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Review

The response of trophic interaction networks to multiple stressors along a large-scale latitudinal range in the Southern Hemisphere

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Abstract

Ecological networks offer valuable insights into community structure, key species identification, and ecosystem management. Understanding how these networks respond to global change stressors is of increasing interest, especially along geographical gradients. This review summarizes potential stressor responses in marine food webs from the Southwest Atlantic to the Antarctic (45–78°S), encompassing areas such as San Jorge Gulf, Beagle Channel, Burdwood Bank, Scotia Sea, Potter Cove, and the Weddell Sea in Antarctica. The objectives are (1) to describe the structure of marine food webs along this latitudinal axis using a network approach; (2) to identify predominant global change-related stressors affecting each ecosystem; and (3) to summarize observed food web changes and hypothesize on stressor impacts. The effects of stressors were primarily reviewed at the species level. Alternative hypotheses for each study area were formulated considering (a) main stressors; (b) impacted parameters; (c) node-level species properties; and (d) network-level food web properties. Global warming emerges as the most common stressor among the studied areas across the latitudinal gradient, except in the Beagle Channel and Burdwood Bank, where alien species introduction and fisheries are more influential. We offer a series of alternative hypotheses on how warming may affect the food webs. This review emphasizes the benefits of using a network approach to understand and predict stressor effects in Southern Hemisphere marine ecosystems. This approach provides a holistic understanding of ecosystems, which enhances our ability to identify key species and their interactions, offering insights for ecosystem management and conservation in the face of global change stressors.

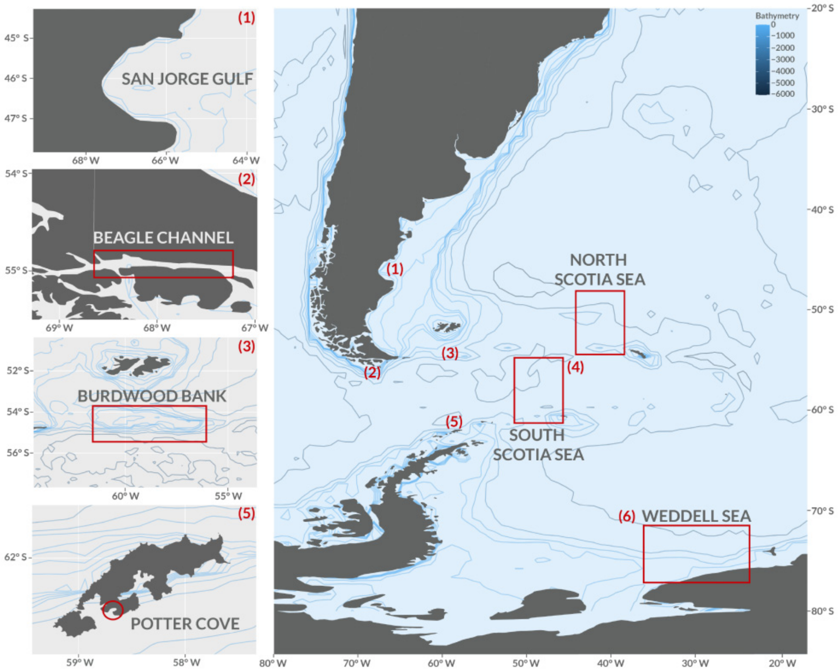
Key words: stressors, global warming, food webs, latitudinal gradient, Southern Hemisphere

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. 2020), 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 stressor responses of marine food webs for areas located along a Southwest Atlantic to Antarctic gradient (45 - 78°S, Fig. 1). We considered proven and expected changes in food webs driven by global change-related stressors in selected areas along this large-scale latitudinal range. 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 global change-related stressors for each marine ecosystem containing the food webs; and (3) review proven food web changes and

Fig. 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.



elaborate on a series of alternative hypotheses on how the identified stressors might affect food web features (energy flow, stability, and topology), combining information on node- and network-level properties. To identify the main stressors, we performed an exploratory and configurative review (Haddaway et al. 2015), where we considered more than 200 peer-reviewed articles retrieved mainly from Google Scholar using keywords combining location ("San Jorge Gulf", "Beagle Channel", "Burdwood Bank", "Scotia Sea", "Weddell Sea", "Potter Cove") and stressors ("acidification", "alien species", "climate change", "contamination", "fishery", "glacier retreat", "global warming", "ice scouring", "invasive species", "marine contaminant", "microplastics", "mercury", "pollution", "sea ice", "sea warming", "urban waste"). Additionally, we specifically searched for publications by authors we know may have conducted related studies in the area including grey literature. We performed this type of review because our objective was to formulate evidenced-based hypotheses rather than providing an exhaustive list of species-level stressors for each ecosystem. 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. Assessment of the food web structure and stressors in the Southwest Atlantic–Antarctic region

The Southwest and the Atlantic sectors 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 (45°S) in the Patagonian shelf to the Weddell Sea (78°S) in the Southern Ocean and covers a well-connected oceanic area (Matano et al. 2010; Guihou et al. 2020).

Throughout this region, many studies address the ecology of predator–prey relationships but most of these studies are restricted to a few interacting species or certain components of the food web such as fish, crustaceans, and benthos (e.g., Vinuesa and Varisco 2007; Padovani et al. 2012; Pasotti et al. 2015; Riccialdelli et al. 2020; Saunders et al. 2019; Pasti et al. 2021; Cordone et al. 2022). Only few studies consider the complexity of trophic interactions within highly resolved food webs containing hundreds of species, ranging from phytoplankton, zooplankton, benthos, fish, and seabirds to whales (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. 2024*b*). 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).

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). Here, we consider a stressor as a global change variable if it causes a quantifiable change, irrespective of its direction (increase or decrease), in a biological response (Orr et al. 2020). This aligns with the framework established during the early years of the International Geosphere–Biosphere Programme for classifying

Table 1. Complexity and structure properties of the marine food webs considered in the present review.

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. (2024*b*)
Potter Cove	110	649	0.05	2.33	2.22	0.46	Marina et al. (2018); Rodriguez et al. (2022)
N Scotia Sea	218	10 008	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	16 041	0.07	2.19	2.62	0.51	Jacob et al. (2011)

Note: Refer to Table S2 for definition of properties. mean TL: mean trophic level. Food webs are ordered by increasing latitude.

driving forces. These driving forces are grouped into those that modify the composition of the Earth's fluid envelopes (e.g., sea warming and acidification), and those that originate as local processes but attain global importance due to their widespread impact (e.g., species invasion and fisheries) (Vitousek 1992; Sage 2020). 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 this review, we included six large 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: (1) San Jorge Gulf (∼45–47°S, 65–68°W) (Funes et al. 2022), (2) Beagle Channel (∼54°S, 68°W) (Rodriguez et al. 2022), (3) Burdwood Bank (∼54°S, 59°W) (Marina et al. 2024*b*), (4) Scotia Sea (∼48–58°S, 50°W) (López-López et al. 2022), (5) Potter Cove (62°S, 58°W, Antarctica) (Marina et al. 2018), and (6) Weddell Sea (74–78°S, 30°W, Antarctica) (Jacob et al. 2011; Marina et al. 2024*a*) (Fig. 1). The geographic locations of these marine biomes span from temperate Atlantic waters to Antarctic and are exposed to global change stressors (e.g., sea warming, glacial retreat, fishery, and pollution) (Sage 2020), of which some are locally more important, e.g., fisheries in the San Jorge Gulf or glacial retreat in the Antarctic.

In the following subsections, we describe the complexity and structure of the mentioned marine food webs, identify the main stressors, the species (or trophic species), and the parameters affected. Table 1 summarizes the properties of the marine food webs (number of nodes, trophic interactions, connectance, path length, mean trophic level, and omnivory); Table 2 provides a list of the main stressors affecting species inhabiting each area, considering stressors' nature, species and parameter affected, and locality.

2.1. San Jorge Gulf

San Jorge Gulf is the northernmost study area considered in this review (Fig. 1), located from Cabo dos Bahias (44°55'S) to Cabo tres Puntas (47°06'S). It is a partially enclosed basin spanning approximately 34 000 km^2 and ∼100 m of maximum depths. The gulf's productivity supports large invertebrate and vertebrate fisheries (Góngora et al. 2012), as well as marine mammal and seabird populations (Yorio 2009). Two prominent frontal systems meet in the shallower northern and southern ends of the gulf (with depths ∼40 m), which are also the places of highest productivity (Glembocki et al. 2015).

The San Jorge Gulf food web contains 165 nodes (trophospecies) and 1015 trophic interactions with a connectance of 0.04. The percentage of top predators is 16%, 78% of the nodes are intermediate and 6% are basal; 60% of the consumers are omnivorous (Table 1). The most connected nodes are the Argentine red shrimp *Pleoticus muelleri*, the squat lobster *Gimothea gregaria*, squids (*Illex argentinus* as dominant species), and Amphipoda. Notably, these nodes are positioned at mid-trophic levels in the food web (3, 2.5, 3.6, and 2, respectively) (Funes et al. 2022).

The gulf is subject to several global change stressors (Table 2), especially fisheries (González-Zevallos and Yorio 2006, 2011; Galván et al. 2022). By discarding species, trawl fisheries add new trophic interactions to the food web, which results in decreasing trait variability and stability of the system (Rincón-Díaz et al. 2021; Funes et al. 2022). Moreover, this has changed the availability of resources to some predators. For example, the Argentine hake *Merluccius hubbsi*, one of the main bycatch species, has become a prey item of non-diving seabirds, like the kelp gull *Larus dominicanus* (González-Zevallos and Yorio 2006) and reef fish (Funes et al. 2019). Although juveniles of *M. hubbsi* is largely the main bycatch species, 29 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 has triggered a shift in the functional diversity of fish assemblages in the gulf, homogenizing their trophic function (Rincón-Díaz et al. 2021), for example, in the sites with the historical highest fishing activity, the fish assemblage experienced a relative increase in midwater fusiform species and lost variability in their depth range (Rincón-Díaz et al. 2021). Other functional changes were a decrease in the maximum sizes of individual fish, together with a drop in elasmobranch biomass and an increase in crustacean biomass (Funes 2020). The significant increase in crustacean biomass was mainly due to the increase in the Argentine red shrimp and the squat lobster (Funes 2020). These species have become the most important prey for the most abundant fish in the area, the Argentine hake and the narrownose smooth-hound

Table 2. Environmental and anthropogenic stressors reported for the study areas: San Jorge Gulf, Beagle Channel, Burdwood Bank, Scotia Sea (North and South), Potter Cove, and Weddell Sea. Stressor categories: sea warming; glacial retreat; sediment in the water column; iceberg scouring; sea ice extent; ocean acidification; ocean acidification + plastics; microplastics; mercury; urban and industrial pollution; fishery; alien species.

Study area	Stressor	Species affected	Parameter affected	Locality	Reference
San Jorge Gulf					
	Sea warming	Fish assemblage and its prey	Distribution	In situ	Galván et al. (2022)
	Fishery	Demersal fish community	Biomass	In situ	Galván et al. (2022)
	Fishery	Macroinvertebrates, fish and seabirds	Diet	In situ	González-Zevallos and Yorio (2006); González-Zevallos and Yorio (2011); Yorio et al. (2017)
	Alien species	Fish assemblage and its prey	Distribution	In situ	Galván et al. (2022); Ciancio et al. (2010)
	Urban and industrial pollution	Seabirds and benthic assemblage	Biomass	Elsewhere	Moore and Dwyer (1974); Buskey et al. (2016)
Beagle Channel					
	Urban and industrial pollution	Macroalgae; *Mytilus edulis chilensis*, *Patagonotothen tessellata*	Metabolism	In situ	Giarratano and Amin (2010); Ferreira et al. (2021); Kaminsky et al. (2023)
	Mercury	Phytoplankton, zooplankton, *Grimothea gregaria*	Metabolism	In situ	Fioramonti et al. (2022)
	Microplastics	*Mytilus edulis chilensis*, *Nacella magellanica*	Metabolism	In situ	Pérez et al. (2020); Ojeda et al. (2021)
	Alien species: Chinook salmon *Oncorhynchus tshawytscha*	*Patagonotothen tessellata*, *Sprattus fuegensis*	Diet/biomass	In situ (the presence); Elsewhere (changes in prey biomass)	Fernández et al. (2010); Ciancio et al. (2008)
Burdwood Bank					
	Mercury	*Dissostichus eleginoides*, *Sprattus fuegensis*, *Patagonotothen ramsayi*, *Cottoperca trigloides* (fish), and squids	Metabolism	In situ	Fioramonti et al. (2022)
	Microplastics	*Henricia obesa* and *Odontaster penicillatus* (sea stars); *Patagonotothen guntheri* and *P. ramsayi* (fish)	Metabolism	In situ	Cossi et al. (2021); Pérez et al. (2021)
	Fishery	Target: *Dissostichus eleginoides*. Bycatch: *Macrourus* sp., *Coelorinchus* sp. (fish), *Daption capense*, *Thalassarche melanophris*, *Macronectes giganteus*, *T. chrysostoma*, *Diomedea epomophora* (seabirds), 30+ spp macrobenthos	Biomass	Elsewhere	Gaitán and Marí (2016); Martínez et al. (2022); Administración de Parques Nacionales (2022); Tamini et al. (2023)
	Fishery	*Thalassarche melanophris*, *Macronectes giganteus*, *Daption capense*, *Diomedea epomophora*, *Macronectes halli*, *Procellaria aequinoctialis* (seabirds)	Diet	Elsewhere	Tamini et al. (2023)
Scotia Sea, North and South					
	Mercury	*Krefftichthys anderssoni*, *Protomyctophum bolini*, *Electrona antarctica*, *Gymnoscopelus nicholsi*, *Gymnoscopelus braueri*, *Dissostichus eleginoides*	Metabolism	In situ	Seco et al. (2021)
	Ocean acidification + plastics	*Euphausia superba*, *Limacina retroversa* (Pteropoda)	Metabolism	In situ	Rowlands et al. (2021); Manno et al. (2022)

Table 2. (*concluded*).

Study area	Stressor	Species affected	Parameter affected	Locality	Reference
	Sea warming	*Euphausia superba*	Metabolism	In situ	Murphy et al. (2007); Perry et al. (2020)
	Sea warming	*Euphausia superba*	Distribution	In situ	Atkinson et al. (2019)
	Fishery	*Euphausia superba*	Biomass	In situ	Trathan et al. (2021)
Potter Cove (Antarctica)					
	Sediment in water column	Microphytobenthos, macroalgae, benthic filter feeders (ascidians), pelagic filter feeders (krill, salps)	Metabolism	In situ	Sahade et al. (2015); Deregibus et al. (2016); Fuentes et al. (2016); Hoffmann et al. (2019)
	Sea ice extent	Krill	Biomass	Elsewhere	Flores et al. (2012)
	Sea ice extent	Benthic community (macroalgae, invertebrates)	Metabolism	Elsewhere	Clark et al. (2013); Campana et al. (2018)
	Glacial retreat	Benthic community (macroalgae, invertebrates)	Biomass	In situ	Quartino et al. (2013); Lagger et al. (2017); Lagger et al. (2018)
	Iceberg scouring	Benthic community	Biomass	In situ	Deregibus et al. (2017); Deregibus et al. (2023)
	Sea warming	Phytoplankton	Metabolism, biomass	In situ	Antoni et al. (2020); Latorre et al. (2023)
	Sea warming	Zooplankton	Metabolism, biomass, diet	In situ	Garcia et al. (2016); Garcia et al. (2019)
	Sea warming	Fish	Metabolism	In situ; Elsewhere	Strobel et al. (2013); Souza et al. (2018); Saravia et al. (2021)
Weddell Sea (Antarctica)					
	Iceberg scouring	Macrobentos	Biomass	In situ	Isla (2023); Gutt et al. (2015); Smale et al. (2008); Gutt et al. (1996)
	Iceberg scouring	Hexactinellida sponges	Biomass	In situ	Gutt and Starmans (2001); Pineda-Metz et al. (2020); Gutt (2001); Gutt and Piepenburg (2003)
	Ocean acidification	Primary producers / krill / foraminifera / flagellates	Metabolism	Elsewhere	Deppeler et al. (2020); Isla (2023); Gutt et al. (2015); Moy et al. (2009)
	Ocean acidification	*Euphausia superba*, *Pleuragramma antarcticum*	Metabolism	In situ	Kawaguchi et al. (2010); Kawaguchi et al. (2013); Piñones and Fedorov (2016); Mintenbeck et al. (2012)
	Sea warming	Large (diatoms) and small (cryptophytes) phytoplankton, zooplankton (salps)	Metabolism	Elsewhere	Isla (2023); Gutt et al. (2015); Trebilco et al. (2020)
	Sea warming	*Euphausia superba*, Nototheniid fish, *Pleuragramma antarcticum*	Metabolism	In situ	Meyer et al. (2017); Hill et al. (2013); Mintenbeck et al. (2012); Constable et al. (2014); Mintenbeck et al. (2012)
	Sea ice extent	Phytoplankton, *Lobodon carcinophaga*, *Hydrurga leptonyx*, *Leptonychotes weddellii*, *Ommataphoca rossii*, *Mirounga leonina*, *Arctocephalus gazella*	Metabolism	In situ	Pineda-Metz et al. (2020); Wege et al. (2021); Siniff et al. (2008)
	Sea ice extent	*Euphausia superba*, *Pleuragramma antarcticum*, *Pagodroma nivea*, *Thalassoica antarctica*, *Pygoscelis adeliae*	Metabolism	In situ	Orgeira et al. (2021); Braithwaite et al. (2015); Hill et al. (2013); Mintenbeck et al. (2012)
	Sea ice extent	*Megaptera novaeangliae*	Metabolism	Elsewhere	Pallin et al. (2023)
	Sea ice extent	*Aptenodytes forsteri*	Metabolism	Elsewhere	Orgeira et al. (2021)

Note: The species affected were considered at the node level, whereas effects were considered at the organism and population levels. Categories of affected parameters and variables: metabolism; biomass; distribution; diet (see text for explanation). "Locality" indicates whether a stressor for a given species was reported for the study area ("In situ") or in another area ("Elsewhere").

Mustelus schmitti (Belleggia et al. 2017; Pasti et al. 2021). However, since commercial fisheries ceased their activities in the San Jorge Gulf in 2015 (Annex I, Resolution CFP No. 7/2018), the effects mentioned above from trawl fisheries on the structure and function of the ecosystem may have changed since then. Nowadays only small-scale trawling from artisanal fishery is practiced in the gulf. Sea warming is another important stressor in the San Jorge Gulf, because of the southward shifts of northern fish populations to the area (Galván et al. 2022). Signs of sea warming have been detected in the gulf and nearby regions. Anomalous bottom temperature increments of up to 2 °C have been observed in the gulf since 2000 (Isla and Cortizo 2024), and a positive trend in sea surface temperature of 0.3 °C/0.4 °C per decade over a 30-year series (Risaro et al. 2022); Saraceno et al. 2022). Additionally, a positive trend in sea surface temperature (∼0.5 °C increase in the last 20 years) has been reported for the Nuevo and San Jose Gulfs, both located close to and northward of the San Jorge Gulf (Williams and Nocera 2023). The region is especially prone to be affected by climate-driven shifts in species ranges because it is situated in the ecotone of two biogeographic provinces, the Argentine (30°S–44°S) and the Magellanic (43°S–55°S) (Balech and Ehrlich 2008). In addition to tropicalization from northern fish populations, alien species are also documented to affect demersal assemblages of fish and macroinvertebrates in the gulf (Galván et al. 2022). Finally, the gulf is exposed to urban and industrial pollution (Verga et al. 2020). In particular, there is 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 the oil spill have shown extraordinary mortality events for cetacean (Litz et al. 2014), sea turtles (Wallace et al. 2017), and important decrease in marine bird populations (Irons et al. 2000) sea otters (Garrott et al. 1993) and macroalgae (Southward and Southward 1978), with cascading effects throughout the food web (Peterson 2001).

2.2. Beagle Channel

Located at a more southern latitude (∼54°S, 68°W), the Beagle Channel (Fig. 1) is an interoceanic passage at the southernmost tip of South America, spanning 240 km in length and 5 km in width (∼1200 km^2), with a depth range of 0–140 m. 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) suggest that locally produced suspended particulate organic matter (mostly composed of 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.

The Beagle Channel food web includes 145 nodes and 1115 trophic interactions with a connectance of 0.05 (Table 1). This food web is hypothesized to have a wasp–waist structure (i.e., the structure and dynamics of the ecosystem are regulated primarily by mid-trophic level species), 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 *Patagonotothen tessellata*, frogmouth *Cottoperca trigloides*, and squat lobster *G. gregaria* (Riccialdelli et al. 2020). Moreover, the squat lobster has been identified as a species linking food web modules and connecting the entire food web (Rodriguez et al. 2022).

One of the main local stressors in the Beagle Channel is the introduction of invasive species (Table 2). Salmonidae were introduced to Tierra del Fuego in the 1930s. Especially, the Chinook salmon *Oncorhynchus tshawytscha* causes concern. The detection of this species 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, the Chinook salmon can compete for resources with several native predators in the Beagle Channel (Correa and Gross 2008) but also prey on them. This is the case for Notothenioids (*Eleginops maclovinus*, *Patagonotothen tessellata*, *Patagonotothen cornucola*, *Patagonotothen sima*, *Paranotothenia magellanica*, *Harpagifer bispinis*), the Atherinidae *Odontesthes smitti* and *Odontesthes nigricans*, the Fuegian sprat, and larvae of king crabs (*Lithodes antarcticus* and *Paralomis granulosa*) (Fernández et al. 2010). Ciancio et al. (2008) observed that Chinook salmon primarily feeds on sprats in the Southern Patagonian Shelf Ecosystem area and display trophic levels comparable to those of intermediate-sized fish and cephalopod predator species, showing significant dietary overlap with the Magellanic penguin *Spheniscus magellanicus*. Another potential competitor for Chinook salmon in the Beagle Channel, sharing a similar diet, is the native Commerson's dolphin *Cephalorhynchus commersonii* (Riccialdelli et al. 2013). In invaded ecosystems, predation emerges as the primary driver of significant damage, often leading to cascading effects impacting even primary producers (David et al. 2017). In the Beagle Channel, other stressors include contaminants like metals, perfluorinated compounds, hydrocarbons, and microplastics found in animal tissue (algae, mussel, fish, and guano) and sediments (Duarte et al. 2011; Llorca et al. 2012). Carbon and carbohydrate levels in Ushuaia Bay's (54°48'S, 68°18'W) surface sediments are similar to hypertrophic ecosystems (i.e., greater input of nutrients than an eutrophic situation), along with hydrocarbons and heavy metals linked to port and industrial activities (Gil et al. 2011; Commendatore et al. 2012). Ferreira et al. (2021) showed that the black southern cod in Ushuaia Bay may be exposed to endocrine-disrupting compounds from urban and industrial pollution. Moreover, Pérez et al. (2020) and Ojeda et al. (2021) found microplastics in the Chilean mussel *Mytilus chilensis* and the sea snail *Nacella magellanica*, respectively. These studies link pollutants to port and industrial activities of Ushuaia; we therefore expect the area of the Beagle Channel closest to the city to be the most affected by contaminants. Contaminants potentially spread through the food web, from lower to higher trophic level taxa. In the Beagle Channel and Atlantic coast of Tierra del Fuego food webs, mercury concentrations rose with benthivory, and higher mercury was found in phytoplankton and the squat lobster. This latter species connects 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 also seen changes in composition along with a decrease in biodiversity as a result of urban pollution (Kaminsky et al. 2023). It is important to note that sea warming might be a less significant stressor in the Beagle Channel compared to the other areas, as global warming is melting glaciers and the influx of cold freshwater is actually slightly cooling the seawater (Saraceno et al. 2022).

2.3. Burdwood Bank

The so-called Burdwood Bank ecosystem comprises Marine Protected Areas Namuncurá–Burdwood Bank I and II (~54°S, 59°W), 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) (Fig. 1). Physical features in the plateau are fairly stable, with salinity averaging 34 all year round and temperature ranging between 4 and 8 °C (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 km^2). 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 (48%), and the network displays a small-world pattern (Marina et al. 2024*b*) (Table 1). This network pattern implies a rapid spread of a perturbation (e.g., contaminant, population fluctuation, and local extinction) throughout the food web due to a short distance among species but, at the same time, a greater resistance caused by the confinement of perturbations mainly within subnetworks as a result of a high clustering coefficient (Bornatowski et al. 2017; Dormann et al. 2017).

The main stressors reported for the ecosystem of the Marine Protected Areas Namuncurá within Burdwood Bank I and II are related to human activities such as fisheries and contamination (Table 2). Several fisheries targeting demersal fish operate in the vicinity and within the Marine Protected Areas. The fishery of the Patagonian 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 bycatches do occur, where demersal fish 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, eight species are indicator taxa of vulnerable marine ecosystems (Gaitán and Marí 2016; Schejter and Albano 2021). However, independent assessments of these bycatches suggest no significant impact on the populations (Gaitán and Marí 2016; Martínez et al. 2022). Besides bycatches, seabirds are being affected by fisheries due to discards, altering their 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 *Macronectes halli*, and white-chinned petrel *Procellaria aequinoctialis* (Tamini et al. 2023). Nevertheless, there is a lack of knowledge considering their role in the ecosystem and the potential joint effect of both target fish and bycatch in a broader food web framework. Contaminants such as microplastics and mercury occur in the water column of the Burdwood Bank ecosystem (Cossi et al. 2021; Di Mauro et al. 2022; Fioramonti et al. 2022). Microplastics are distributed along the entire 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 fish (*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 is the longtail southern cod *P. ramsayi*. This species 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 occurring at a greater pace than near coastal areas such as the Beagle Channel (Fioramonti et al. 2022). The Fuegian sprat *S. fuegensis*, a pelagic fish with a mid-trophic level in the food web, has the highest levels of mercury recorded (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). Despite evidence of warming of surface, mid-water and bottom layers (100 m) in Burdwood Bank (Franco et al. 2020*a*), studies on the oceanographic aspects of the system are lacking. Warming impacts on the species and trophic interactions in Burdwood Bank are also unknown.

2.4. Scotia Sea

The Scotia Sea is a deep-sea basin (~48–58°S, 50°W), 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 × 106 km^2 and a depth range of 0–3000 m (Murphy et al. 2006) (Fig. 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, characterized by higher and more variable temperatures, and the Southern Scotia Sea, characterized by lower and more stable temperatures and influenced by seasonal sea ice (Raymond 2011).

Analysis of the Northern and Southern Scotia Sea food webs shows that the former is relatively more complex in terms of number of species and links than the latter: with more species richness (218 vs. 192) and interactions (10 008 vs. 7241) and a slightly higher connectance (0.21 vs. 0.20). Mean path length is shorter in the Northern Scotia Sea food web, whereas the Southern Scotia Sea network displays a greater proportion of omnivores and a lower mean trophic level (López-López et al. 2022) (Table 1).

The Scotia Sea is a vast and heterogenous oceanic region, where especially the zone around South Georgia island represent an area of interest, here referred to as ''Northern Scotia Sea''. The majority of studies analyzing the stressors' effects come from this area (e.g., Murphy et al. 2007; Whitehouse et al. 2008; Trathan 2023) (Table 2). The main stressor of the Scotia Sea is commercial fisheries. Krill fishery on *Euphausia superba* not only impacts 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 that 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 *D. eleginoides* and *Dissostichus 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). Recently, Trathan (2023) has identified several concerns regarding aspects of these fisheries, highlighting that it is crucial to recognize ongoing changes such as the recovery of baleen whales and climate change. These factors increase the uncertainty for fishery managers, necessitating direct consideration in the management of harvested and dependent species.

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 Antarctic krill *E. superba* also showed an increase in mean body length (Atkinson et al. 2019), likely altering predator–prey interactions. Moreover, it allows krill to reach colder feeding grounds near the seabed, with the potential to link krill to unexpected predators such as demersal fish (Schmidt et al. 2011). Because of warming, the krill distribution has shifted southward (Atkinson et al. 2019), changing the food web from a krill-based to a non-krill-based, where myctophid fish and squid are playing important roles as key species in a wasp–waist controlled system (Saunders et al. 2019). While the krill distribution has shifted southward, the most abundant calanoid copepods have maintained their distribution (Tarling et al. 2018). 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 fish (e.g. *D. 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).

2.5. Potter Cove (Antarctica)

In the Antarctic realm, Potter Cove is a ∼9 km^2 fjord with a depth range of 0–200 m located at 25 de Mayo/King George Island (62°S, 58°W) on the South Shetland Islands of the West Antarctic Peninsula (Fig. 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 Boraso 2008).

The Potter Cove food web includes 110 nodes and 649 interactions, and a connectance of 0.05 (Table 1). It presents an asymmetric degree distribution and a modular structure, i.e., groups of species interact more strongly with each other within modules than with species belonging to other modules (Rodriguez et al. 2022).

Regional warming in the West Antarctic Peninsula recorded in the last half-century (Chown et al. 2022) has been one of the main stressors driving changes in Potter Cove (Table 2), a system highly dependent on glacier and sea ice dynamics (Deregibus et al. 2017). This has caused drastic environmental and biological transformations such as shifts in dominance within the benthic community (Schloss et al. 2012; Quartino et al. 2013; Sahade et al. 2015). In Potter Cove, there has been a decreasing trend in total sea ice cover since 1991 (Schloss et al. 2012). Changes in the annual timing of landfast ice formation and the breakup of the sea ice cover has multiple effects on species (Michel et al. 2019). Warmer winters and springs result in earlier sea ice melt, causing an abrupt increase in the light available for 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 their associated consumers, including copepods and the Antarctic 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 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 Antarctic 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 (i.e., 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 rate and in the quality of the fatty acid composition (Latorre et al. 2023).

2.6. Weddell Sea (Antarctica)

Located between 74 and 78°S, the high Antarctic Weddell Sea shelf spans approximately 450 km from East to West (Jacob et al. 2011) (Fig. 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. The shelf area is characterized by a complex three-dimensional benthic habitat, substantial benthic biomasses, and an intermediate to high diversity (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 (16 041) among the marine food webs of the Southern Hemisphere (Table 1). Its connectance (0.07), mean trophic level (2.62), and omnivory (51%) are intermediate compared to the other food webs (Table 1). Recently, the interaction strengths of this food web were estimated, revealing the presence of numerous weak and few strong interactions (Marina et al. 2024*a*).

In the Weddell Sea, the main stressors are related to warming impacts (sea warming, sea ice extent, and iceberg scouring) (Table 2), where sea warming has been substantial since the early 1980s (Turner et al. 2020). For example, in 2017, the mean temperature for February reached 1.45 °C, the highest monthly mean ever recorded, i.e., 0.56 °C above the climatological mean (Turner et al. 2020). Warming has caused spatial and temporal reductions in sea ice, impacting both pelagic and benthic communities (Constable et al. 2014; Gutt et al. 2021). Since the start of satellite imaging in 1978, sea ice extent has reached new record lows. Some of the most pronounced impacts of decreasing sea ice are negative changes in primary productivity (Atkinson et al. 2004) and declines of the Antarctic krill. Moreover, reduced sea ice cover allows increased access to krill by its predators (Kawaguchi et al. 2009), which further contributes to its decline. Some outcomes of the krill decline are reduced energy intake by higher trophic levels such as humpback whales *Megaptera novaeangliae* Braithwaite et al. (2015), which rely heavily on krill for foraging, as well as reduced carbon export due to fewer fecal pellets (Pauli et al. 2021). Many higher trophic level species in the Weddell Sea are greatly impacted by sea ice reductions due to loss of habitat and food source availability, such as the Antarctic petrel *Thalassoica antarctica*—one of the most abundant seabirds in the Weddell Sea (Orgeira et al. 2021). Other impacted sea bird species are the emperor penguin *Aptenodytes forsteri*. Reductions in sea ice constrain its population 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. Thus, continued warming is expected to gradually erode the abundance and distribution of marine seabirds in the Weddell Sea (Orgeira et al. 2021). Many marine mammals depend on for breeding and foraging such as the Weddell and Crabeater seals (*Leptonychotes weddellii* and *Lobodon carcinophagus*) (Wege et al. 2021), and the Humpback whale. Reduced sea ice can significantly affect the breeding success of seals (Wege et al. 2021) and body condition of whales (Turner et al. 2020). Notothenioid fish, with *Pleuragramma antarcticum* being the most abundant species, confront numerous stressors such as sea warming, sea ice decline, and ocean acidification, posing significant threats to their survival. While certain species exhibit physiological plasticity to cope with increased oxygen demand, most notothenioid fish are stenothermal and incapable of adjusting their metabolic functioning (Mintenbeck et al. 2012). Projections suggest that the preferred thermal habitat of the Antarctic toothfish, *D. mawsoni*, an important fish species in the Weddell Sea ecosystem, may contract over the next three decades, underscoring the potential impact of global warming on these species (Constable et al. 2014). Iceberg scouring is a major factor in driving 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 increase iceberg scouring frequency (Gutt 2001; Smale et al. 2008), disrupting the environment (Smale and Barnes 2008) with the potential for tipping points (Gutt et al. 2015).

3. From species' stressors to food web effects: a qualitative approach

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).

Global change 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 2), 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 effects of the main stressors on the selected food webs, given the current information, we formulated a series of alternative 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, population biomass, distribution, and diet (Fig. 2). ''Metabolism'' refers to any change related to metabolic rate, such as reproduction, hatching, larval development, growth and mortality (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). ''Population 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).

3.1. Hypotheses on the 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 2, Table 2). The main characteristics of global warming in the region, and the most plausible drivers of change, are sea warming, glacial retreat, elevated sediment input to 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 or even amplifying 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, e.g., body size (Vucic-Pestic et al. 2011; Klein et al. 2018), population 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).

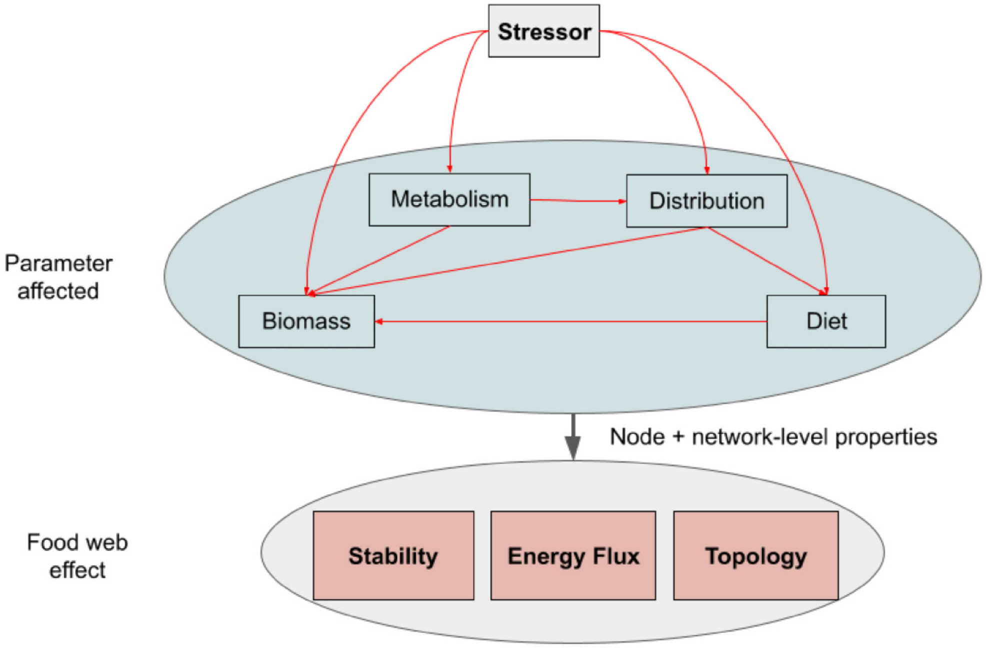
3.1.1. San Jorge Gulf

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, concerning 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, 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 increases 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).

3.1.2. Scotia Sea

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). 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

Fig. 2. Conceptual diagram: from species' stressors to food web effects. A stressor (e.g., global warming) will affect one of the following species' characteristics: metabolism, population biomass, distribution, and diet. "Metabolism" refers to any change related to metabolic rate, such as reproduction, hatching, larval development, growth and mortality, and contamination due to pollutants. "Population biomass" indicates an effect at the population level, where the density/abundance is being impacted. "Distribution" entails a change at the population level in the geographic space occupied by a species. "Diet" includes alterations in the prey items of a species at the population level. Next, we considered node- and network-level properties relevant to the hypothesized stressor effects on the food webs. At the node-level, we included (*a*) degree, (*b*) trophic position, (*c*) omnivory index, and (*d*) relative abundance. At the network-level, we considered: (*a*) connectance, (*b*) path length, (*c*) mean trophic level, and (*d*) omnivory. Finally, we elaborate a series of competing hypotheses on how the identified stressors might affect food web features (stability, energy flow, and topology), combining information on node- and network-level properties.



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 because the dominant copepod species have maintained their distribution (Tarling et al. 2018), but most importantly shown an abundance increase in recent decades likely due to reduced predation and competition for food (Ward et al. 2018). The potential compensation for the decrease in krill by increasing abundance of copepod may buffer against structural and functional changes in the food web (Table 3), since krill and copepod play similar (central) roles in the food web, characterized by a high degree and mid-trophic position.

3.1.3. Potter Cove (Antarctica)

In Potter Cove, a fjord-like Antarctic ecosystem, the repercussions of climate change extend across numerous species. Noteworthy, these effects are non-uniform within the food web, manifesting differently across its pelagic and benthic compartments. Potter Cove has recently experienced frequent events of marine heatwaves, i.e., prolonged periods of anomalously high sea surface temperature (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 and zooplankton low mean degree (Table S1), resulting in weak interaction strengths between these low trophic levels and higher ones (Rodriguez and Saravia 2024), added to the modular configuration of the food web (Rodriguez et al. 2022), we hypothesize that changes in these nodes due to warming will be retained at the lower trophic levels of the pelagic compartment and will not expand to higher trophic levels. Macroalgae, important benthic primary producers, are being influenced 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 local effect of climate change on macroalgae is a net increase in their production and macroalgal detritus (Braeckman et al. 2019; Deregibus et al. 2023; Iken et al. 2023). On the other hand, increased glacial runoff lead to a decrease in net primary production of benthic microalgae (Hoffmann et al. 2019); reduced secondary benthic production; changes on the benthic community composition; and an expansion of its distribution towards newly free-ice areas, specially filter and deposit feeders species (Pasotti et al. 2015; Sahade et al. 2015; Braeckman et al. 2024). In an increasing glacial melt disturbance scenario, it is expected a shift in the food sources of benthic species towards grazing on macroalgal

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

Study area	Stressor	Hypothesis on 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	↑ FW chain length and | ↑ Trophic niches |
Weddell Sea (Antarctica)		
	Sea ice decline + iceberg scouring	Shifts in main energy fluxes
		↑ Likelihood of regime shifts
		↓ Resilience

*Industrial trawl fishery ceased in 2015 remaining artisanal trawling activity.

and their detritus (Braeckman et al. 2024). It has been proposed that larger diversity in primary sources can support a more diverse food web with more specialized consumers (Iken et al. 2023). Given the high relative abundance and the high degree of the macroalgae functional group (Table S1), we expect a longer benthic food web (i.e., number of interactions connecting low and high trophic levels), wider consumer trophic niches, meaning an increase in omnivory, and a more stable benthic food web as sea ice cover decreases and glaciers retreat due to global warming. As a net effect of climate change on the overall Potter Cove food web, we expect a significant shift in energy fluxes, rather than drastic alterations in the topological structure, affecting the transfer of energy from lower to higher trophic levels.

3.1.4. Weddell Sea (Antarctica)

In the southernmost food web, the Weddell Sea, 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), decreasing their population biomasses 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 affecting mean food web attributes, local extinctions may produce changes in the interactions, especially impacting benthic species (Gutt and Piepenburg 2003). Given that the impacted species—whether individually like krill, or collectively like macrobenthos and notothenioids (e.g., *P. antarcticum*)—present a mid-trophic position, high population biomasses 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).

3.1.5. Beagle Channel and Burdwood Bank

The Beagle Channel and Burdwood Bank—the two ecosystems in the subantarctic region—are more affected by other stressors than warming. That said, there are impacts of warming in these ecosystems, especially affecting vertebrate and invertebrate species (Franco et al. 2020*a*), but generally studies addressing these impacts are lacking for the 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 2). 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 highly connected, key species (Table S1)—as well as smaller changes in the population biomass of four mid-trophic level fish species, five top trophic 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).

4. Gaps and future perspectives

In the selected study areas along the Southwest Atlantic to Antarctic latitudinal axis, several stressors may directly affect consumers' diets triggered by modified environmental conditions (sea warming and 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 population biomass shifts should be investigated 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 and decreases in robustness.

Since this review deals with qualitative data of predator–prey interactions and stressor effects influencing them, adding quantitative data to the food webs (e.g., interaction strength) and to the stressors (e.g., magnitude) would lead to a better understanding 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 reflects 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 and energy fluxes within food webs as a response to stressors (Gellner et al. 2023; Gauzens 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 (sea warming, glacial retreat, and ocean acidification) on communities in these ecosystems, although warming of mid-water and bottom layers has been shown at a regional scale (Franco et al. 2020*a*). Yet, in Beagle Channel, recent experimental studies have tested the tolerance of fish to scenarios of sea warming and (or) acidification, suggesting high vulnerability to projected climate-driven environmental conditions (Lattuca et al. 2018, 2023).

Analyzing the impact of multiple stressors through observational studies is challenging (Gutt et al. 2021). This complexity arises partly because of the 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.

In this review, we proposed a series of alternative hypotheses on how global stressors may affect food webs in the Southwest Atlantic to Southern Ocean. Despite being qualitative, this is a first important step in synthesizing food webs and stressor effects on species and food webs for this region. These qualitative assessments must be complemented with further investigations that test their validity. To achieve this, we suggest using a combination of observational data such as reported biomass changes and historic records of sea temperature for the region (e.g., Laptikhovsky et al. 2013;

Funes et al. 2019; Franco et al. 2020*b*; Winter and Arkhipkin 2023), and food web modeling methods such as stressor-response matrices (Bracewell et al.2019) and flux modeling (e.g., Gauzens et al. 2019; Beauchesne et al. 2021; Polazzo et al. 2022).

5. Conclusions

We reviewed global change 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. Apart from an important amount of uncertainty, 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.

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Data availability

All data used in this manuscript are publicly available and compiled on a Github repository https://github.com/EcoComplex/SouthFWReview and Zenodo https://zenodo.org/doi/10.5281/zenodo.11060734.

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The authors declare there are no competing interests.

Supplementary material

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