The response of trophic interaction networks to multiple stressors in a marine latitudinal gradient of the Southern Hemisphere

Running Title: Marine stressors in the Southern Hemisphere

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Abstract

Ecological networks offer valuable insights into community structure, key species identification, and ecosystem management for biodiversity conservation. Understanding how these networks react to environmental and anthropogenic stressors, especially along geographical gradients, is of increasing interest. This review presents a pioneering analysis of stressor responses in marine food webs from the southwest Atlantic to the Antarctic (45 - 78ºS), encompassing areas such as San Jorge Gulf, Beagle Channel, Burdwood Bank, Scotia Sea, Potter Cove, and the Weddell Sea in Antarctica. Our objectives are to: 1) describe the structure of marine food webs along this axis using a network approach; 2) identify predominant environmental and anthropogenic stressors affecting each ecosystem; and 3) summarize observed food web changes and hypothesize on stressor impacts. Our collaborative team, comprising regional experts and global authorities on high-latitude marine food webs and stressor effects, ensures a comprehensive and credible literature review. We assessed the effects of stressors primarily at the species level, with notable exceptions like fisheries in San Jorge Gulf. Hypotheses for each study area were formulated considering: a) stressors; b) impacted parameters; c) node-level species properties; and d) network-level food web properties. Global warming emerges as the most common stressor across the gradient, except in the Beagle Channel and Burdwood Bank, where alien species introduction and fisheries are more influential, respectively. We offer specific hypotheses on how warming may affect food webs. Our findings highlight the benefits of a network approach in understanding and predicting stressor effects in Southern Hemisphere marine ecosystems. This approach provides a holistic understanding of ecological networks, enhances our ability to identify key species and interactions, and offers insights for ecosystem management and conservation in the face of various stressors.

Keywords: anthropogenic stressors, environmental stressors, food webs, latitudinal gradient, Southern Hemisphere

1. Introduction

The application of a network perspective has emerged as a powerful tool to tackle the complexity of species interactions, facilitating a better understanding of the structure and functioning of ecosystems (Belgrano et al. 2005; Thompson et al. 2012). Trophic networks (or food webs) allow identifying properties and key species that may be crucial for ecosystem stability, and hence important for ecosystem management and biodiversity conservation (Thompson et al. 2012). There is a growing interest in understanding how ecological networks respond to environmental and anthropogenic stressors along geographical gradients (Cirtwill et al. 2015; Bauer et al. 2022). Yet, only a few studies have described variation in food web structure along latitudinal gradients in marine ecosystems. The few that have come from the Global North (Wood et al. 2015; Kortsch et al. 2019; Pecuchet et al. 2022), whereas no studies, nor meta-analyses, on geographical variation in marine food webs exist for the Global South (Southern Hemisphere).

Here we review for the first time the state-of-the-art knowledge on stressor response of marine food webs along the southwest Atlantic to Antarctic gradient (45 - 78ºS, Figure 1). We focus on proven and expected changes in food webs driven by stressors in selected areas along this large-scale latitudinal gradient. We recruited food web experts from different marine systems of Argentina and the world (see co-authors' list). Throughout the year 2023 we maintained regular discussion meetings, typically held every two or three weeks. The aim of this review is threefold: 1) describe the complexity and structure of marine food webs along the southwest Atlantic to Antarctic axis from a network perspective; 2) identify the ongoing environmental and anthropogenic stressors for each marine ecosystem containing the food webs; and 3) resume proven food web changes and elaborate hypotheses on how the identified stressors might affect food web features (e.g. energy flow, stability), combining information on node- and network-level properties. Finally, we suggest which additional data and analyses are needed to gain insights into the stressors' effects on food web properties in the southwest Atlantic to Antarctic region.

2. The structure of marine food webs in the Southwest Atlantic - Antarctic region

Together, the southwest and the Atlantic sector of the Southern Ocean comprise one of the most biologically productive regions of the world's oceans (Acha et al. 2004; Latorre et al. 2023). The referred region extends from San Jorge Gulf (45ºS) in the Patagonian shelf to the Weddell Sea (78ºS) in the Southern Ocean, and covers a well-connected oceanic latitudinal gradient (Matano et al. 2010; Guihou et al. 2020).

Throughout this latitudinal gradient, many investigations have been carried out addressing the trophic ecology of specific species and prey-predator relationships (Vinuesa and Varisco 2007; Pasotti et al. 2015; Saunders et al. 2019; Riccialdelli et al. 2020), but few studies have considered the complexity of the ecosystem in terms of a high resolution of species and their prey-predator interactions (but see Jacob et al. (2011), Marina et al. (2018), Funes et al. (2022), López-López et al. (2022), Rodriguez et al. (2022), Marina et al. (in rev.)). Neglecting this complexity might lead to a misunderstanding of the structure and functioning of the ecosystems, and ultimately reduce the ability to predict ecosystem responses to perturbations (Montoya et al. 2009).

In this review, we consider marine areas in the Southern hemisphere for which highly-resolved empirical food webs, in terms of species diversity and trophic interactions, have been previously described. These areas include: (1) San Jorge Gulf (45 - 47ºS, 65 - 68ºW), (2) Beagle Channel (~54ºS, 68ºW), (3) Burdwood Bank (~54ºS, 59ºW), (4) Scotia Sea (48 - 58ºS, 50ºW), (5) Potter Cove (62ºS, 58ºW, Antarctica), and (6) Weddell Sea (74 - 78ºS, 30ºW, Antarctica) (Figure 1). The geographic locations of these marine biomes span from temperate to Antarctic, and are exposed to both environmental (sea warming, glacial retreat) and anthropogenic (fishery, pollution) stressors.

San Jorge Gulf is the northernmost study area considered in this review. It is a partially enclosed basin spanning approximately 34,000 km2 and ~100 m of maximum depths, located from Cabo dos Bahias (44°55'S) to Cabo tres Puntas (47°06'S) (Figure 1). The shallower northern and southern ends of the Gulf (with depths ~40 m) present two prominent frontal systems. These systems are the areas of highest productivity (Glembocki et al. 2015). The Gulf's productivity supports large invertebrate and vertebrate fisheries (Góngora et al. 2012), as well as marine mammal and seabird populations (Yorio 2009). The San Jorge Gulf food web comprises 165 nodes and 1015 trophic interactions with a connectance of 0.04. The percentage of top predators is 16%, 78% of intermediate nodes and 6% of basal nodes; 60% of predators are omnivorous (Table 1). The most connected nodes are: the Argentine red shrimp Pleoticus muelleri, the squat lobster

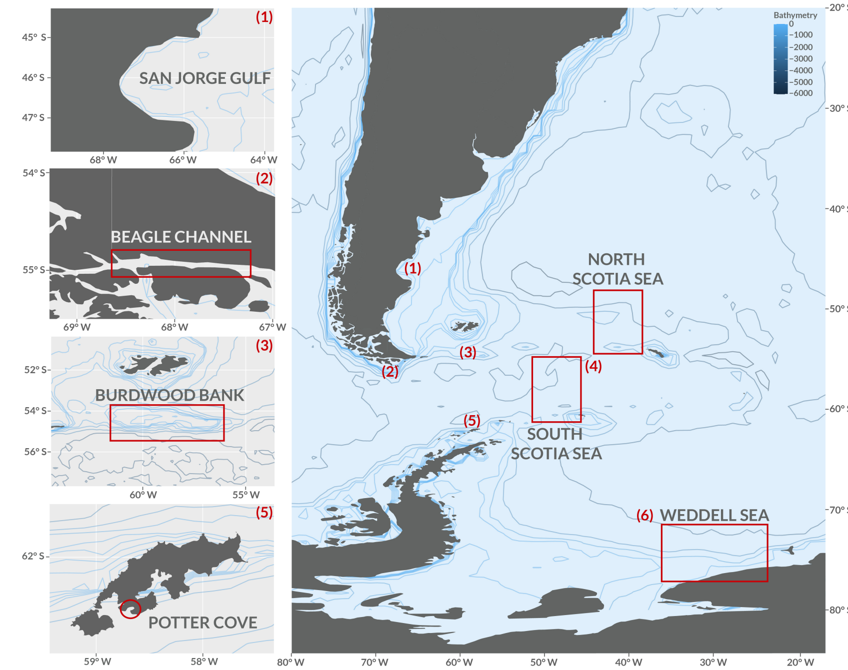

Figure 1: Map of the study areas along the southwest Atlantic - Antarctic latitudinal gradient. The areas are marked with numbers from one to six. Smaller areas (1. San Jorge Gulf, 2. Beagle Channel, 3. Burdwood Bank, and 5. Potter Cove) are shown on the panels to the left, whereas the larger areas (4. North and South Scotia Sea, and 6. Weddell Sea) are marked with a red rectangle on the map. The map was drawn using the 'marmap' R package (Pante et al. 2023). Continental contour shapefiles were obtained from www.ign.gob.ar.

Gimothea gregaria, squids (Illex argentinus as dominant species) and Amphipoda. Notably, these nodes present mid-trophic positions in the food web (3.0, 2.5, 3.6 and 2, respectively) (Funes et al. 2022).

At a southern latitude, the Beagle Channel (54°52'S, 68°8'W) is an interoceanic passage located at the southernmost tip of South America, spanning 240 km in length and 5 km in width (~1200 km2), and a range depth of 0 - 140 m (Figure 1). It features complex coastlines, varying bathymetry, a prevailing west-to-east circulation pattern, and a significant longitudinal gradient of glacial freshwater discharge (Schloss et al. 2023). Bruno et al. (2023) suggests that locally produced suspended particulate organic matter (mostly composed by phytoplankton) and organic matter accumulated in the sediments (macroalgae-originated detritus) are the primary food sources for the marine ecosystem, as opposed to allochthonous materials. Beagle Channel food web includes 145 nodes and 1115 trophic interactions with a connectance of 0.05 (Table 1). The food web is suggested to have a wasp-waist structure, where the following species play a crucial role in the dynamics of the ecosystem: Fueguian sprat Sprattus fuegensis, longtail southern cod Patagonotothen ramsayi, black southern cod P. tessellata, frogmouth Cottoperca trigloides, and squat lobster Grimothea gregaria (Riccialdelli et al. 2020). Moreover, the squat lobster has been identified as a species responsible for linking modules and connecting the entire food web (Rodriguez et al. 2022).

The so-called Burdwood Bank ecosystem comprises Marine Protected Areas Namuncurá - Burdwood Bank I and II, meaning the shallow submarine plateau named Burdwood Bank with a 200 m isobath boundary, and a deep slope that reaches 4000 m in depth, respectively (Administración de Parques Nacionales 2022) (Figure 1). Physical features in the plateau are fairly stable, with salinity averaging 34 all year round and temperature ranging between 4 and 8ºC (Acha et al. 2004). The plateau is surrounded by steep flanks of up to 4000 m depth, protected by the Marine Protected Area Namuncurá - Burdwood Bank II (32,000 km2; ~55º - 56ºS, ~58º - 62ºW). Intense upwelling and mixing occur in relation to the slope, entraining deep nutrient-rich waters into the photic layer (Matano et al. 2019), and resulting in a fairly homogeneous water column both spatially and temporally (Matano et al. 2019). The Burdwood Bank food web comprises 379 nodes and 1788 interactions, with a connectance of 0.01, and an asymmetric degree distribution (i.e. most of the species have a relatively low number of interactions and few species concentrate most of them). Almost half of the consumers are omnivores (0.48), and the network displays a small-world pattern (Marina et al. in rev.) (Table 1).

The Scotia Sea is a deep-sea basin, 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 x 106 km2 and a depth range of 0 - 3000 m (Murphy et al. 2006) (Figure 1). Its oceanography is dominated by the Antarctic Circumpolar Current, which is spatially structured by frontal systems (Whitworth 1980). The South Antarctic Circumpolar Current Front subdivides the Scotia Sea into two biogeographic regions: the Northern Scotia Sea is characterized by higher and more variable temperatures, and the Southern Scotia Sea by lower and more stable temperatures and influenced by seasonal sea ice (Raymond 2011). The analysis of the Northern and Southern Scotia Sea food webs shows that the former is relatively more complex than the latter: with higher species richness (218 vs 192) and interactions (10008 vs 7241) and a higher connection overall (0.21 vs 0.20). As expected from a more complex network, the path length is shorter in the Northern Scotia Sea food web. In the same sense, the Southern Scotia Sea network displays a greater proportion of omnivores and a lower mean trophic level (López-López et al. 2022) (Table 1).

In the Antarctic realm, Potter Cove is a ~9 km2 fjord with a depth range of 0 - 200 m located at 25 de Mayo/King George Island (62°14'S, 58°38'W, South Shetland Islands) on the West Antarctic Peninsula (Figure 1). The cove, bordered by the Fourcade Glacier, is divided into three areas: a) the internal cove, a high glacier-influenced, soft sediment zone with a 50 m maximum depth; b) the central cove, a mixed substrate area with low meltwater influence and an 80 m maximum depth; and c) the external cove, ice-free for 60 years with a 185 m maximum depth and rocky substrate (Jerosch et al. 2018). Potter Cove's high-latitude location results in variable environmental conditions due to photoperiod length seasonality. Sea ice often covers this area in winter (Schloss et al. 2012). With low phytoplankton biomass, macroalgae, and microphytobenthos are likely the primary food sources for secondary benthic production (Quartino and Boraso de Zaixso 2008). The Potter Cove food web includes 110 nodes and 649 interactions, with an asymmetric degree distribution, and a connectance value of 0.05 (Table 1). It presents a modular structure (groups of species interact more strongly with each other than with species belonging to other groups), that's positively associated with stability, since perturbation can be retained within modules (Rodriguez et al. 2022).

Located between 74 and 78ºS, the high Antarctic Weddell Sea shelf spans approximately 450 km from East to West (Jacob et al. 2011) (Figure 1). The water depth ranges from 200 to 500 m, with shallower regions being covered by continental ice that forms the coastline along the eastern and southern parts of the Weddell Sea. Within this shelf area, exists a complex three-dimensional benthic habitat characterized by substantial benthic biomasses and an intermediate to high diversity when compared to benthic boreal communities (Teixidó et al. 2002). The Weddell Sea food web exhibits a high level of network complexity, featuring the greatest number of nodes (490) and trophic interactions (16041) among the analyzed food webs in this review (Table 1). Its connectance (0.07) and other structural properties are intermediate compared to the other food webs. Recently, the interaction strengths of this food web were estimated, revealing the presence of numerous weak and few strong interactions, which is consistent with findings in other complex food webs (Nilsson and McCann 2016). Notably, this asymmetric distribution of interaction strength is likely to promote community persistence.

Table 1. Complexity and structure properties of the marine food webs considered in the present review. Refer to Table 2 for definition of properties. mean TL: mean trophic level. Food webs are ordered by increasing latitude.

Food web	Nodes	Links	Connectance	Path length	mean TL	Omnivory	Reference
San Jorge Gulf	165	1015	0.04	2.17	3.02	0.63	Funes et al. (2022)
Beagle Channel	145	1115	0.05	2.12	2.37	0.55	Rodriguez et al. (2022)
Burdwood Bank	379	1788	0.01	2.99	2.52	0.49	Marina et al. (in rev.)
Potter Cove	110	649	0.05	2.33	2.22	0.46	Marina et al. (2018); Rodriguez et al. (2022)
N Scotia Sea	218	10008	0.21	1.87	3.29	0.73	López-López et al. (2022)
S Scotia Sea	192	7241	0.20	1.90	3.21	0.71	López-López et al. (2022)
Weddell Sea	490	16041	0.07	2.19	2.62	0.51	Jacob et al. (2011)

3. Environmental and anthropogenic stressors in the Southwest Atlantic - Antarctic region

A stressor is any environmental or anthropogenic variable that causes a quantifiable change, irrespective of its direction (increase or decrease), in a biological response (Orr et al. 2020). In the light of this, the southwest Atlantic - Antarctic marine biota has been and is currently subjected to a variety of stressors (e.g. sea warming, glacial retreat, ice changes, acidification, species invasion, fisheries, and contamination). Although it is well-known that multiple stressors act in concert at any given time (e.g. warming and fishery; acidification and contaminants) (Gutt et al. 2021), to date stressor assessments have been performed individually. Moreover, the potential for interactive effects of two or more stressors (synergy or antagonism) (Côté et al. 2016) is almost unknown for the region (Rowlands et al. 2021).

In the following subsections, we describe the main environmental and anthropogenic stressors, and the species (or trophic species) and parameters affected reported for the marine ecosystems that contain the food webs considered in this review. In Table S2 we provide an exhaustive list of all stressors affecting species inhabiting each area, considering: the type of stressor, species and parameter affected, and locality.

3.1 San Jorge Gulf

San Jorge Gulf experienced several environmental and anthropogenic stressors (Table S2). Trawl fisheries discard several species and add new trophic interactions to the food web which resulted in a decrease in trait variability and the stability of the system (Rincón-Díaz et al. 2021; Funes et al. 2022). Moreover, it changed the availability of prey to several predators. For example, Merluccius hubbsi one of the main bycatch species, became prey item to non-diving seabirds, like the kelp gull Larus dominicanus (González-Zevallos and Yorio 2006) and reef fishes (Funes et al. 2019). Although juveniles of M. hubbsi are largely the main bycatch item, 29 other cartilaginous and 69 bony local fish species were also registered as incidental catch between 2005 and 2014 (Bovcon et al. 2013; Ruibal Nuñez 2020). This level of impact triggered a shift in the functional diversity of the assemblages homogenizing the trophic function of fishes (Rincón-Díaz et al. 2021). Other functional changes were a decrease in the maximum sizes of individual fish, together with a drop in elasmobranchs biomass and an increase in crustaceans biomass (Funes 2020). The significant increase in crustacean biomass was mostly due to the increase in Pleoticus muelleri and Grimothea gregaria populations (Funes 2020). These species rapidly became the most important prey for the most abundant fishes in the area: M. hubbsi and Mustelus schmitti (Pasti et al. 2021). However, the above-mentioned effects of trawl fisheries on the structure and function of the San Jorge Gulf community may have changed again, since the fisheries ceased activity in 2015 (Annex I, Resolution CFP No 7/2018), remaining a small trawling artisanal fishery.

Sea warming is another important environmental stressor in the San Jorge Gulf, because of the southward shifts of northern fish populations to the Gulf (Galván et al. 2022). The San Jorge Gulf is especially prone to be affected by climate-driven shifts in species ranges, because it is located in the ecotone between two biogeographic provinces, the Argentine (30°S - 44°S) and the Magellanic (43°S - 55°S) (Balech and Ehrlich 2008). In addition to this tropicalization from northern fish populations, alien species are also documented to affect the demersal assemblage (fish and macroinvertebrates) in the Gulf (Galván et al. 2022). Finally, San Jorge Gulf is exposed to urban and industrial pollution due to an oil monobuoy from which oil manipulation and general oil transport along the Patagonian coast registered several oil spills and chronic oil discharges (García-Borboroglu et al. 2008). Other marine systems impacted by oil spill showed an important decrease in marine bird populations (Irons et al. 2000), seals and macroalgae (e.g. Paine et al. (1996)), with examples of cascading effects throughout the food web (Peterson 2001).

3.2 Beagle Channel

A main anthropogenic stressor in the Beagle Channel is the introduction of invasive species (Table S2). Salmonidae were introduced to Tierra del Fuego in the 1930s. Especially Chinook salmon Oncorhynchus tshawytscha causes concern. The detection of Chinook salmon in Tierra del Fuego dates back to April 2006, and its population has been expanding since then (Nardi et al. 2019). Being a top predator Chinook salmon can compete with several native species in the Beagle Channel (Correa and Gross 2008), and prey over native species such as Notothenioids (Eleginops maclovinus, Patagonotothen tessellata, P. cornucola, P. sima, Paranotothenia magellanica, Harpagifer bispinis), the Atherinidae Odontesthes smitti and O. nigricans, the Fuegian sprat Sprattus fuegensis, and larvae of king crabs (Lithodes antarcticus and Paralomis granulosa) (Fernández et al. 2010). Ciancio et al. (2008) observed that Chinook salmon in the Southern Patagonian Shelf Ecosystem Area primarily feed on sprats and display trophic levels comparable to those of intermediate-sized fish and cephalopod predators species, showing significant dietary overlap with Magellanic penguins (Spheniscus magellanicus). Another potential competitor for Chinook salmon in the Beagle Channel is the Commerson's dolphin (Cephalorhynchus commersonii), which shares a similar diet (Riccialdelli et al. 2013).

In the Beagle Channel, other anthropogenic stressors include contaminants like metals, perfluorinated compounds, hydrocarbons, and microplastics found in animal tissue and sediments. Some studies reported varying heavy metal levels in sea mussel tissues and sediments, indicating bioavailability differences (Duarte et al. 2011). Other research found similar carbon and carbohydrate levels in Ushuaia Bay's surface sediments to those in hypertrophic ecosystems, along with hydrocarbons and heavy metals linked to port and industrial activities (Gil et al. 2011). Commendatore et al. (2012) identified three distinct hydrocarbon accumulation zones in the Bay. Llorca et al. (2012) found high levels of perfluorinated compounds in algae, fish, and guano. Ferreira et al. (2021) showed that black southern cod in Ushuaia Bay may be exposed to endocrine-disrupting compounds from urban and industrial pollution. Pérez et al. (2020) and Ojeda et al. (2021) found microplastics in M. edulis chilensis and Nacella magellanica, respectively. These studies link pollutants to Ushuaia (54°48 S 68°18 W) and its port and industrial activities. We expect the Beagle Channel area closest to the city to be most affected. Contaminants can spread through the food web, magnifying the risk to higher-level organisms. Fioramonti et al. (2022) studied mercury transfer in three southwest Atlantic Ocean food webs and found biodilution in the Beagle Channel and Atlantic coast of Tierra del Fuego webs. However, mercury concentrations rose with benthivory in these webs, and higher mercury was found in phytoplankton and Grimothea gregaria. Squat lobsters connect pelagic and benthic habitats, so any disruption to them could disrupt the food web (Rodriguez et al. 2022). Dodino et al. (2022) found the highest mercury levels in Magellanic penguin feathers from offshore colonies in Tierra del Fuego. Recently, Ushuaia's kelp forests have seen a decrease in biodiversity and changes in macroalgae composition due to urban pollution (Kaminsky et al. in prep.).

3.3 Burdwood Bank

The stressors reported for the ecosystem of the Marine Protected Areas Namuncurá within Burdwood Bank I and II are mostly anthropogenic; there is a lack of studies focusing on the environmental stressors that are known to be occurring at a regional scale (e.g. sea surface warming, Franco et al. (2020)) (Table S2). Several fisheries targeting demersal fishes operate in the vicinity and within the ecosystem of the Marine

Protected Areas (i.e. Marine National Reserve management category). The Patagonian fisheries on the toothfish Dissostichus eleginoides has gained prominence in recent years (Allega et al. 2020; Gorini et al. 2021). Although these are regulated by the Argentinean government, incidental catches do occur, where demersal fishes of the genera Coelorinchus and Macrourus, seabirds and benthic invertebrates (30+ taxa) are the most common bycatches (Gaitán and Marí 2016; Martínez et al. 2022). Noteworthy, among the invertebrates caught, 8 species are indicator taxa of vulnerable marine ecosystems (Gaitán and Marí 2016; Schejter and Albano 2021). Independent assessments of these bycatches suggest no significant impact on the communities (Gaitán and Marí 2016; Martínez et al. 2022). Besides bycatch, species of seabirds are being affected by the fishery due to discards, altering its diet; the most frequently encountered species are Black-browed albatross Thalassarche melanophris, Southern giant petrel Macronectes giganteus, Cape petrel Daption capense, Southern royal albatross Diomedea epomophora, Northern giant petrel M. halli, and White-chinned petrel Procellaria aequinoctialis (Tamini et al. 2023). Nevertheless, there is a lack of knowledge considering the species' role in the ecosystem and the potential joint effect of both target fishes and bycatch in a broader food web framework.

Anthropogenic contaminants such as microplastics and mercury are present in the water column of the Burdwood Bank ecosystem (Cossi et al. 2021; Fioramonti et al. 2022; Di Mauro et al. 2022). Microplastics are distributed all along the water column, from surface to deep waters (3-2450 m) (Di Mauro et al. 2022). More importantly, microplastics were found in soft tissues of benthic macroinvertebrates (sea stars Henricia obesa and Odontaster penicillatus) and benthopelagic fishes (Patagonotothen guntheri and P. ramsayi), which not only incorporated the contaminant from the environment through their filter-feeding system but could also get it indirectly from prey organisms already containing plastics in their tissues (Cossi et al. 2021). Notably, one of the contaminated species, the long tail southern cod Patagonotothen ramsayi, is part of the core group of species that drive the ecosystem through the suggested wasp-waist control (Riccialdelli et al. 2020). Mercury transfer and biomagnification are ongoing processes in the ecosystem, which are occurring at a greater pace than near coastal areas (Beagle Channel) (Fioramonti et al. 2022). It's important to note that the Fuegian sprat Sprattus fuegensis, a pelagic fish with a mid-trophic level in the food web, presented the highest levels of mercury (Fioramonti et al. 2022). Considering the wasp-waist control of the Fuegian sprat in the food web (Riccialdelli et al. 2020), a rapid and widespread contamination to the top predators is expected (Fioramonti et al. 2022).

In recent years, licenses for seismic studies and exploration of hydrocarbon resources have been granted all along the northwestern limit of the Marine Protected Areas (Secretaría de Gobierno de Energía Res. Nº 65/2018). Although effects from these types of surveys on marine mammals and seabirds are well-known for other regions of the world (Nowacek et al. 2015), there is no particular knowledge for this ecosystem. However, several documents warn of the potential negative effects this may have on the species inhabiting the Burdwood Bank area (Allega et al. 2019; de Haro et al. 2022).

Despite evidence of warming at surface, mid-water and bottom layers (100 m) in Burdwood Bank (Franco et al. 2020), specific studies on the oceanographic aspects of the system are lacking. In this sense, there is a big question mark about the environmental stressors impact on the species and trophic interactions in Burdwood Bank.

3.4 Scotia Sea

The Scotia Sea is a vast and heterogenous oceanic region, where especially the areas around South Georgia island represents an area of interest, here referred to as 'Northern Scotia Sea'. The majority of studies analyzing the stressors' effects come from this area.

The Scotia Sea has experienced one of the largest levels of warming within the polar regions (Whitehouse et al. 2008). Together with the Southern Annular Mode anomalies this has caused a long-term decrease in krill abundance; more pronounced in the northern than in the southern Scotia Sea (Murphy et al. 2007). Over the past 90 years, the krill also showed an increase in mean body length (Atkinson et al. 2019), which may also alter predator-prey interactions and allow reaching cooler feeding grounds near the seabed, with the potential to link krill to unexpected predators (Schmidt et al. 2011). Another consequence of the mentioned environmental stressors, is a change in krill distribution due to a southward contraction (Atkinson et al. 2019). It is noteworthy here, that the distributional shift has not affected all species inhabiting the Northern Scotia Sea, and most abundant calanoid copepods have maintained their distribution (Tarling et al. 2018). Considering the above, food web models of the Northern Scotia Sea have suggested shifts in the structure and functioning of the food web, from krill-based to non-krill-based, where myctophid fishes and squid are playing important roles (Saunders et al. 2019).

The principal anthropogenic stressor of the Scotia Sea is commercial fisheries. Krill fishery not only stresses the targeted species, but also the many predators that depend on it as a food source (Hilborn et al. 2017). Yet, data currently available from monitoring of krill and its predators remain insufficient, hence identifying the potential fishery impacts on the ecosystem is difficult (Trathan et al. 2021). Apart from krill fishery, two other commercial fisheries operate in the Scotia Sea, targeting Patagonian toothfish species Dissostichus eleginoides and D. mawsoni. The D. eleginoides stock is linked to the stock at South Georgia ('Northern Scotia Sea') (Collins et al. 2010), while the D. mawsoni stock is linked to the Antarctic continental shelf ('Southern Scotia Sea') (Soeffker et al. 2022). Despite the fact that the mentioned fisheries are certified by the Marine Stewardship Council standards, Trathan (2023) identified several concerns regarding aspects of fisheries itself, other species' population status (i.e. recovery of baleen whales), and environmental stressors (i.e. sea warming), which could have synergistic effects on the food web structure and functioning that are still unknown.

Mercury transfer and biomagnification are current processes occurring in the Scotia Sea, where the total concentration of contaminants increase with trophic level and are highest in notothenioid and myctophid fishes (e.g. Dissostichus eleginoides, Gymnoscopelus nicholsi), and seabirds (Seco et al. 2021). During years of low Antarctic krill abundance, predators must deal with both the stress of reduced prey availability and the concurrent rise in mercury exposure (Seco et al. 2021).

3.5 Potter Cove (Antarctica)

Regional warming in the last half century has been one of the main factors driving changes in Potter Cove (Western Antarctic Peninsula) (Chown et al. 2022). Sudden environmental changes have occurred, such as sea surface temperature increase, salinity decrease, suspended particulate matter loading and chlorophyll-a increase, all linked to climatic cycles (Southern Annular Mode and El Niño Southern Oscillation) (Schloss et al. 2012). Particularly, sea warming has produced drastic environmental and biological transformations (e.g. shifts in dominance of benthic community) in the Potter Cove ecosystem (Schloss et al. 2012; Quartino et al. 2013; Sahade et al. 2015), a system highly dependent on sea-ice dynamics (Table S2). In Potter Cove, total sea ice cover has decreased since 1991 (Schloss et al. 2012). Changes in the annual timing of landfast ice formation and breakup of the sea ice cover has multiple effects on species in the food web (Michel et al. 2019). Warmer winters and springs result in earlier sea-ice melt, causing an abrupt increase in the light available benthic primary producers (Deregibus et al. 2020). Sea ice also mediates physical disturbances to the benthos by influencing sedimentation and iceberg scouring. These factors affect the production of macroalgae, albeit in opposite ways (Deregibus et al. 2017), and microphytobenthos (Hoffmann et al. 2019). On the other hand, sea ice is an important habitat for diatoms and its associated consumers, including copepods and krill (Flores et al. 2012), and thus important for bentho-pelagic nutrient and carbon cycling during winter. Additionally, a decrease in winter sea ice cover produces an increase in physical perturbation on benthic shallow communities in coastal shallows due to ice scouring (Deregibus et al. 2017). The glacier surrounding Potter Cove has been receding at an increasing rate since 1950 (Rückamp et al. 2011), which has caused a massive discharge of sediment-laden meltwater (Meredith et al. 2018). Large quantities of suspended particles affect growth, survival and reproduction of benthic species. This had led to a major shift in the benthic community structure, from a filter feeders–ascidian domination to a mixed assemblage with scavengers and opportunistic species (Sahade et al. 2015), and the metabolic balance in benthos went from net autotrophy to heterotrophy (Braeckman et al. 2021). Additionally, massive stranding events of the tunicate Salpa thompsoni and the euphausiid Euphausia superba (krill) linked to the presence of glacial meltwater have been reported (Fuentes et al. 2016). Rising temperatures leading to ice and glacial melting has also substantial impacts on pelagic primary productivity, since it reduces water salinity, affecting water column stratification, light penetration and nutrient availability for photosynthesis (Schloss et al. 2012). In Potter Cove, changes in biomass of most phytoplankton species have been observed under heat wave conditions, resulting in a shift from a microplankton to a nanoplankton dominated community (Antoni et al. 2020; Latorre et al. 2023). This means that in areas strongly affected by glacier melt, the planktonic food web is dominated by the microbial loop (ciliates and heterotrophic dinoflagellates preys upon nanophytoplankton, which are sequentially available prey for small omnivorous copepods), instead of being predominantly herbivorous (Garcia et al. 2016, 2019). In addition, phytoplankton species under these warming conditions showed a decrease in metabolic rates and in the quality of the fatty acids composition (Latorre et al. 2023).

3.6 Weddell Sea (Antarctica)

In the Weddell Sea several stressors have already been triggered by global warming effects (Table S2), from which spatial and temporal reduction in sea ice is suggested to be driving changes in pelagic and benthic communities (Constable et al. 2014; Gutt et al. 2021). Sea ice extent has reached new record lows since the satellite era began in 1978. Sea warming has been substantial in recent years: in 2017 the mean temperature for February reached 1.45°C, the highest monthly mean ever recorded (0.56°C above the climatological mean) (Turner et al. 2020). In this context, it has been suggested that Antarctic krill Euphausia superba has already declined as a result of productivity changes caused by sea ice declines (Atkinson et al. 2004). Declining sea ice cover allows increased access to krill by predators (Kawaguchi et al. 2009), which further contributes to decreased krill abundances. This in turn can result in reduced carbon export due to decreased fecal pellets from krill (Pauli et al. 2021).

On the other hand, sea ice loss increases light availability, triggering primary production by phytoplankton in the short-term (Pineda-Metz et al. 2020). Furthermore, a warmer and more stable water column with a shallow upper mixed layer, is expected to enhance the dominance of cryptophytes over diatoms which may favor salp populations over krill populations; thereby reducing the magnitude of energy transfer to higher trophic levels and the seabed (Isla 2023).

Higher trophic level species are expected to respond differently to global warming in the Weddell Sea. In this regard, Notothenioid fishes (e.g. Pleuragramma antarcticum) face multiple stressors (sea warming, sea ice decline, ocean acidification) that threaten their survival. While some species exhibit physiological plasticity to compensate for increased oxygen demand, most notothenioid fishes are stenothermal and unable to adjust their metabolic functioning (Mintenbeck et al. 2012). It is anticipated that the thermal habitat preferred by the Antarctic toothfish Dissostichus mawsoni could undergo contraction in the coming three decades (Constable et al. 2014), further emphasizing the potential impact of global warming effects on these species. Marine mammals, Weddell and crabeater seals (Leptonychotes weddellii and Lobodon carcinophagus), exhibit varying levels of sensitivity. The latter exhibits a preference for breeding in close proximity to krill swarms, and thus is particularly susceptible to reductions in sea ice concentrations and sea surface temperatures. Rescued sea ice can significantly affect their post- and future breeding foraging success (Wege et al. 2021). In addition, the Antarctic petrel Thalassoica antarctica, which is one of the most abundant seabirds in the area, is a sea ice dependent forager and breeder (Orgeira et al. 2021); therefore the loss of this habitat will degrade its foraging success and reproductive output over time. The snow petrel Pagodroma nivea also relies heavily on sea ice for foraging and its colonies in the Weddell Sea may be affected. The emperor penguin Aptenodytes forsteri uses sea ice for breeding; any reductions could constrain its populations, as evidenced by recent observations in the Bellingshausen Sea region (Fretwell et al. 2023). The Arctic tern Sterna paradisaea spends the summer in the Weddell Sea exploiting krill swarms under receding ice edges, then declines in ice cover may reduce prey availability and quality of molting habitats. Continued warming is thus expected to gradually erode the abundance and distribution of these 'primary species' that dominate the avifauna of the Weddell Sea through loss of critical sea ice habitat (Orgeira et al. 2021). Variations in sea ice extent have implications for great whales, such as the Humpback whale Megaptera novaeangliae, since their primary prey resource is the Antarctic krill (Braithwaite et al. 2015). Decreased winter ice coverage results in reduced suitable habitat and lower krill abundance (Braithwaite et al. 2015), with flow-on effects for whale body condition observed historically in harvest data. With climate projections indicating ongoing sea ice losses, further threats to critical krill populations pose risks to the energy intake and reproductive success and long-term viability of humpback whale populations dependent on consistent Antarctic feeding (Pallin et al. 2023).

Iceberg scouring is a major factor in the high biodiversity of benthic communities in the Weddell Sea (Gutt and Starmans 2001). Even at 600 m depths, iceberg scouring has a strong effect on the benthic environment, disrupting the upper layers of the seabed and removing macrofauna. This patchy disturbance and distribution pattern occurs roughly every 200 square meters on the Antarctic continental shelf. Global warming is predicted to raise iceberg scouring frequency (Gutt 2001; Smale et al. 2008), disrupting the environment (Smale and Barnes 2008). Gutt et al. (2015) expects tipping points are significant due to these effects and lack of knowledge.

4. From species' stressors to food web effects

A major challenge in contemporary ecology lies in predicting the effects of stressors on complex multispecies systems, such as food webs. Network analysis has proved to be a powerful tool to tackle this issue, since it can capture the effects of individual and multiple stressors on communities and ecosystems (Montoya et al. 2009; O'Gorman et al. 2012; Bruder et al. 2019).

Environmental and anthropogenic stressor effects in the southwest and the Atlantic sector of the Southern Ocean have been mostly assessed individually and at the organism and/or population, i.e., at the node level (Table S2), with one exception: the effect of fisheries in the San Jorge Gulf food web (see section below for more details). To address the most plausible stressors effects on the selected food webs, given the current information, we built hypotheses for each study area. To this aim, we developed a theoretical framework considering the following: a) stressor(s), b) parameter(s) affected, c) node-level properties of the affected species, and d) network-level properties of the food web.

We considered that a stressor will affect one of the following species' characteristics or parameters: metabolism, biomass, distribution, and diet (Figure 2). 'Metabolism' refers to any change related to metabolic rate, such as reproduction, hatching, larval development, growth and mortality, and contamination due to pollutants (e.g. growth effect in filter-feeders due to sediment in water column in Potter Cove; endocrine disruption in fish due to urban pollutants in Beagle Channel). 'Biomass' indicates an effect at the population level, where the density/abundance is being impacted (e.g. abundance decreases in macrobenthos due to iceberg scouring in Weddell Sea). 'Distribution' entails a change at the population level in the geographic space occupied by a species, e.g. southward contraction of Antarctic krill due to sea warming of the Scotia Sea. 'Diet' includes alterations in the prey items of a species at the population level, e.g, due to prey switching, having a direct effect on the structure of the food web, e.g. new prey item (discards) for seabirds due to fishery activities in Burdwood Bank. Next, we considered node- and network-level properties relevant to the hypothesized stressor effects on the food webs, and which have been previously calculated for the studied food webs (Table 2). At the node-level, we included: a) degree, b) trophic position, c) omnivory index, and d) relative abundance (see Table S1 in Supporting Information for properties of stressed nodes). At the network-level, we considered: a) connectance, b) path length, c) mean trophic level, and d) omnivory (Table 1).

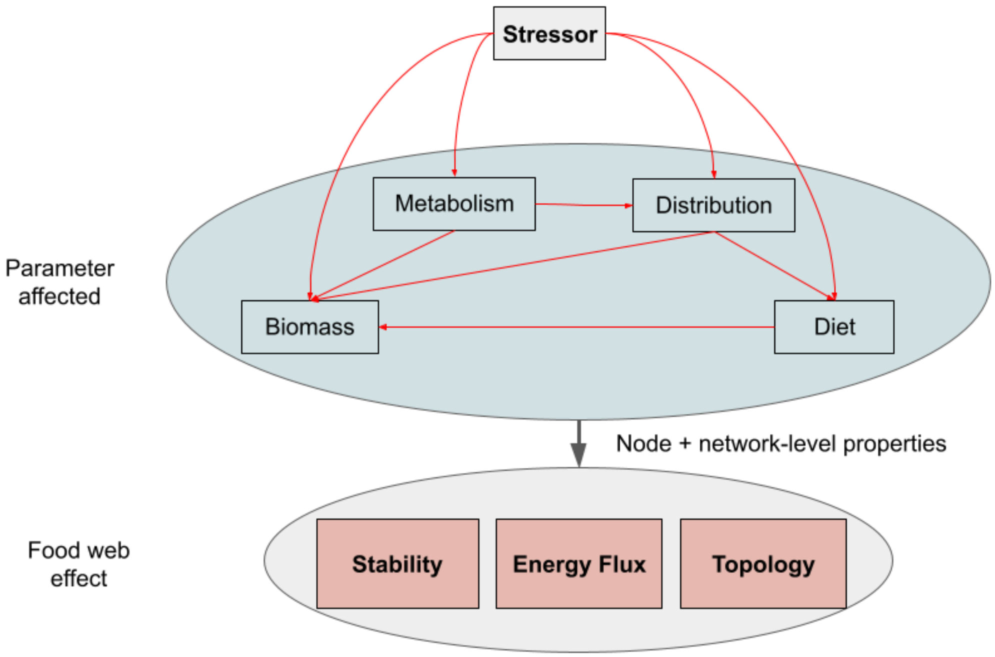

Figure 2: Conceptual diagram: from species' stressors to food web effects. See text for explanation.

Table 2. Node and network-level properties used to build hypotheses on the stressors' effects.

Property	**Definition**	**Relevance for stressor effects**	**Reference**
Node-level			
Degree	Number of feeding interactions in which the species participates as prey and/or predator.	Perturbations to high-degree species may have more significant effects on the food web robustness to perturbations than low-degree species.	Dunne et al. (2002b); Jordán et al. (2007)
Trophic position	Place in the food web relative to the basal resources that support the community. Classifies species in: basal, intermediate and top.	Perturbations on basal resources, intermediate species and top predators are expected to have large effects on the rest of their communities if ecosystem control is bottom-up, wasp-waist or top-down, respectively.	Williams and Martinez (2000); Thompson et al. (2007)
Omnivory	Consumer resource use across trophic levels.	High-omnivore species (generalists) are more flexible than low-omnivore species to diet changes.	Thompson et al. (2007)
Relative abundance	Species' density in proportion to the other species of the food web.	Perturbations on abundant (dominant) species are expected to have large effects on the stability and energy flux of the food and ecosystem, respectively.	Nilsson and McCann (2016)
Network-level			
Conectance	Proportion of actual interactions among possible ones.	Estimator of community sensitivity to stressors. High connectance gives resistance and resilience to the food web.	Dunne et al. (2002a)
Path length	Average distance, accounted by the number of interactions, between any pair of species.	Short distances enhance rapid and broad propagation of perturbations.	Albert and Barabási (2002)
Mean TL	Average of all species' trophic position contained in the food web.	Influences the magnitude and efficiency of trophic transfer. A higher mean food chain length reflects increased energy availability and productivity.	Duffy et al. (2007); Olivier et al. (2019)
Omnivory	Proportion of species that feed at different trophic levels.	It provides trophic flexibility to an ecosystem. Reduces probability of trophic cascades.	Kratina et al. (2012)

4.1 Main stressor effects in food webs in a southwest Atlantic - Antarctic gradient

The most common stressor reported along the southwest Atlantic - Antarctic gradient is global warming, except for Beagle Channel and Burdwood Bank, which are more influenced by the introduction of an alien species and fisheries, respectively (section 3, Table 3). The main characteristics of global warming in the region, and the most plausible drivers of change, are: sea warming, glacial retreat, elevated sediment input in the water column, and reduction of the sea ice extent. These drivers act in different ways and magnitudes in the studied locations along the latitudinal gradient. Despite emphasizing global warming in this section, this does not mean that no other stressors act or interact with global warming in the study systems, potentially buffering the overall effect on the food web (e.g. sea warming and fishery in San Jorge Gulf). Climate change has led to several well-documented impacts on marine species regarding distributional shifts induced by warming of marine currents (Wu et al. 2012; Poloczanska et al. 2013; Vergés et al. 2019). Furthermore, warmer temperatures increase species metabolic rates (Brown et al. 2004). Changes in metabolic rates can subsequently translate into shifts in species traits (body size, Vucic-Pestic et al. (2011); Klein et al. (2018)], biomass (Perry et al. 2020) and distribution (Kortsch et al. 2015). Alterations in the species body size and distributions have ripple effects on feeding interactions, for example, it can introduce new feeding interactions (Vergés et al. 2014; Pecuchet et al. 2020), modify existing ones, and shorten energy pathways (Bartley et al. 2019; O'Gorman et al. 2019), and reduce trophic efficiencies (Vucic-Pestic et al. 2011).

In recent years, several new fish (Galván et al. 2022) and macroinvertebrates species (Vinuesa 2005; López-Gappa 2022) were registered in Patagonia, mostly in San Jorge Gulf in relation to the southward range shift of warm-temperate species. This distributional change is driven by the tropicalization of temperate waters caused by sea warming (Vergés et al. 2014; Vergés et al. 2019). Because of its location in the ecotone between two biogeographic provinces, the Argentine (30°S - 44°S) and the Magellanic (43°S - 55°S) (Balech and Ehrlich 2008), the San Jorge Gulf is prone to changes in species composition. We hypothesize that sea warming will alter the food web structure topologically, by increasing the number of species and interactions. Newcomers are, in general, mid-trophic level species with generalist diets, hence an increase in food web connectance may be expected (Bartley et al. 2019). In another temperate ecosystem, an increase in the number of fish species, led to an increase in functional diversity and predation rate (Sgarlatta 2023); consequences that may also be expected in San Jorge Gulf. Given the short path length of the San Jorge Gulf food web, the disturbances from the listed stressors are expected to spread to many species of the food web (Table 3). However, it has to be acknowledged that the increase in functional diversity driven by the range expansion of warm-temperate species is contrary to the process of homogenization and loss of functional diversity in the area driven by trawl fisheries (Rincón-Díaz et al. 2021).

In the middle of the latitudinal gradient (considered in this study), the Scotia Sea has experienced one of the largest levels of sea warming of any polar region (Whitehouse et al. 2008; Atkinson et al. 2019). López-López et al. (2022) suggested that the southward distributional shift of generalist predators from the northern towards southern Scotia Sea increases network connectance of the latter, while decreasing its modularity. The lower modularity may increase the probability of perturbations spreading through the network (Stouffer and Bascompte 2011), which may be offset by increased connectance enhancing robustness to species loss (Dunne et al. 2002b). In the northern Scotia Sea around South Georgia Island, we suggest that the declining krill biomass driven by sea warming (Atkinson et al. 2019), ocean acidification and pollution synergy (Rowlands et al. 2021), will reduce the energy transfer to top predators like seabirds and marine mammals. However, this may be buffered since the dominant copepod species have maintained their distribution (Tarling et al. 2018), but most importantly, showed an abundance increase in recent decades likely due to reduced predation and competition for food (Ward et al. 2018). All this is significant for the structure of the food web given the central role of krill and copepods, characterized by high degree and mid-trophic position (Table S1). Overall, the food web's inherent resilience, marked by high connectance and omnivory, added to the potential compensation for the krill decrease due to a copepod increase, may buffer against structural changes (Table 3).

In Potter Cove, a fjord-like Antarctic ecosystem, the impacts of climate change affect many species within the food web. Potter Cove has recently experienced frequent events of marine heatwaves, i.e. prolonged periods of anomalously high sea surface temperatures (Oliver et al. 2018; Latorre et al. 2023). This has led to decreases in biomasses of different planktonic functional groups (Garcia et al. 2019; Latorre et al. 2023). Given the relatively low abundance of phytoplankton, zooplankton's low degree, and the modular configuration of the food web, we hypothesize that changes in these nodes, due to increased sea temperatures, will be retained in the basal pelagic compartment of the food web and will not expand to higher trophic levels. Benthic primary producers in Potter Cove are being influence by the decrease in winter sea ice cover (higher light availability), the increased levels of sediments in the water column due to glacial melt run-off (lower light penetration) and the newly free-ice areas available for colonization associated to glacier retreat. The overall local effect of climate change on macroalgae is a net increase in their production (Deregibus et al. 2023). It has been proposed that larger diversity in primary producers can support a more diverse food web with more specialized consumers (Iken et al. 2023). We expect to see differential effects of climate change on hard and soft bottom associated food webs (Cordone et al. 2020). Given the high relative abundance and the high degree of the macroalgae functional group (Table S1), we expect a longer hard bottom food web, wider consumer trophic niches, and that it will become more stable as sea ice cover decreases and the glacier retreats due to global warming. In soft bottom areas of the Cove, multiple food web nodes are being affected by ongoing warming effects: decrease in net primary production of benthic microalgae (Hoffmann et al. 2019), and changes in the benthic community biomass, distribution and composition (Sahade et al. 2015; Pasotti et al. 2015). Given that the Potter Cove food web's present low connectance and omnivory, we suggest fragility and potential trophic cascade effects (Marina et al. 2018) with pronounced changes in energy fluxes (Table 3).

The southernmost location of the latitudinal gradient is the Weddell Sea, where the main effect of global warming is the decrease in sea ice extent, with reported anomalies in the past summer seasons (Fretwell et al. 2023). Declining sea ice extent has reduced the abundance of krill (Atkinson et al. 2004; Flores et al. 2012), and produced an increase in phytoplankton productivity (Pinkerton et al. 2021; Isla 2023), altering the plankton community structure, and benefiting cryptophytes over diatoms (Lin et al. 2021). Moreover, habitat loss from sea ice decline will reduce the foraging success and breeding sites of seabirds (e.g., snow petrel Pagodroma nivea and emperor penguin Aptenodytes forsteri), decreasing their biomassess and modifying their distributions. The projected rise in iceberg scouring is expected to significantly alter the biomass and community structure of macrobenthos, which in turn will impact mid-trophic level predators such as demersal fish (Gutt 2001; Mintenbeck et al. 2012). While we do not anticipate large-scale topological changes in the food web, local extinctions could lead to such changes, particularly affecting benthic species (Gutt and Piepenburg 2003). Given that the impacted species—whether individually like krill, or collectively like macrobenthos—present a mid-trophic position, high biomass and high degree (Table S1), we hypothesize that significant shifts in energy fluxes will occur (Table 3). Additionally, the food web's low proportion of omnivores suggests reduced system resilience (Table 1), increasing the likelihood of regime changes (Gutt et al. 2015).

The two ecosystems in the subantarctic region, the Beagle Channel and Burdwood Bank, are more affected by other anthropogenic stressors than warming. Although these areas are being impacted by sea warming, potentially affecting vertebrate and invertebrate species (Franco et al. 2020), to date no studies exist for Beagle Channel and Burdwood Bank ecosystems. In the Beagle Channel, the introduction of chinook salmon, a non-native species, poses a significant risk to the existing food web (Fernández et al. 2010). We hypothesize that chinook salmon's predation on Fuegian sprat and black southern cod will disrupt the established patterns of interaction within the food web. Both of these prey species are crucial for food web dynamics due to their mid-trophic positions and relatively high abundance (Table S1). Moreover, we expect that changes in the black southern cod population will have a more significant impact on the food web than changes in the Fuegian sprat population, as the black southern cod has a higher degree (Table S1). Overall, these disruptions could have far-reaching effects on the ecosystem. This is particularly concerning given the short path length of the food web, which means that changes can quickly propagate through the system, affecting many species and potentially destabilizing the entire network. This phenomenon is further heightened by the ecosystem's inherent vulnerability to changes at mid-trophic levels, often referred to as wasp-waist control (Table 3). In the Burdwood Bank region, fishing activities may be the main stressor causing shifts in the food web (Table S2). We hypothesize that a combination of factors will destabilize the already fragile ecosystem, characterized by low connectance and low omnivory (Table 1). These factors include a decline in the biomass of the Patagonian toothfish -a key, highly-connected species (Table S1)- as well as smaller changes in the biomass of four mid-level fish species, five top-level seabird species, and over 30 types of benthic macroinvertebrates due to bycatch (Gaitán and Marí 2016; Martínez et al. 2022; Tamini et al. 2023). Additionally, alterations in the diets of six seabird species, caused by discarded catch (Tamini et al. 2023), are expected to disrupt the energy flow and further reduce the stability of the food web (Table 3).

Table 3. Summary of food web (FW) effects according to the main stressors reported for each study area. *Industrial trawl fishery

ceased in 2015 remaining artisanal trawling activity.

Study area	Stressor	Food web effects
San Jorge Gulf		
	Fishery*	↑ FW connectance ↓ FW stability ↓ functional diversity
	Sea warming	Shifts in FW topology ↑ FW connectance ↑ functional diversity
Beagle Channel		
	Alien species	Shifts in FW topology ↑ spread of perturbations
Burdwood Bank		
	Fishery	Shifts in main energy fluxes ↓ FW stability
Scotia Sea		
	Sea warming	↑ FW connectance ↓ FW modularity ↓ energy transfer to high TLs ↑ spread of perturbation
Potter Cove (Antarctica)		
	Sea warming	↓ perturbation spreading
	Sea ice decline + glacial retreat	Differential impacts, by substrate: hard (HS) or soft (SS) ↑ FW chain length & ↑ trophic niches (HS) ↑ FW fragility & trophic cascades (SS)
Weddell Sea (Antarctica)		
	Sea ice decline + iceberg scouring	Shifts in main energy fluxes ↑ likelihood of regime shifts ↓ resilience

5. Gaps and future perspectives

In the selected study areas along the southwest Atlantic to Antarctic latitudinal gradient, several stressors may directly affect consumers' diets triggered by modified environmental conditions (sea warming, reduced sea ice extent) and new species (due to species' distributional shifts and introductions). Moreover, the population trends (biomasses and abundances) of important species are also changing (Funes 2020; Hindell et al. 2020; Woods et al. 2023) driving shifts in their roles as either predators or prey (e.g. Belleggia et al. (2017), Pasti et al. (2021)). These diet and biomass shifts should be investigated in order to generate reliable predictions of food web responses to multiple stressors in the southwest Atlantic - Antarctic region. One could argue that both shifts might increase the complexity of food webs in the short term by adding generalist predators or new prey (e.g., Cordone et al. (2023)) or by enabling discard consumption (e.g. Funes et al. (2022)). However, in the long term, both stressors may lead to the biological extinction of certain prey and competitors (e.g. Anton et al. (2019)) or a significant reduction in target and incidental catch species (e.g. Dulvy et al. (2014)), thereby promoting food web simplification.

Since this review deals with qualitative data of prey-predator interactions and stressor effects influencing them, adding quantitative data to the food webs (i.e. interaction strength) and to the stressors (i.e. magnitude) would lead to a better comprehension of how a given stressor acts on specific species which might translate into food web effects. In this context, it would be useful to develop quantitative food web models where the strength of interactions reflect energy fluxes among species (Nilsson and McCann 2016; Kortsch et al. 2021). Emerging methods such as bioenergetic food web modeling have been proposed in this regard and present promising ways to estimate shifts in species interactions within food webs as a response to stressors (Gellner et al. 2023; Gauzens et al. n.d.). Shifts that can lead to changes in overall ecosystem functioning and stability.

Regarding knowledge and data gaps on species and their stressors, especially the Beagle Channel and Burdwood Bank are poorly sampled study regions. Almost no information exists on the impact of global warming effects (sea warming, glacial retreat, ocean acidification) on communities in these ecosystems, though warming of mid-water and bottom layers have been shown at a regional scale (Franco et al. 2020). Yet in Beagle Channel recent experimental studies have tested the tolerance of fishes to scenarios of sea warming and/or acidification suggesting potential metabolic impacts on species (Lattuca et al. 2018; Lattuca et al. 2023).

Analyzing the impact of multiple stressors through observational studies is challenging (Gutt et al. 2021). This complexity arises partly because of potential for antagonistic effects, where impacts cancel each other out, or synergistic effects, where the combined impact is greater than the sum of individual effects (Boyd et al. 2015; Côté et al. 2016). Moreover, these interactive effects are complicated to handle in the framework of complex food webs. The number of pathways through which a species may affect or be affected by other species, and through which stressors may permeate communities, increases exponentially with the number of species and interactions in a network (Menge 1995). To tackle this complexity, Beauchesne et al. (2021) developed a theory-grounded approach using motifs (i.e. groups of species that, when put together, construct whole food webs) to simplify food webs; a methodology that could be applied to our food web study cases.

Conclusions

We have reviewed the main environmental and anthropogenic stressors acting in six different areas along a large-scale latitudinal gradient, from temperate Atlantic to cold Antarctic ecosystems. Using a theoretical framework that combines species and food web level data, we suggest how warming effects may impact food web structure and functioning. These qualitative predictions are intended to serve as the basis for future studies in marine ecosystems of the Southern Hemisphere that aim at quantifying the magnitude of these stressors and how they are affecting quantitative food web properties, such as energy fluxes and stability. There is an urgent need to assess these changes using a holistic and quantitative framework where the magnitude of stressors and species interactions are taken into account.

Acknowledgements

This review is a product of the project "¿Cuáles son los efectos de los cambios ambientales antropogénicos en las interacciones tróficas de las comunidades de los ecosistemas marinos en el gradiente latitudinal Atlántico Sudoccidental - Antártida?", funded by Consejo Nacional de Investigaciones Científicas (CONICET, code PIP 2022-2024 #0907).

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