\frac{\Sigma_{i=1}^{N} L_{Ci}}{N}}$ Where L_{Ci} is the number of consumers of node i.	Relates to the vertical structure of the network and the existence of bottom-up controls.	Bersier et al., 2002; Dunne and Williams, 2009	Network3D
Modularity	Network	Number of groups of nodes interacting more strongly among themselves than with other groups.	$M = \sum_{s=1}^{N_M} \left(\dfrac{I_S}{L} - \left(\dfrac{d_S}{2L} \right)^2 \right)$ Where N_M is the number of modules, I is the number of links between nodes in modules, L is the number of links in the network and d_s is the sum of degrees of all species in modules. We used the simulated annealing algorithm by Reichardt and Bornholdt, 2006; which aims at maximising the partition between modules based on stochastic optimisation.	The compartmentalisation of food-webs into distinct modules, containing species which are more densely connected among themselves than with the rest of the network, can limit the spread of perturbations through the network, increasing food web persistence.	May 1972; Stouffer and Bascompte, 2011; Newman & Girvan 2004; Reichardt & Bornholdt, 2006	cluster_spinglass() R: iGraph package
Clustering coefficient	Node	Number of triplets of nodes, i.e. how many of the nodes, which are both linked to a third node, are also linked	$CC_i = \dfrac{2I_i}{L_i \cdot (L_i - 1)}$ Where L_i is the degree of a node and I_i is the number of triplets (i.e., connections between the nodes connected to node i)	Informs on the density of links locally, by considering the density of triplets in neighbouring nodes. Relates to the stability of the network.	Watts and Strogatz, 1998; Montoya and Solé, 2002	Network3D
Prey-Averaged	Node	Mean trophic level of all trophic	$TL_i = 1 + \sum_{i=j}^{n} \dfrac{TL_j}{n_i}$	As the average position of a species in all the	Williams and Martinez,	Network3D

Trophic Level		resources +1	Where n_i is the number of prey species in the diet of predator i, and TL_j is the trophic level of each of its prey.	food chains it is a part of, trophic level characterizes the vertical structure of the web.	2004	
	Network	Mean prey-averaged trophic level	$$TL = \frac{\sum_{i=1}^{N} TL_i}{N}$$ Where TL_i is the trophic level of each individual node.	Informs on the relative contribution of trophic levels to the vertical structure of the network.		TrophInd() R: NetIndices package
Omnivory index	Network	Standard deviation associated to the trophic level of each taxa	$$OI = \frac{\sum_{i=1}^{N} sd(TL_{Ri})}{N}$$ Where TL_{Ri} is the trophic level of the resources of node i.	Intermediate levels of omnivory are believed to stabilize communities by mitigating top-down controls and thereby reducing the probability of trophic cascades	McCann and Hastings, 1997; Bascompte and Melián, 2005; Dunne and Williams, 2009; Curtsdotter and others, 2011	TrophInd() R: NetIndices package

1