



FEATURE ARTICLE

Complex network of trophic interactions in Burdwood Bank, a sub-Antarctic oceanic marine protected area

Tomás I. Marina^{1,*}, Irene R. Schloss^{1,2,3}, Gustavo A. Lovrich¹, Claudia C. Boy¹, Daniel O. Bruno^{1,3}, Fabiana L. Capitano^{4,5}, Sergio M. Delpiani⁶, Juan Martín Díaz de Astarloa⁶, Cintia Frayse¹, Virginia A. García Alonso^{4,5}, Andrea Raya Rey^{1,3,7}, Laura Schejter⁸, Mariela L. Spinelli^{4,5}, Marcos Tatián^{9,10}, Diego Urteaga¹¹, Luciana Riccialdelli¹

¹Centro Austral de Investigaciones Científicas (CADIC-CONICET), V9410 Ushuaia, Argentina

²Instituto Antártico Argentino (IAA), 1650 San Martín, Argentina

³Instituto de Ciencias Polares, Ambiente y Recursos Naturales (ICPA), Universidad de Tierra del Fuego (UNTDF), V9410 Ushuaia, Argentina

⁴Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires (UBA), C1428EGA Ciudad Autónoma de Buenos Aires, Argentina

⁵Instituto de Biodiversidad y Biología Experimental y Aplicada (IBBEA), Universidad de Buenos Aires-CONICET, C1428EGA Ciudad Autónoma de Buenos Aires, Argentina

⁶Instituto de Investigaciones Marinas y Costeras (IIMYC), Universidad Nacional de Mar del Plata-CONICET, 7600 Mar del Plata, Argentina

⁷Wildlife Conservation Society (WCS), Representación Argentina, C1526AKC Ciudad Autónoma de Buenos Aires, Argentina

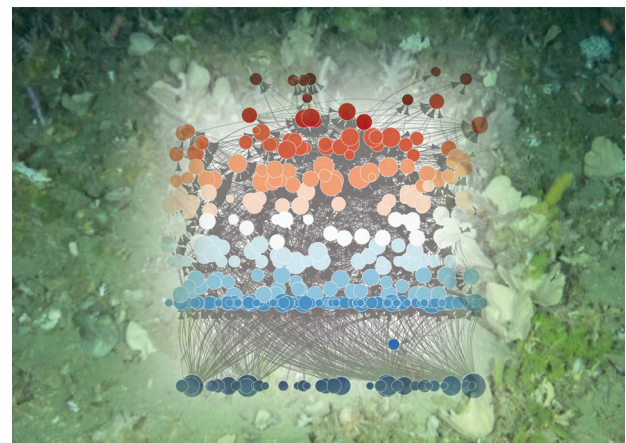
⁸Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), B7602HSA Mar del Plata, Argentina

⁹Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba (UNC), X5016GCA Córdoba, Argentina

¹⁰Instituto de Diversidad y Ecología Animal (IDEA-CONICET), 5000 Córdoba, Argentina

¹¹Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', C1405DJR Ciudad Autónoma de Buenos Aires, Argentina

ABSTRACT: The world's oceans designated under marine protection have increased recently. Most marine protected areas (MPAs) target vulnerable, key-stone, charismatic, and/or endemic species. In the sub-Antarctic, ocean protection is associated with oceanic islands, except for the MPAs Namuncurá – Burdwood Bank I and II (MPA N-BB; ~53–55° S, ~56–62° W), which are associated with a submarine plateau and a southern deep slope, respectively. We present the first analysis of the predator–prey network for the MPA N-BB, applying a topological network approach to characterise the complexity and structure of the food web and to identify the species' role. The MPA N-BB food web consists of 1788 interactions and 379 species, with a connectance of 0.01. Almost half of the consumers feed at more than one trophic level (0.48), and the network displays a small-world pattern (short path length, high clustering of compartments). This network pattern suggests that the ecosystem might be vulnerable to perturbations targeting highly connected species, although some properties might provide resilience and resistance, resulting in a rearranged structure that preserves its original functions. Several species arise as being important in trophic structure and functioning and response to perturbations. Generalist species, mainly fishes, play a crucial role in the benthic–pelagic coupling and should be considered as relevant energy transfer agents for the ecosystem. We



Network of predator–prey interactions in the MPA Namuncurá – Burdwood Bank showing the area's seafloor in the background.

Image: Luciana Riccialdelli

argue that the diversity of species, including both the benthic and pelagic habitats, is responsible for securing the connectivity within the food web to withstand perturbations, thereby contributing to the structure and stability of the ecosystem.

KEY WORDS: Food web · Complexity · Structure · Namuncurá · Burdwood Bank · Southwest Atlantic

*Corresponding author: tomasimarina@gmail.com

1. INTRODUCTION

In recent years, there has been an unparalleled rise in marine protected areas (MPAs) worldwide, driven by both the compelling evidence of their benefits and the pressing need for ocean protection (Roberts et al. 2017, Sala et al. 2018). In total, the world ocean designated under marine protection is approximately 29 600 000 km², distributed among 18 444 MPAs covering 8.16% of the ocean's surface (IUCN & UNEP-WCMC 2023). This approaches the 10% goal of the Convention of Biological Diversity (Secretariat of the Convention on Biological Diversity 2004). Although some progress has been made, it has become apparent that the level of protection has been inflated due to the inclusion of regions that have only been declared as protected, as well as areas where significant extractive operations are allowed (Sala et al. 2018).

In the sub-Antarctic region, the level of ocean protection is mainly associated with oceanic islands, such as the South Georgias and South Sandwich, Bouvet, Prince Edward, and Macquarie Islands (IUCN & UNEP-WCMC 2023). Interestingly, the case of the Argentine MPAs Namuncurá–Burdwood Bank I and II (MPA N-BB; ~53–55° S, ~56–62° W), which is the focus of this work, is unique since these MPAs are associated with a submarine plateau and its southern adjacent deep slope region, respectively (Falabella 2017, Schejter et al. 2020). In addition, such MPAs are part of a network of protected areas in the sub-Antarctic area (jointly with MPA Yaganes) that aims to protect this southern region in order to contribute to global ocean health.

Many MPAs focus on the presence of keystone, charismatic or particularly vulnerable species, large proportions of endemic species, and/or considerable biodiversity throughout taxonomic levels (Hogg et al. 2016). Indeed, the MPA N-BB was created to protect a potentially sensitive and biodiverse benthic habitat that was scarcely known (Schejter et al. 2016, Falabella 2017). The benthic community is characterised by high biomass of vulnerable and fragile species (mainly Porifera, Bryozoa, and Cnidaria) that, considered along with their environment, meet the characteristics of vulnerable marine ecosystems (Schejter & Albano 2021), defined here as sites that present densities of indicator taxa of >10 kg per 1200 m² (CCAMLR 2009). The benthic realm also provides habitat to several small-sized species (López-Gappa et al. 2018, Martin Siritto 2019, Schejter & Bremec 2019), and has an important role in the life history of fishes as a food source, refuge, and nursery area (García Alonso et al. 2018, Vazquez et al. 2018, Delpiani et

al. 2020, Troccoli et al. 2020, Covatti Ale et al. 2022, Fischer et al. 2022, Matusевич et al. 2023). The persistence of this particular community is linked to the interplay of local and regional oceanographic dynamics, encompassing the influence of the nutrient-rich Malvinas current (Piola & Gordon 1989, Guerrero et al. 1999), and occurrences of upwelling and mixing. Moreover, the influx of nutrients carried by the Malvinas current fosters a varied planktonic ecosystem (Guinder et al. 2020). Given the cooling trend of this current in a warming regional context (i.e. adjacent waters of the Patagonian shelf and Southwest Atlantic Ocean) (Franco et al. 2022), the MPA N-BB might play an essential role as a refuge maintaining not only biodiversity but also fisheries populations of the region (Franco et al. 2020b).

Maintaining ocean ecosystem services relies on a healthy ocean, and biological species play a key role in this process. It is essential to identify the main species involved in sustaining this health for effective management and conservation purposes. In this regard, Bergagna et al. (2020) identified the principal ecosystem services that are provided by species inhabiting the MPA N-BB, including nursery and feeding areas for commercially important fishes (e.g. Patagonian grenadier *Macruronus magellanicus*, Patagonian toothfish *Dissostichus eleginoides*), and water purification by filter feeders (e.g. sponges), among others. These species are part of a complex system in terms of biodiversity. There is robust knowledge on the complexity considering the richness of the benthic and plankton communities in the MPA N-BB ecosystem (Schejter et al. 2016, 2020, Guinder et al. 2020, Administración de Parques Nacionales 2022). Overall, 811 benthic and plankton species have been identified in the MPA N-BB ecosystem, where 349 were reported for the first time in the area in recent years (Administración de Parques Nacionales 2022). Recently, the structure of the southwestern South Atlantic Ocean has been hypothesised to be under a 'wasp-waist' control, meaning that the structure and dynamics of the ecosystem are regulated primarily by mid-trophic level species (e.g. fishes, crustaceans) (Padovani et al. 2012, Saporiti et al. 2015, Riccialdelli et al. 2020). In particular, the ecosystem of the MPA N-BB shows a more pronounced 'wasp-waist' structure, characterised by a shorter average food chain and a greater trophic overlap and redundancy in high trophic levels compared to other sub-Antarctic areas, such as the continental shelf off Tierra del Fuego (Riccialdelli et al. 2020).

The high abundance of a limited number of prey species at the intermediate trophic level of the food web leads to a specific feeding reliance among high-

trophic level predators. This phenomenon shortens the length of the food web, as the diet of top predators is expected to be dominated by the intermediate-trophic level species, thus lowering their trophic position. Simultaneously, it amplifies trophic overlap and redundancy between such predators. The Fuegian sprat *Sprattus fuegensis* and longtail southern cod *Patagonotothen ramsayi* have been considered the most plausible 'wasp-waist' species for the MPA N-BB (Ricciardelli et al. 2020), since they are species with high regional abundances (Madirolas et al. 2000, Arkhipkin & Laptikhovsky 2013), they occupy intermediate trophic levels (Ricciardelli et al. 2010, 2020), many predators feed on them (Ricciardelli et al. 2020), and their population dynamics appear to depend on the environment (e.g. climatic variations) (Diez et al. 2018). These recent efforts have increased our understanding of the biological communities and their complexity, but an understanding of the complexity and structure of species interactions is lacking. Such understanding will provide a more complete picture of the ecosystem, generate a baseline to comprehend climate change effects (Franco et al. 2020b), and serve as input to decision makers on conservation actions (Administración de Parques Nacionales 2022).

A better understanding of the ecosystem can be gained by analysing one of the most frequent relationships between species: the predator–prey interaction (Bascompte 2009). The assembly of these interactions in a particular region is referred to as a food web, representing the roadmap for matter and energy flow in an ecosystem. Here it is important to distinguish the inference power of topological food web models, which rely on presence/absence interactions among species, versus the so-called dynamic food web models that account for biomass of species, along with the magnitude and direction of energy flows among them (Brose & Dunne 2009). While the latter might better capture the ecosystem properties given that food webs are inherently dynamical systems, the former ones are the necessary first step, providing a map of biological and ecological-constrained possibilities. In recent years, topological network approaches have been successfully applied to study complex high-latitude marine ecosystems, improving our knowledge on structure, functioning, and response to environmental/anthropogenic changes (Kortsch et al. 2015, Cordone et al. 2018, Funes et al. 2022, Marina et al. 2024). Among the anthropogenic threats reported for the MPA N-BB ecosystem, it is worth mentioning contaminants like mercury and microplastics (Cossi et al. 2021, Di Mauro et al. 2022, Fioramonti et al. 2022), and fishing vessels are allowed to operate in the

western section of the MPA N-BB (i.e. marine national reserve category), altering the stocks of commercially important fish species (Martínez et al. 2021, Administración de Parques Nacionales 2022). Moreover, there is a potential hazard related to the effects of offshore activities (exploration and exploitation of gas and oil) to the west of the MPA N-BB (Administración de Parques Nacionales 2022).

In this work, we present the first detailed analysis of the network of predator–prey interactions, hereafter food web, for the MPA N-BB ecosystem. For this, we applied a topological network approach to a highly resolved food web. The objective was 2-fold: (1) to characterise the food web in terms of complexity and structure, and (2) to identify the species' role in the network. For the former, we considered all species and interactions in the food web, and calculated the number of species (S), number of interactions (links, L), link density (L/S), connectance (L/S^2), and proportion of omnivorous species, and we assessed the small-world pattern (see Section 2.3). For the latter objective, we considered the interactions and species related to a focal species and analysed the following properties: betweenness, closeness, trophic similarity, topological role, and trophic level.

2. METHODS

2.1. Study area

The MPAs Namuncurá–Burdwood Bank I and II, created by Argentine National Laws 26 875 in 2013 and 27 490 in 2017, comprise a shallow submarine plateau called Burdwood Bank (BB) and a deep slope to the south that reaches 4000 m in depth (N-BB I and N-BB II, respectively) (Tombesi et al. 2020, Administración de Parques Nacionales 2022) (Fig. 1). They are located 150 km east of Isla de los Estados and 200 km south of Malvinas/Falkland Islands. MPA N-BB I comprises nearly 28 900 km² circumscribed by the 200 m isobath, between ~54–55° S and ~56–62° W, with a slight slope extending nearly 370 km east–west. The physical characteristics of the deep waters of BB are relatively stable, with a consistent salinity of 34 psu throughout the year and a temperature range of 4–8°C (Guerrero et al. 1999, Acha et al. 2004, Piola & Falabella 2009). The BB is enclosed by high, steep slopes that plunge to depths of up to 4000 m, where powerful currents flow (Piola & Gordon 1989, Matano et al. 2019). N-BB II includes such a deep slope, protecting about 32 000 km² (~55–56° S, ~58–62° W). Intense upwelling and mixing take place in connec-

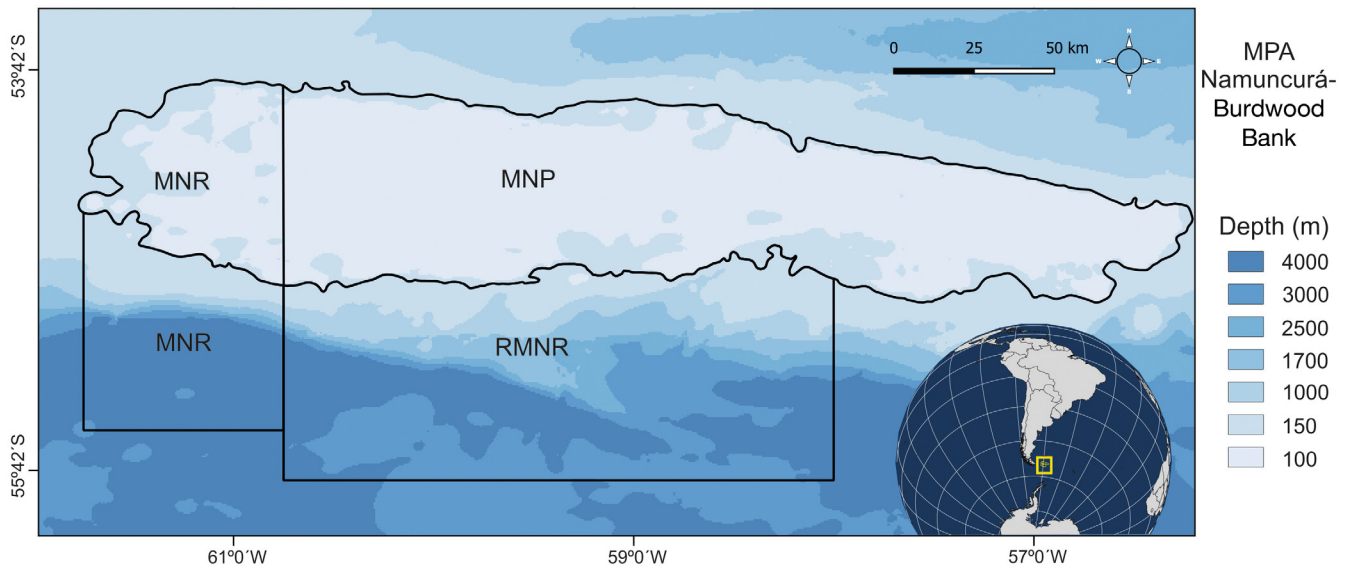


Fig. 1. Marine Protected Areas Namuncurá–Burdwood Bank I (Marine National Reserve [MNR] and Marine National Park [MNP], northern section) and II (MNR and Restricted Marine National Reserve [RMNR], southern section); abbreviations indicate categories according to the management plan

tion with the slope, bringing deep, nutrient-rich waters into the photic layer (Piola & Falabella 2009, Matano et al. 2019) and resulting in a relatively uniform water column both horizontally and vertically, both in space and time (Glorioso & Flather 1995, Guerrero et al. 1999, Matano et al. 2019).

Given the evidence collected during several research cruises about the oceanographic and ecological processes connecting MPAs N-BB I and II (references in Administración de Parques Nacionales 2022), a joint management plan was recently proposed (Administración de Parques Nacionales 2022). This is why the study area of the present work includes both MPAs.

2.2. Network construction

In order to build the network of predator–prey interactions, we started by searching trophic information for the species reported by Schejter et al. (2016) and Falabella (2017). Subsequently, we performed a literature search using the name of the species in question and the keywords 'diet', 'prey', 'predator', 'feeding ecology', and 'trophic ecology' in Google Scholar and Scopus. This process identified more than 170 references including peer-reviewed published articles, PhD theses, public databases, and reports belonging to 16 research cruises conducted in the MPAs N-BB I and II during 2014–2019 (Fig. S2 in Supplement 1 at www.int-res.com/articles/suppl/m736p001_supp1.pdf). We considered that one reference

showing evidence of a predator–prey relationship was enough to add that interaction to the network. Finally, we consulted with experts belonging to the working group of the study area (<https://www.pampazul.gob.ar/tag/banco-burdwood/>) that filtered the list of trophic interactions and discarded those unlikely to occur in the MPAs N-BB I and II. The diversity of the authors' expertise contributing to the present study was a key factor in enhancing the quality of the network, and inherently improved the network representation. A list of the references used to build the network is presented in Table S1 in Supplement 2 at www.int-res.com/articles/suppl/m736p001_supp2.xlsx.

Due to a lack of trophic data resolution for some species inhabiting the study area, we followed the concept of trophic species, defined here as taxa collapsed into a single node in the network. In most cases, we followed this concept when specific data on species, in the taxonomic sense, were not available. In some cases, we collapsed species when taxa shared the same set of predators and prey (trophic similarity, Martinez 1991), one of the aggregation methods that better preserve food web functional properties (Gauzens et al. 2013). In addition, for endemic species (e.g. bryozoan *Burdwoodipora paguricola*) and other species with no trophic studies so far, we inferred their feeding interactions applying a conservative approach that assumes that the set of prey and predators are at some point preserved in time. In those cases, we gathered information from upper taxo-

nomic levels (i.e. genus, family, order, class, phylum) as a good proxy variable (Morales-Castilla et al. 2015, Pomeranz et al. 2019). Details about this can be found in Table S2 in Supplement 2. Furthermore, we considered non-living food sources, such as detritus and necromass, as prey species in the food web context.

With the gathered trophic data, we constructed a matrix of pairwise interactions; a value of 1 or 0 was assigned to each element a_{ij} of the matrix depending on whether or not predator j preyed on prey i . We then transformed such a matrix into a directed graph with L trophic interactions between S nodes or species (Fig. S1 in Supplement 1). The direction of the interaction within the graph follows the flow of energy and matter in the network, from prey to predator.

2.3. Network analysis

We analysed the MPA N-BB network of trophic interactions, or food web, at 2 levels: (1) network, considering species and interactions of the whole network; and (2) species, considering direct and indirect interactions to a given species (Table 1).

The network-level analysis aims to characterise the food web in terms of complexity and structure. For this, we calculated several network properties commonly used to describe empirical food webs (Pascual & Dunne 2005): (1) number of species S ; (2) number of interactions or links L ; (3) link density L/S ; (4) connectance L/S^2 ; (5) omnivory; and (6) small-world pattern. In order to explore the small-world phenomenon, we analysed the characteristic path length (CPL) and the clustering coefficient (CC). The CPL is the average shortest path length between all pairs of nodes (Watts & Strogatz 1998, Marina et al. 2018b). Here, CPL was calculated as the average number of nodes in the shortest path $CPL_{\text{Min}}(i,j)$ between all pairs of nodes $S(i,j)$ in a network averaged over $S(S-1)$ nodes:

$$CPL = \frac{2}{S(S-1)} \sum_{i=1}^S \sum_{j=1}^S CPL_{\text{Min}}(i,j) \quad (1)$$

The CC quantifies the local interconnectedness of the network and is defined as the fraction of the number of existing links between neighbours of node i among all possible links between these neighbours. In this study, the CC was determined as the average of the individual clustering coefficients CC_i of all nodes in the network. Individual CC_i were determined as follows:

$$CC = \frac{2E_i}{K_i(K_i-1)} \quad (2)$$

where E_i is the effective number of interactions between K_i nearest-neighbour nodes of node i and the maximal possible number of such interactions (Newman 2003). To test whether the food web presented the small-world pattern, we compared the empirical values of CPL and CC with those resulting from 1000 randomly generated networks with the same size (S) and number of interactions (L) following Marina et al. (2018b). Random webs were created using the Erdős-Rényi model, where links are added to the complete set of nodes (S) and chosen uniformly randomly from the set of all possible links (Erdős & Rényi 1959). The preciseness of our method lies in the use of confidence intervals (99% CI) for the empirical-random comparison of the CPL and CC properties. If the empirical value is positioned within or to the left (= lower than) the CI 99% of the random CPL, and to the right (= higher than) the CI 99% of the CC, then the food web is considered to present the SW topology (Marina et al. 2018b).

We also estimated (7) the degree distributions for the food web, prey and predators, and each functional group (e.g. Amphipoda, Ascidiacea, Bivalvia, fish, marine mammals, seabirds, among others). The prey and predator distributions indicate the frequency of prey among predators, and vice versa; the degree distribution of functional groups shows the distribution of interactions within groups.

The species-level analysis aims to describe the species' role in the food web. For this, we considered the following properties: betweenness (Btw), closeness (Cl), trophic similarity (TS), topological role (TR), and trophic level (TL) (Table 1). Topological roles refer to the fact that food webs tend to naturally organise in non-random, modular patterns, where modules are defined as a group of species that interact more frequently among themselves than with species that are not members of the module (Guimerà & Nunes Amaral 2005). This implies that prey and predator groups exhibit greater interaction within their respective modules compared to interactions with species outside of those modules. Therefore, modularity assesses the intensity of interactions among these modules relative to interactions with species from different modules. Species can play different roles in this respect, according to the pattern of interactions within their own module and/or across modules. We computed the topological role for each species, classified as 'module hub', species with a relatively high number of interactions, but most within its own module; 'module specialist', species with relatively few interactions and most within its own module; 'module connector', species with relatively few interactions mainly between

Table 1. Network and species-level properties analysed, definitions, and relevant ecological implications related to food web complexity and structure

Name	Definition	Implications	Reference
Number of species	Number of trophic species in a food web	Represents species diversity and has implications for the persistence of the ecosystem	May (1973), Tilman (1996)
Number of interactions	Total number of trophic interactions in a food web	Represents the number of pathways along which matter and energy can flow	Dunne et al. (2002a)
Link density	Ratio of interactions to species in a food web	Represents the average number of interactions per species; informs about how connected species are in the food web	Dunne et al. (2002a)
Connectance	Proportion of potential links among species that are actually realized. Range = 0–1	Measures the probability of interactions and is a fundamental measure of network complexity. Connectance can be negatively or positively associated with food web robustness, depending on the network structure (random vs. non-random) or how the strengths of the interactions are distributed	Martinez (1992)
Degree distribution	Frequency of trophic species that have k or more interactions	Affects the vulnerability of complex food webs to random failures and intentional attacks (i.e. species extinctions)	Albert & Barabási (2002)
Trophic level (TL)	Indicator of the position a species occupies in a food web, reflecting the distance of each species to the source of matter and energy	Low values of mean TL indicate efficient energy transfer from basal assemblage to top predators. Contributes to food web stability	Lindeman (1942), Borrelli & Ginzburg (2014)
Omnivory	Species feeding on prey from more than one TL	Influences stability of the food web; intermediate levels of omnivory may stabilize it and may diffuse top-down effects, thus reducing the probability of trophic cascades	McCann & Hastings (1997)
Small-world pattern	Network with short path length (distance between nodes) and high clustering coefficient (formation of compartments) compared to random networks	Consequences of this structural pattern in food webs are of great importance in recognizing evolutionary paths and the vulnerability to perturbations	Watts & Strogatz (1998), Montoya & Solé (2002)
Betweenness	Number of shortest paths through a species	Species with high betweenness act as 'bridges'; if removed, would have rapidly spreading effects in the food web	Freeman (1978), Lai et al. (2012)
Closeness	Number of steps required to reach every other species from a given species	Removal of a species with high closeness will affect most other species in the food web	Freeman (1978), Lai et al. (2012)
Trophic similarity	Trophic overlap based on shared and unique resources (prey) and consumers (predators)	Measures one of the most important aspects of species' niches, the trophic niche, and functional aspects of biodiversity	Martinez (1992)
Topological role	Role of a species according to interactions within and across modules (subgroups of species)	Four roles are defined: module hub, module specialist, module connector, and network connector. Network connector and module connector roles maintain the connectivity of the food web	Guimerà & Nunes Amaral (2005)

modules; and 'network connector', species with high connectivity between and within modules (Guimerà & Nunes Amaral 2005, Rodríguez et al. 2022). Refer to Supplement 1 for the equations used to calculate the species-level properties.

We also studied the relationship between species TL and the other species properties by fitting analyses. Thus, we considered the TL as the dependent variable and the given property (i.e. betweenness, closeness, trophic similarity) as the independent variable. Fitting was done locally, meaning that for the fit at point x , the fit is made using points in a neighborhood of x , weighted by their distance from x (Cleveland et al. 1992). We also explored the topological role categories with the species TL. These species-level properties provide an appropriate description of the roles of species in empirical complex food webs (Cirtwill et al. 2018).

All network analyses and graphs were performed in R version 4.3.1 (R Development Core Team 2023), mainly using the packages 'igraph' (Csárdi et al. 2024) and 'multiweb' (Saravia 2022). Fitting between species TL and the other species properties were performed using the 'loess' function in the 'stats' package (R Development Core Team 2023). The

source code and data are available at Zenodo (<https://zenodo.org/doi/10.5281/zenodo.10854750>).

3. RESULTS

3.1. Network-level properties

In terms of complexity, the MPA N-BB food web consisted of 1788 predator–prey interactions and 379 species, of which 93% were defined at the species taxonomic level (Fig. 2; Table S2). The food web presented a link density (e.g. the average number of interactions per species) of 4.72, and a connectance of 0.01. Almost half of the consumers were omnivores (0.49), feeding on sources at different trophic levels. The food web displayed a small-world pattern, meaning that the path length was lower and the clustering coefficient higher than the random networks (Table 2).

The degree distribution of the food web showed an asymmetric frequency in the number of interactions, whereby most of the species had a relatively low number of interactions and few species concentrated most of them (Fig. 3A). The distribution of prey among predators showed that most consumers fed on a low number of prey, whereas few had multiple prey (Fig. 3B). The top 5 predators in number of prey were yellowfin notothen *Patagonotothen guntheri* (notothenioid fish, 50 prey), rock cod *P. ramsayi* (notothenioid fish, 49 prey), broad nose skate *Bathyraja brachyurops* (chondrichthyan, 33 prey), Patagonian toothfish *Dissostichus eleginoides* (notothenioid fish, 30 prey), and graytail skate *B. griseocauda* (Chondrichthyan, 28 prey). Following the same distribution pattern, few prey were targeted by multiple predators (Fig. 3C). The top 5 prey (or food sources) in number of predators were: detritus (non-living, 153 predators), the 3 categories of diatoms considered (benthic, centric, and pennate, 72.5 predators on average), and species of the genus *Euphausia* (zooplankton, 46 predators). Finally, aggregating the interactions by functional group (Fig. 3D), most interactions were concentrated in a few species. The most evident species were *Doryteuthis gahi* (Cephalopoda); *Grimothea* (= *Munida*) *gregaria* (Decapoda); *Patagonotothen ramsayi*, *P. guntheri*, and

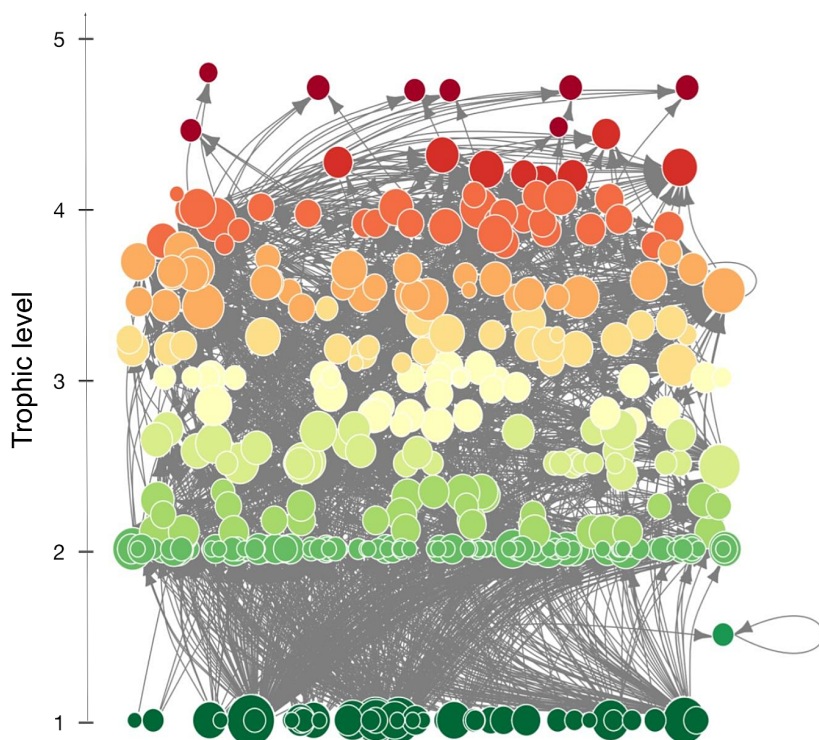


Fig. 2. Food web of the MPA Namuncurá–Burdwood Bank. Circles represent trophic species and arrows show trophic interactions. Circle diameter is relative to the number of interactions (see Table S3 in Supplement 2 for the exact number of interactions per species). Colour gradient indicates the trophic level

Table 2. Network-level properties of the marine protected area (MPA) Namuncurá–Burdwood Bank food web. Omn: fraction of omnivorous groups; CPL: characteristic path length; CC: clustering coefficient; SW: small-world pattern

Species	Number of interactions	Link density	Connectance	Omn	CPL	CC	SW
379	1788	4.72	0.01	0.49	2.99	0.08	True

Dissostichus eleginoides (benthopelagic fish); *Sprattus fuegensis* and *Micromesistius australis* (pelagic fish); and species of *Euphausia* and *Themisto gaudichaudii* (zooplankton). Overall, there is an evident asymmetry in the distribution of interactions among species at different levels (i.e. considering the entire food web, gathered by prey, predator, and functional group) in the MPA N-BB food web. A list of the distribution of interactions per species is presented in Table S3.

3.2. Species-level properties

We found different relationships between the species trophic level (TL) and the rest of the analysed species-level properties (Fig. 4). The most evident relationship was with trophic similarity, which described an exponential-like decline; i.e. the higher the species' TL, the lower the trophic similarity or the higher the uniqueness in terms of trophic role (Fig. 4A). Here, it is noteworthy to highlight those high TL species (TL >3.1) with low values of trophic similarity: *Bathyraxia macloviana* and *Squalus acanthias* (Chondrichthyans); *Diplopteraster clarki* and *Pteraster* sp. (echinoderms); *Daption capense* and *Eudyptes chrysolome* (seabirds); and Ziphiidae and *Lagenorhynchus cruciger* (marine mammals) (Table S3).

We also found a general negative relationship between TL and closeness, meaning that species with relatively low TLs are closer to any other species in the food web (Fig. 4B). Specifically, species in the TL range of 2–3 showed a hump-shaped distribution, while for TL >3, closeness decreased consistently. Detritus, species of genera *Calanus* and *Euphausia*, and Foraminifera, all with TL <3, registered the highest closeness values (Table S3).

Regarding betweenness, as expected, species of mid-TLs (3–4.2) showed the highest values, meaning that those species participated in the highest number of shortest paths between species (Fig. 4C). The following are the species with the highest values (descending order): *Patagonotothen ramsayi*, *Salilota australis*, *Dissostichus eleginoides* (fishes); *Doryteuthis gahi* (Cephalopoda); and *P. guntheri* (notothenioid fish) (Table S3). Here, we should note that species with highest TLs

(>4.2, top predators) show values equal to zero since no 'betweenness' role is possible for them.

Considering the topological role, 'module specialist' species were the most frequent and presented a wide TL range (1–4.78), followed by 'module hub' species (TL = 1–3.92); 'module connectors' were constrained to mid-level TLs (2–3.86); and 'network connectors' were represented by only 1 trophic species: detritus (Fig. 4D; see Fig. S3 in Supplement 1 for species' topological roles in a food web graph framework). Here, it is important to highlight the 2 latter topological roles because they are responsible for linking modules and maintaining the connectivity of the food web: 42 species (1 network connector + 41 module connectors) from 19 different functional groups with a TL range of 1–3.86. The 41 species with a module connector role represented these functional groups: Amphipoda, Bivalvia, Brachiopoda, Bryozoa, Hydrozoa (as 'Cnidaria_benthic'), Copepoda, Cumacea, Decapoda, Echinodermata, fish (benthopelagic and demersal Osteichthyes, and Chondrichthyes), Foraminifera, Polychaeta, Porifera, Pycnogonida (as 'Benthos_Misc'), and zooplankton (see Table S3 for the identity of the species). An exhaustive list of the species-level properties is presented in Table S3.

4. DISCUSSION

4.1. Food web of the MPA N-BB ecosystem

The food web of the MPA N-BB ecosystem analysed in this study is one of the most highly resolved networks of trophic interactions ever studied, not only for a high-latitude open-ocean ecosystem but also for any marine protected area worldwide to our knowledge. It is of paramount importance to consider the complexity of species interactions in order to gain insights into the structure and functioning of the ecosystem, since some aggregation criteria (i.e. body size) might mask food web properties and produce type II errors (false negatives, e.g. when an effect is not significant before aggregation but significant after considering a particular food web property) (Martinez 1993, Gauzens et al. 2013).

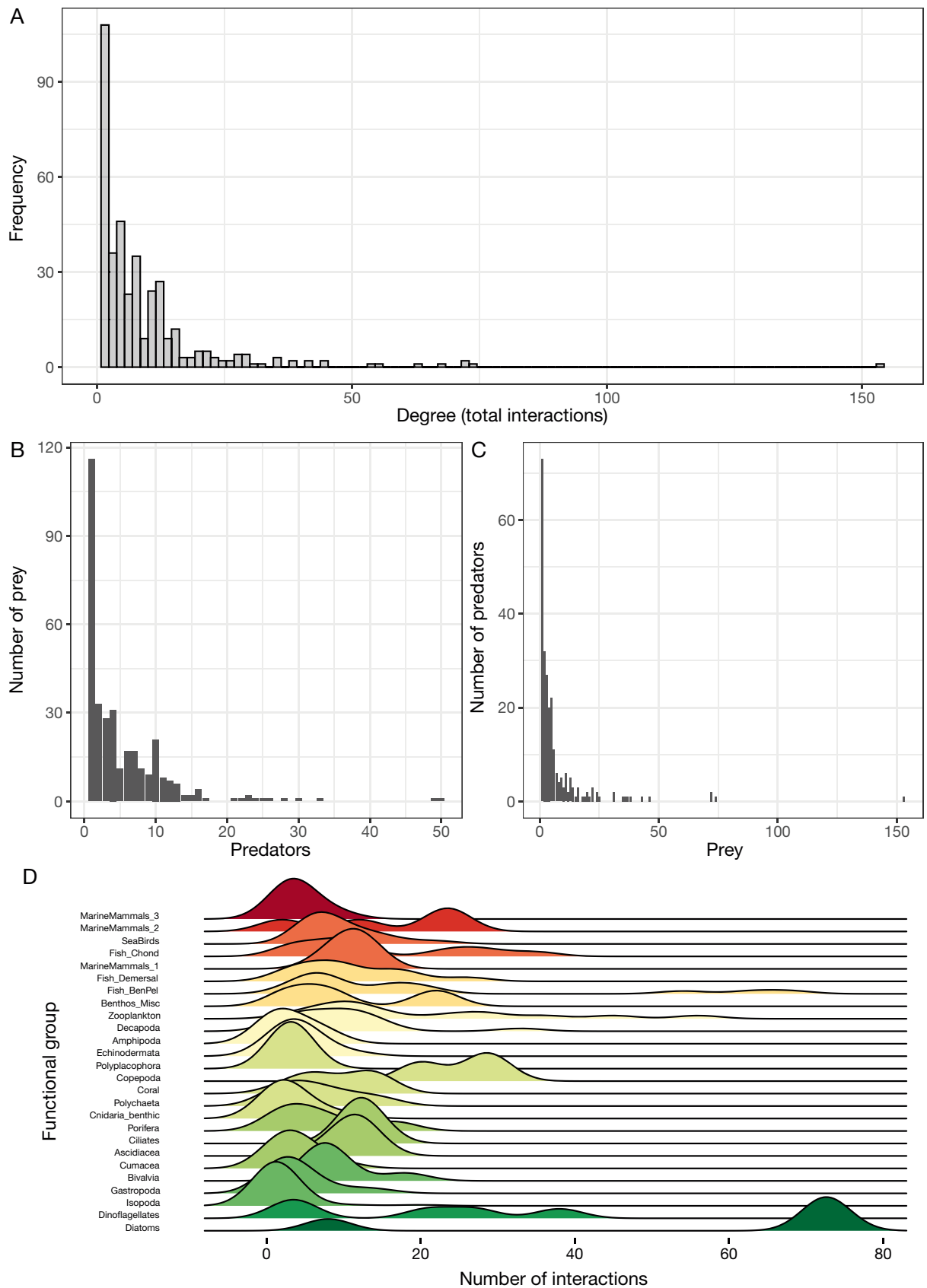


Fig. 3. Degree distributions for (A) the food web, (B) prey among predators, (C) predators among prey, and (D) each functional group. Groups are vertically ordered by increasing trophic level (following coloration of Fig. 2); groups with fewer than 3 species were not plotted (e.g. pelagic fish). All functional groups and the species that comprise them are shown in Table S3

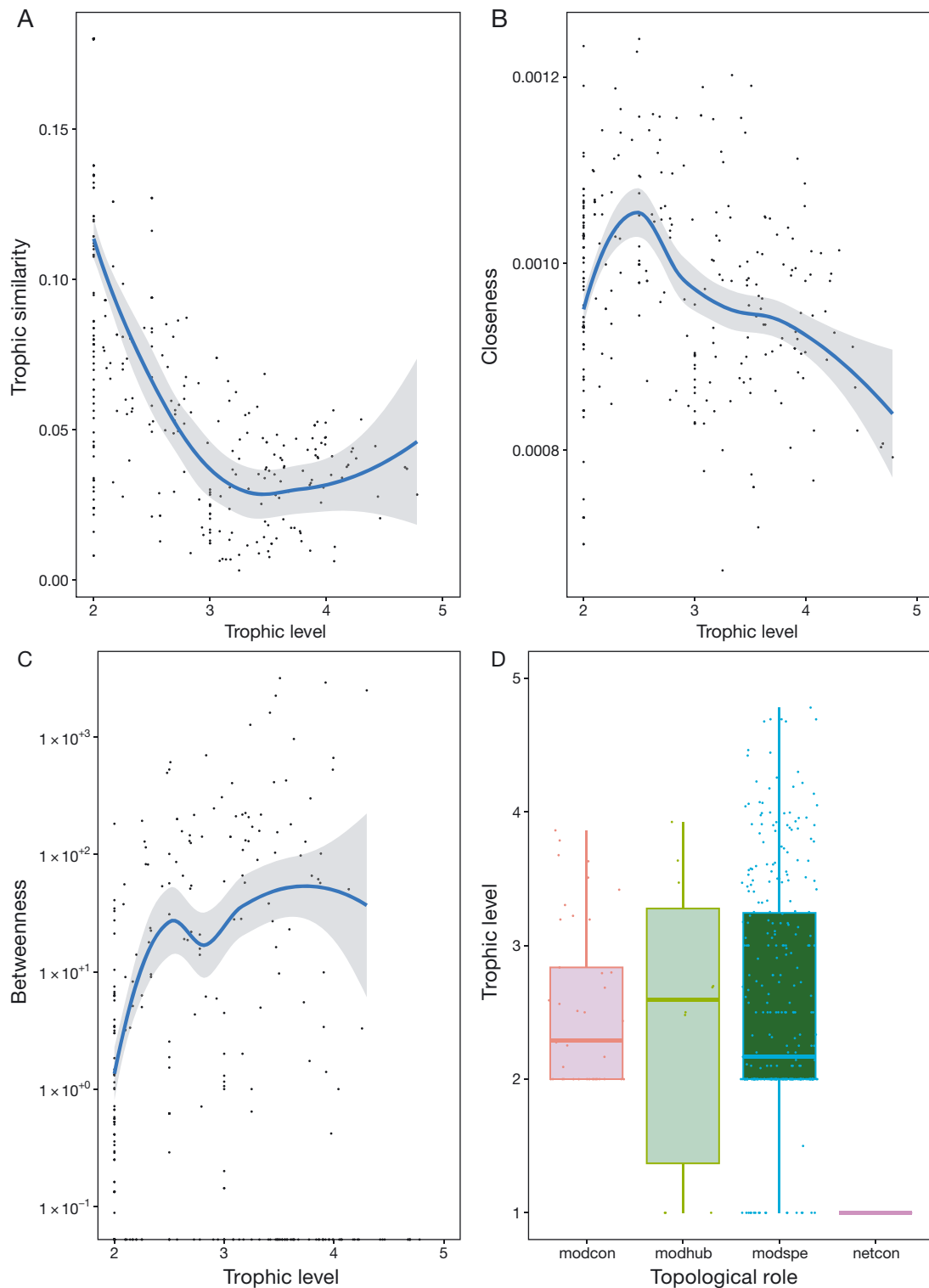


Fig. 4. Species-level properties by trophic level (TL): (A) trophic similarity, (B) closeness, (C) betweenness, and (D) topological role. Topological roles are 'modcon' = species with relatively few interactions mainly between modules; 'modhub' = species with a relatively high number of interactions, but most within its own module; 'modspe' = species with relatively few interactions and most within its own module; and 'netcon' = species with high connectivity between and within modules. Each point represents a species. Note that for panels A, B, and C, only species with TLs ≥ 2 were considered. In the boxplot in panel D, the horizontal line in the middle of each box represents the median of the data and the coloured box represents the interquartile range (containing the middle 50% of data points). The upper whisker extends from the 3rd quartile to the largest value no further than $1.5 \times$ interquartile range; the lower whisker extends from the 1st quartile to the smallest value at most $1.5 \times$ interquartile range

Food web connectance is a feature that summarises the complexity of the network, but more importantly, it is an emergent property of pairwise species interactions (Poisot & Gravel 2014). It contains information regarding how interactions within an ecological network are distributed and predicts reasonably well key dynamical properties of ecological networks (Dunne et al. 2002a). Complex marine food webs (i.e. with more than 25 trophic species) show connectance values ranging from 0.01 to 0.27 (Marina et al. 2018b). In particular, food webs from high-latitude regions tend to exhibit a connectance closer to the minimum (between 0.01 and 0.05) (de Santana et al. 2013, Kortsch et al. 2015, Rodriguez et al. 2022). The connectance of the food web of the MPA N-BB (0.01) is one of the lowest reported so far for these regions; in particular, it appears to be much lower than that of Beagle Channel (0.05), an adjacent coastal area (Rodriguez et al. 2022). Whether food webs display a low or a high connectance helps to better comprehend synthetic ecosystem properties like robustness. Empirical research indicates that ecological networks with high connectance are resilient to external perturbations, including the introduction of new or invasive species (Smith-Ramesh et al. 2017), as well as the removal of species due to local extinction (Dunne et al. 2002b, Montoya & Solé 2003).

The degree distribution, the frequency distribution of the number of interactions per species, makes up the core of the structure of species interactions, which influences the opportunities for multiple species to persist in the long term and, therefore, their coexistence (Godoy et al. 2018). The food web of the MPA N-BB presents an asymmetric degree distribution. This pattern was identified at different levels of analysis: food web, predator, prey, and functional group. Such asymmetry is a well-known feature in empirical complex food webs in particular (Dunne et al. 2002a, Montoya & Solé 2003, Stouffer et al. 2005), and has received great attention in complex networks in general (Albert & Barabási 2002, Newman 2003). The degree distribution affects the resilience of complex food webs against random failures and pressure on a particular component of the web: food webs showing right-skewed distributions, like the one described in this study, are more vulnerable to the removal of the most connected species or hubs, with the potential for producing secondary extinctions and a catastrophic fragmentation of the network (Albert et al. 2000, Dunne et al. 2002b, Eklöf & Ebenman 2006).

It is suggested that the small-world pattern, i.e. a network with short path length and high clustering coefficient, is not frequent in complex marine food

webs, mainly due to a low clustering coefficient compared to random networks (Dunne et al. 2002c, Marina et al. 2018b). However, the food web of the MPA N-BB does display a small-world pattern. Consequences of this could be of great importance in recognizing species' evolutionary paths and the vulnerability to perturbations (Montoya & Solé 2002). On the one hand, a short path length implies a rapid spread of an impact (e.g. contaminant, population fluctuation, local extinction) throughout the network but, at the same time, more potentially adaptive dynamics in the face of external perturbations (Montoya & Solé 2002, Williams et al. 2002). On the other hand, a high clustering coefficient indicates the formation of subnetworks composed only of the neighbours of particular species. This translates into a greater resistance of the network due to the confinement of perturbations mainly within subnetworks and not spreading between them (Kortsch et al. 2019, Heer et al. 2020). Overall, a small-world topology provides ecological networks with greater resilience and resistance (Bornatowski et al. 2017, Dormann et al. 2017).

Omnivory acts as a buffer to changes as the ecosystem presents alternative energy pathways in the face of perturbations, i.e. reducing the risk of cascading extinctions following the primary loss of species (Borrvall et al. 2000). This is supported by the fact that omnivores adapt at a faster rate and to a wide range of environmental conditions due to their flexibility to feed on the most abundant prey (Fagan 1997). Furthermore, omnivory can be analysed from the interaction point of view: theoretical studies have identified omnivorous interactions as possible candidates for keystone interactions, *sensu* Kadoya et al. (2018), highlighting the importance of omnivory in stabilizing food web dynamics (McCann & Hastings 1997, Neutel et al. 2002). The high proportion of omnivory in the food web of the MPA N-BB suggests that the network might be robust to variations in prey abundances, which could increase food web persistence and stability (Stouffer & Bascompte 2010).

In summary, the food web of the MPA N-BB presents a combination of network properties that makes it unique in terms of network resolution, complexity, and structural pattern. All this suggests that the food web might be fragile to external perturbations targeting highly connected species, which in this case are commercially exploited fishes (Laptikhovskiy et al. 2013, Martínez et al. 2015, Winter & Arkhipkin 2023). However, structural properties may provide resilience and resistance with the final outcome of a rearranged structure maintaining its functions.

4.2. Dominant consumers and food sources

The degree distribution allows identification of important species, such as potential keystone species (i.e. highly connected) (Solé & Montoya 2001, Dunne et al. 2002b), generalist/specialist species, and dominant food sources (Kondoh et al. 2010). We have identified that most of the consumers in the food web of the MPA N-BB either have a narrow diet or are specialists, while few present a broad or generalist diet. The most evident generalist species are *Patagonotothen guntheri* (Covatti Ale et al. 2022), *P. ramsayi* (Fischer et al. 2022), juveniles of *Dissostichus eleginoides* (Troccoli et al. 2020), *Bathyraja brachyurops* (Belleggia et al. 2008), and *B. griseocauda* (Belleggia et al. 2014), each with more than 25 potential prey. Since these species present mid-trophic positions in the food web (with the exception of adults of *Dissostichus eleginoides* that are top predators), acting as both predators and prey, they might be important links between lower and higher trophic levels. This result is in agreement with the sole analysis, using stable isotopes, that exists so far for the trophic structure of the MPA N-BB (Ricciardelli et al. 2020), and resembles other high-latitude marine systems of the Southwest Atlantic and Antarctic regions (Arkhipkin & Laptikhovskiy 2013, Marina et al. 2018a). The importance of these particular generalist species also arises since they feed in benthic and pelagic habitats (Troccoli et al. 2020, Covatti Ale et al. 2022, Fischer et al. 2022), enhancing benthic-pelagic coupling and contributing to vertical carbon flow.

On the other hand, a low number of prey are consumed by many predators in the food web of the MPA N-BB. This suggests that there are dominant food sources on which most consumers depend and from where the ecosystem energy is being transferred to the upper trophic levels. The source in most demand that we identified in this study (i.e. detritus) supports the abundant benthic community of filter-feeders (Schejter et al. 2016), components of the animal forest (Schejter et al. 2020), likely feeding on detritus that is constantly resuspended from the bottom (Martin & Flores Melo 2021). Furthermore, we found that the second and third most-consumed prey were diatoms and species of *Euphausia*, respectively, which are essential sources for the diverse zooplankton community (Spinelli et al. 2020), mid-TL consumers like the Fuegian sprat *Sprattus fuegensis* (Padovani et al. 2021) and *Patagonotothen ramsayi* (Fischer et al. 2022), and top predators such as albatrosses (black-browed *Thalassarche melanophris* and grey-headed *T. chrysostoma*) (Catry et al. 2004) and

baleen whales (species of the genera *Balaenoptera* and *Eubalaena*) (Valenzuela et al. 2018).

4.3. Role of species in relation to their trophic level

Describing species' roles in food webs provides a toolbox to assess the significance of species in terms of community functioning and overall stability (Thébault & Fontaine 2010, Cirtwill et al. 2018). Closeness and betweenness are defined as 'mesoscale' properties because they consider direct and indirect interactions, therefore describing the ability of focal species to influence the rest of the species in the food web (Freeman 1978, Lai et al. 2012). Closeness quantifies how many steps away species *i* is from all other species in the food web, and is proportional to how rapidly the indirect effects of the focal species can spread to other species in the network (Scotti & Jordán 2010). Considering the relationship between this property and TL in the food web of the MPA N-BB, it is worth highlighting that species with the highest closeness values are low-TL consumers (TL = 2–3): species of the zooplankton community, *Calanus* and *Euphausia*, *Zygochlamys patagonica* (Bivalvia), and Brachiopoda. Any perturbation affecting these species, such as the recently confirmed contaminants mercury (Fioramonti et al. 2022) and microplastics (Cossi et al. 2021, Di Mauro et al. 2022), and the warming trend reported for surface and subsurface waters in the Southwest Atlantic Ocean (Franco et al. 2020a, Galván et al. 2022), should be of concern since it might reach many other species in the food web. Otherwise, betweenness measures the number of shortest paths between species, providing information on the importance of species as 'bridges' for energy transfer: a species with high betweenness takes part in more food chains and therefore affects more energy flows (Scotti & Jordán 2010). We have identified the longtail southern cod *Patagonotothen ramsayi* as the most important species in this sense. Moreover, in light of our analysis, other species like the Patagonian toothfish *Dissostichus eleginoides* (juveniles), the Patagonian cod *Salilota australis*, the yellowfin notothenioid *P. guntheri*, and the Patagonian longfin squid *Doryteuthis gahi* should be considered as relevant in the energy transfer in the ecosystem. All of these species have a mid-trophic position in the food web, supporting the 'wasp-waist' control hypothesis for the MPA N-BB (Ricciardelli et al. 2020).

Ecosystems with a pronounced 'wasp-waist' structure are suggested to present high trophic redun-

dancy, since many species feeding at intermediate TLs would show similar trophic habits (Saporiti et al. 2015). Such trophic redundancy is expected to be greater for species in TLs above the waist that depend on a very few species at this intermediate level. However, our results show a negative relationship between trophic similarity (or redundancy) and TL, indicating functional similarity among low- and mid-TL species compared to higher TL species for the MPA N-BB food web. This contradiction might reflect the potential discrepancy that could arise between qualitative (this study) and quantitative food web studies. Here, it is important to note that our analyses considered all potential predator–prey interactions in the food web, assigning equal importance to each of them. Although this could be a disadvantage when inferring energy flows, one of the main advantages of qualitative food web studies is that they consider the diversity of the communities inhabiting a particular study area, therefore providing a more representative picture of all components (species) acting on the ecosystem. In this sense, our study highlights the uniqueness in terms of the trophic role of high-TL predators. Not only the expected pelagic animals such as marine mammals and seabirds arise as relevant, but also demersal vertebrate (chondrichthyans *Bathyraja macloviana* and *Squalus acanthias*) and benthic invertebrate (echinoderms *Diplopteraster clarki* and *Pteraster* sp.) species are noteworthy. The role that such species play in the MPA N-BB ecosystem is unique, and perturbations on them might result in unprecedented changes at the trophic structure and functioning level. In this regard, we should mention the potential threat of the fisheries operating in the western section of the MPA N-BB, where this activity is allowed and mostly focuses on the Patagonian toothfish *Dissostichus eleginoides* and the southern blue whiting *Micromesistius australis* (Martínez et al. 2015). Although fishing effort is concentrated outside the limits of the MPA N-BB, the impact on the MPA ecosystem should not be neglected (Martínez et al. 2021).

Roles of species can also be assessed in a module-based context. Among the varying numbers of topological roles into which species can be divided, 2 are remarkable: ‘module connector’ and ‘network connector’. Here, our results point out that there are several species, belonging to a wide range of trophic positions (TL 1–3.86) and representing 17 different functional groups, that should be considered as influential species for the connectivity of the food web. Thus, we propose that the diversity of species (benthic and pelagic) maintains the connectivity of

the food web, therefore contributing to the trophic structure and ecosystem stability.

4.4. Caveats and future perspectives

The food web studied in the present work might be more representative of the shallow ecosystem of the submarine plateau called Burdwood Bank, on which most of the research was focused as the MPA N-BB I was first created. This is related to the sampling effort made during the research cruises in the former MPA compared to the MPA N-BB II (i.e. deep flanks to the south). As a consequence, most of the data we used to build the network come from studies performed in the MPA N-BB I. Despite this fact, we decided to build the food web considering both MPAs due to the tight oceanographic and ecological connection that exists between them (Administración de Parques Nacionales 2022 and references therein).

The MPA N-BB I presents complex oceanographic conditions that generate an internal spatial heterogeneity, mainly along its longitudinal axis (Matano et al. 2019). Thus far, this heterogeneity has been reflected in phytoplankton and zooplankton communities (Bértola et al. 2018, García Alonso et al. 2020, Spinelli et al. 2020), and in fish assemblages (Delpiani et al. 2020). Moreover, seasonal variations also occur in some physical and biological aspects of the MPA N-BB I (García Alonso et al. 2018, Matano et al. 2019). Considering both MPAs (N-BB I and II), seasonal variation in the community composition of marine mammals and seabirds was recorded recently (Dellabianca et al. 2023). The spatial and seasonal variations in the plankton community might affect the energy and matter flow to higher levels of the food web. This has been recently studied in the vicinity of the MPA N-BB I, in the Beagle Channel, where a differential energy flow pattern of the plankton community was recognized in 2 micro-basins of the channel separated by a sill, each with different physicochemical properties (Giesecke et al. 2021), nutrient concentrations (Latorre et al. 2023), and dominant components of the plankton community (Bruno et al. 2023, Presta et al. 2023). Although we were aware of the above, we decided to characterise a food web representing the whole MPA N-BB I year round since this is the first study of its type in the area. In future studies, environmental variables such as depth, current speed, and/or nutrient availability should be included in food web studies, as was done recently (Cordone et al. 2020).

It is important to note that we did not consider quantitative data (i.e. abundance, biomass) to assess

the roles of species in the food web. Although such data exist for some species (Schejter & Albano 2021), it would not be possible to include this information in the food web framework described here due to a taxonomical resolution mismatch. In this regard, we should mention the case of *Zygochlamys patagonica* (Bivalvia) and Brachiopoda that are highlighted by our species-level analyses although they have been found in low abundances in the area (Schejter & Albano 2021).

Taking into account the mentioned caveats, and with the aim of improving knowledge regarding the structure, functioning, and stability of the MPA N-BB, we suggest that the future perspectives should (1) incorporate spatial heterogeneity between MPA N-BB I and II (Schejter & Albano 2021), which might lead to distinct food web properties in terms of structure and functioning (Kortsch et al. 2019, Cordone et al. 2020); (2) include species traits, like body size and mass, since they are known to be important drivers in predator–prey interactions (Brose et al. 2019); (3) simulate the anthropogenic impacts already present in the MPA N-BB ecosystem (e.g. microplastics, mercury) (Cossi et al. 2021, Di Mauro et al. 2022, Fioramonti et al. 2022) as perturbations within the framework of the described complex food web; and (4) estimate the interaction strength of each predator–prey relationship in the food web considering species and interaction traits (i.e. diet preference, body size, body mass, interaction dimensionality, or whether the predator–prey relationship occurs in a 2- or 3-dimensional space), and species density data (Pawar et al. 2012, Nilsson & McCann 2016).

5. CONCLUSION

We compiled information on the species and trophic diversity of the oceanic MPA N-BB, generating an unprecedented, well-resolved network of trophic interactions for a sub-Antarctic ecosystem, identifying the complexity and structure of the system, and the role of the main species in a network framework. Particular properties at the network level allowed us to identify ecosystem vulnerability and potential response to perturbations in the presence of highly connected species, with a rearranged structure maintaining their functions due to its potential resilience and resistance.

We identified several species as important regarding different aspects of trophic structure and functioning and their response to perturbations (i.e. environmental/anthropogenic changes). On the one hand, we suggest that generalist species, mainly fishes, play

a crucial role in the benthic–pelagic coupling process in this ecosystem. At the same time, we propose that other species besides the longtail southern cod *Patagonotothen ramsayi* and the Fuegian sprat *Sprattus fuegensis* should be considered relevant energy transfer agents for the ecosystem. Finally, we argue that it is the diversity of species, representing benthic and pelagic habitats, that maintains the connectivity and resilience of the food web against perturbations, therefore contributing to the structure and stability of the ecosystem.

Our work provides valuable information for supporting the management of the MPA N-BB in the sense that it disentangles the multiple ecosystem players and their roles. Moreover, by building the network of predator–prey interactions, we have set the baseline to model the environmental and anthropogenic perturbations affecting this oceanic ecosystem. This knowledge becomes important at the regional scale given that the MPA N-BB ecosystem is a known spawning ground for many species of commercial interest (Administración de Parques Nacionales 2022) and a potential area of high carbon storage and sequestration due to the characteristics of the benthic community (Bax et al. 2022, L. Bergagna et al. unpubl.).

Acknowledgements. We are indebted to all those experts of the working group 'Banco Burdwood' who provided their knowledge to enhance the quality of the present research. Most of them are authors of the present work, but we also thank the following researchers: Brenda L. Doti (IBBEA, CONICET-UBA; Universidad de Buenos Aires, Argentina), Sofía L. Callá (Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Argentina), Sandra Gordillo (IDACOR-CONICET; Universidad Nacional de Córdoba, Argentina), Mariano I. Martínez (Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Argentina) and Luciano Padovani (Instituto Nacional de Investigación y Desarrollo Pesquero, INIDEP, Argentina). We thank the MPA Namuncurá–Burdwood Bank administration. Research cruises were funded by national funds under the Law 26 875. This study was funded by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Agencia Nacional de Promoción Científica y Tecnológica (PICT 2020 SERIEA 01617), Argentina. This work is contribution no. 77 of the MPA Namuncurá (Law 26 875).

LITERATURE CITED

- ✦ Acha EM, Mianzan HW, Guerrero RA, Favero M, Bava J (2004) Marine fronts at the continental shelves of austral South America: physical and ecological processes. *J Mar Syst* 44:83–105
- Administración de Parques Nacionales (2022) Plan de gestión AMP Namuncurá Banco Burdwood. Tech Rep. Dirección Nacional de Áreas Marinas Protegidas, Ciudad Autónoma de Buenos Aires

- Albert R, Barabási AL (2002) Statistical mechanics of complex networks. *Rev Mod Phys* 74:47–97
- Albert R, Jeong H, Barabási AL (2000) Error and attack tolerance of complex networks. *Nature* 406:378–382
- Arkhipkin A, Laptikhovskiy V (2013) From gelatinous to muscle food chain: Rock cod *Patagonotothen ramsayi* recycles coelenterate and tunicate resources on the Patagonian Shelf. *J Fish Biol* 83:1210–1220
- Bascompte J (2009) Disentangling the Web of Life. *Science* 325:416–419
- Bax N, Barnes DKA, Pineda-Metz SEA, Pearman T and others (2022) Towards incorporation of blue carbon in Falkland Islands marine spatial planning: a multi-tiered approach. *Front Mar Sci* 9:872727
- Belleggia M, Mabrugaña E, Figueroa DE, Scenna LB, Barbini SA, Díaz de Astarloa JM (2008) Food habits of the broad nose skate, *Bathyraja brachyurops* (Chondrichthyes, Rajidae), in the south-west Atlantic. *Sci Mar* 72:701–710
- Belleggia M, Scenna L, Barbini SA, Figueroa DE, Díaz de Astarloa JM (2014) The diets of four *Bathyraja* skates (Elasmobranchii, Arhynchobatidae) from the Southwest Atlantic. *Cybium* 38:314–318
- Bergagna L, Chiesa I, Álvarez YP, Ceballos SG, Boy CC, Riccialdelli L, Lovrich GA (2020) En el fondo el Banco es bueno. *Lupa Col Fueguina Divulg Cient* 16:20–24
- Bértola G, Olguín Salinas H, Alder VA (2018) Distribución espacial de *Rhizosolenia crassa*, especie clave del banco Burdwood? In: Menoret A, Güller M (eds) Libro de Resúmenes X Jornadas Nacionales de Ciencias Del Mar. Universidad de Buenos Aires (UBA), Ciudad Autónoma de Buenos Aires, p 74 (Abstract)
- Bornatowski H, Barreto R, Navia AF, de Amorim AF (2017) Topological redundancy and ‘small-world’ patterns in a food web in a subtropical ecosystem of Brazil. *Mar Ecol* 38:e12407
- Borrelli JJ, Ginzburg LR (2014) Why are there so few trophic levels: selection against instability explains the pattern. *Food Webs* 1:10–17
- Borrvall C, Ebenman B, Jonsson TJ (2000) Biodiversity lessens the risk of cascading extinction in model food webs. *Ecol Lett* 3:131–136
- Brose U, Dunne JA (2009) Modelling the dynamics of complex food webs. In: Verhoef HA, Morin PJ (eds) Community ecology: processes, models, and applications. Oxford University Press, New York, NY, p 37–44
- Brose U, Archambault P, Barnes AD, Bersier LF and others (2019) Predator traits determine food-web architecture across ecosystems. *Nat Ecol Evol* 3:919–927
- Bruno DO, Valencia-Carrasco C, Paci MA, Leonarduzzi E and others (2023) Spring plankton energy content by size classes in two contrasting environments of a high latitude ecosystem: the Beagle Channel. *J Mar Syst* 240:103876
- Catry P, Phillips RA, Phalan B, Silk JRD, Croxall JP (2004) Foraging strategies of grey-headed albatrosses *Thalasarche chrysostoma*: integration of movements, activity and feeding events. *Mar Ecol Prog Ser* 280:261–273
- CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) (2009) Vulnerable marine ecosystem taxa classification guide. Tech Rep. <https://www.ccamlr.org/en/system/files/VME-guide.pdf>
- Cirtwill AR, Dalla Riva GV, Gaiarsa MP, Bimler MD, Cagua EF, Coux C, Dehling DM (2018) A review of species role concepts in food webs. *Food Webs* 16:e00093
- Cleveland WS, Grosse E, Shyu WM (1992) Local regression models. In: Hastie TJ (ed) Statistical models in S. Wadsworth and Brooks/Cole, New York, NY, p 479–547
- Cordone G, Marina TI, Salinas V, Doyle SR, Saravia LA, Momo FR (2018) Effects of macroalgae loss in an Antarctic marine food web: applying extinction thresholds to food web studies. *PeerJ* 6:e5531
- Cordone G, Salinas V, Marina TI, Doyle SR, Pasotti F, Saravia LA, Momo FR (2020) Green vs brown food web: effects of habitat type on multidimensional stability proxies for a highly-resolved Antarctic food web. *Food Webs* 25:e00166
- Cossi PF, Ojeda M, Chiesa IL, Rimondino GN, Fraysse C, Calcagno J, Pérez AF (2021) First evidence of microplastics in the Marine Protected Area Namuncurá at Burdwood Bank, Argentina: a study on *Henricia obesa* and *Odontaster penicillatus* (Echinodermata: Asteroidea). *Polar Biol* 44:2277–2287
- Covatti Ale M, Fischer L, Deli Antoni M, Díaz de Astarloa JM, Delpiani G (2022) Trophic ecology of the yellowfin notothen, *Patagonotothen guntheri* (Norman, 1937) at the Marine Protected Area Namuncurá–Burdwood Bank, Argentina. *Polar Biol* 45:549–558
- Csárdi G, Nepusz T, Traag V, Horvát S, Zanini F, Noom D, Müller K (2024) igraph: Network analysis and visualization in R. R package version 2.0.3. <https://r.igraph.org>
- Dellabianca NA, Torres MA, Ordoñez C, Fioramonti N, Raya Rey A (2023) Marine protected areas in the southern south-west Atlantic: insights from marine top predator communities. *Aquat Conserv* 33:472–487
- Delpiani SM, Bruno DO, Vazquez DM, Llopart F and others (2020) Structure and distribution of fish assemblages at Burdwood Bank, the first Sub-Antarctic Marine Protected Area ‘Namuncurá’ in Argentina (Southwestern Atlantic Ocean). *Polar Biol* 43:1783–1793
- de Santana CN, Rozenfeld AF, Marquet PA, Duarte CM (2013) Topological properties of polar food webs. *Mar Ecol Prog Ser* 474:15–26
- Di Mauro R, Castillo S, Pérez A, Iachetti CM, Silva L, Tomba JP, Chiesa IL (2022) Anthropogenic microfibers are highly abundant at the Burdwood Bank seamount, a protected sub-Antarctic environment in the Southwestern Atlantic Ocean. *Environ Pollut* 306:119364
- Diez MJ, Cabreira AG, Madirolas A, De Nascimento JM, Scioscia G, Schiavini A, Lovrich GA (2018) Winter is cool: spatio-temporal patterns of the squat lobster *Munida gregaria* and the Fuegian sprat *Sprattus fuegensis* in a sub-Antarctic estuarine environment. *Polar Biol* 41:2591–2605
- Dormann CF, Fründ J, Schaefer HM (2017) Identifying causes of patterns in ecological networks: opportunities and limitations. *Annu Rev Ecol Evol Syst* 48:559–584
- Dunne JA, Williams RJ, Martinez ND (2002a) Food-web structure and network theory: the role of connectance and size. *Proc Natl Acad Sci USA* 99:12917–12922
- Dunne JA, Williams RJ, Martinez ND (2002b) Network structure and biodiversity loss in food webs: Robustness increases with connectance. *Ecol Lett* 5:558–567
- Dunne JA, Williams RJ, Martinez ND (2002c) Small networks but not small worlds: unique aspects of food web structure. SFI Work Pap 2002-03-010. Santa Fe Institute, Santa Fe, NM
- Eklöf A, Ebenman B (2006) Species loss and secondary extinctions in simple and complex model communities. *J Anim Ecol* 75:239–246
- Erdős P, Rényi A (1959) On random graphs. *Publ Math* 6: 290–297

- ✦ Fagan WF (1997) Omnivory as a stabilizing feature of natural communities. *Am Nat* 150:554–567
- Falabella V (2017) Área Marina Protegida Namuncurá – Banco Burdwood. Contribuciones para la línea de base y el plan de manejo. Tech Rep. Jefatura de Gabinete de Ministros, Ciudad Autónoma de Buenos Aires
- ✦ Fioramonti NE, Ribeiro Guevara S, Becker YA, Riccialdelli L (2022) Mercury transfer in coastal and oceanic food webs from the Southwest Atlantic Ocean. *Mar Pollut Bull* 175: 113365
- ✦ Fischer L, Covatti Ale M, Deli Antoni M, Díaz de Astarloa JM, Delpiani G (2022) Feeding ecology of the longtail southern cod, *Patagonotothen ramsayi* (Regan, 1913) (Notothenioidei) in the Marine Protected Area Namuncurá – Burdwood Bank, Argentina. *Polar Biol* 45:1483–1494
- ✦ Franco BC, Combes V, González Carman V (2020a) Subsurface ocean warming hotspots and potential impacts on marine species: the southwest South Atlantic Ocean case study. *Front Mar Sci* 7:563394
- ✦ Franco BC, Defeo O, Piola AR, Barreiro M and others (2020b) Climate change impacts on the atmospheric circulation, ocean, and fisheries in the southwest South Atlantic Ocean: a review. *Clim Change* 162:2359–2377
- Franco BC, Ruiz-Etcheverry LA, Marrari M, Piola AR, Matano RP (2022) Climate change impacts on the Patagonian shelf break front. *Geophys Res Lett* 49:e2021GL096513
- ✦ Freeman LC (1978) Centrality in social networks conceptual clarification. *Soc Networks* 1:215–239
- ✦ Funes M, Saravia LA, Cordone G, Iribarne OO, Galván DE (2022) Network analysis suggests changes in food web stability produced by bottom trawl fishery in Patagonia. *Sci Rep* 12:10876
- Galván DE, Bovcon ND, Cochia PD, González RA and others (2022) Changes in the specific and biogeographic composition of coastal fish assemblages in Patagonia, driven by climate change, fishing, and invasion by alien species. In: Helbling EW, Narvarte MA, González RA, Villafañe VE (eds) *Global change in Atlantic coastal Patagonian ecosystems: a journey through time* (Natural and Social Sciences of Patagonia). Springer International Publishing, Cham, p 205–231
- ✦ García Alonso VA, Brown D, Martín J, Pájaro M, Capitanio FL (2018) Seasonal patterns of Patagonian sprat *Sprattus fuegensis* early life stages in an open sea Sub-Antarctic Marine Protected Area. *Polar Biol* 41:2167–2179
- ✦ García Alonso VA, Brown DR, Pájaro M, Capitanio FL (2020) Growing up down south: spatial and temporal variability in early growth of Fuegian sprat *Sprattus fuegensis* from the Southwest Atlantic Ocean. *Front Mar Sci* 7:322
- ✦ Gauzens B, Legendre S, Lazzaro X, Lacroix G (2013) Food-web aggregation, methodological and functional issues. *Oikos* 122:1606–1615
- ✦ Giesecke R, Martín J, Piñones A, Höfer J and others (2021) General hydrography of the Beagle Channel, a subantarctic interoceanic passage at the southern tip of South America. *Front Mar Sci* 8:621822
- ✦ Glorioso PD, Flather RA (1995) A barotropic model of the currents off SE South America. *J Geophys Res C Oceans* 100:13427–13440
- ✦ Godoy O, Bartomeus I, Rohr RP, Saavedra S (2018) Towards the integration of niche and network theories. *Trends Ecol Evol* 33:287–300
- Guerrero RA, Baldoni AG, Benavides HR (1999) Oceanographic conditions at the southern end of the Argentine continental slope. Tech Rep. Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata
- ✦ Guimerà R, Nunes Amaral LA (2005) Functional cartography of complex metabolic networks. *Nature* 433:895–900
- ✦ Guinder VA, Malits A, Ferronato C, Krock B, Garzón-Cardona J, Martínez A (2020) Microbial plankton configuration in the epipelagic realm from the Beagle Channel to the Burdwood Bank, a Marine Protected Area in sub-Antarctic waters. *PLOS ONE* 15:e0233156
- ✦ Heer H, Streib L, Schäfer RB, Ruzika S (2020) Maximising the clustering coefficient of networks and the effects on habitat network robustness. *PLOS ONE* 15:e0240940
- ✦ Hogg OT, Huvenne VAI, Griffiths HJ, Dorschel B, Linse K (2016) Landscape mapping at sub-Antarctic South Georgia provides a protocol for underpinning large-scale marine protected areas. *Sci Rep* 6:33163
- ✦ IUCN, UNEP-WCMC (2023) The world database on protected areas (WDPA). <https://www.protectedplanet.net/en/thematic-areas/wdpa?tab=WDPA> (accessed 1 December 2023)
- ✦ Kadoya T, Gellner G, McCann KS (2018) Potential oscillators and keystone modules in food webs. *Ecol Lett* 21: 1330–1340
- ✦ Kondoh M, Kato S, Sakato Y (2010) Food webs are built up with nested subwebs. *Ecology* 91:3123–3130
- ✦ Kortsch S, Primicerio R, Fossheim M, Dolgov AV, Aschan M (2015) Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proc R Soc B* 282:20151546
- ✦ Kortsch S, Primicerio R, Aschan M, Lind S, Dolgov AV, Planque B (2019) Food-web structure varies along environmental gradients in a high-latitude marine ecosystem. *Ecography* 42:295–308
- ✦ Lai SM, Liu WC, Jordán F (2012) On the centrality and uniqueness of species from the network perspective. *Biol Lett* 8:570–573
- ✦ Laptikhovskiy V, Arkhipkin A, Brickle P (2013) From small bycatch to main commercial species: explosion of stocks of rock cod *Patagonotothen ramsayi* (Regan) in the Southwest Atlantic. *Fish Res* 147:399–403
- ✦ Latorre MP, Berghoff CF, Giesecke R, Malits A and others (2023) Plankton metabolic balance in the eastern Beagle Channel during spring. *J Mar Syst* 240:103882
- ✦ Lindeman RL (1942) The trophic-dynamic aspect of ecology. *Ecology* 23:399–418
- ✦ López-Gappa J, Liuzzi MG, Zelaya DG (2018) A new genus and species of cheilostome bryozoan associated with hermit crabs in the subantarctic Southwest Atlantic. *Polar Biol* 41:733–741
- Madirolas A, Sánchez R, Hansen J, Álvarez Colombo G, Reta R (2000) Distribución, abundancia, biología y hábitat de la sardina fueguina (*Sprattus fuegensis*). Tech Rep. Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata
- ✦ Marina TI, Salinas V, Cordone G, Campana G and others (2018a) The food web of Potter Cove (Antarctica): complexity, structure and function. *Estuar Coast Shelf Sci* 200:141–151
- ✦ Marina TI, Saravia LA, Cordone G, Salinas V, Doyle SR, Momo FR (2018b) Architecture of marine food webs: to be or not be a ‘small-world’. *PLOS ONE* 13:e0198217
- ✦ Marina TI, Saravia LA, Kortsch S (2024) New insights into the Weddell Sea ecosystem applying a quantitative network approach. *Ocean Sci* 20:141–153
- Martin J, Flores Melo X (2021) Área Marina Protegida

- Namuncurá Banco Burdwood: aspectos físicos y biogeoquímicos. In: Lovrich G (eds) Tercer taller científico sobre el Área Marina Protegida Namuncurá—Banco Burdwood. Dirección Nacional de Áreas Marinas Protegidas, Ciudad Autónoma de Buenos Aires, p 14–15
- Martin Sirito S (2019) Fauna asociada a corales (Octocorallia) e hidroides (Hydrozoa) del Área Marina Protegida 'Namuncurá' (Banco Burdwood) y zonas profundas adyacentes. PhD dissertation, Universidad Nacional de Mar del Plata
- ✦ Martínez ND (1991) Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecol Monogr* 61: 367–392
- ✦ Martínez ND (1992) Constant connectance in community food webs. *Am Nat* 139:1208–1218
- ✦ Martínez ND (1993) Effects of resolution on food web structure. *Oikos* 66:403–412
- Martínez PA, Wöhler OG, Troccoli GH (2015) La evolución de la pesquería de merluza negra (*Dissostichus eleginoides*) en el espacio marítimo argentino. Periodo 2003–2014. Tech Rep. Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata
- Martínez PA, Wöhler OC, Troccoli GH, Di Marco EJ (2021) Análisis del impacto potencial provocado por el establecimiento de las áreas marinas protegidas Namuncurá—Banco Burdwood I, II y Yaganes en la pesquería argentina de merluza negra (*Dissostichus eleginoides*). Tech Rep. Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata
- ✦ Matano RP, Palma ED, Combes V (2019) The Burdwood Bank circulation. *J Geophys Res C Oceans* 124:6904–6926
- ✦ Matusevich F, Vazquez DM, Gabbanelli V, Díaz de Astarloa JM, Mabragna E (2023) Chondrichthyans from the southern tip of South America with emphasis on the marine protected area Namuncurá—Burdwood Bank: exploring egg nursery grounds. *Polar Biol* 46:357–372
- May RM (1973) Stability and complexity in model ecosystems. Princeton University Press, Princeton, NJ
- ✦ McCann K, Hastings A (1997) Reevaluating the omnivory—stability relationship in food webs. *Proc R Soc B* 264: 1249–1254
- ✦ Montoya JM, Solé RV (2002) Small world patterns in food webs. *J Theor Biol* 214:405–412
- ✦ Montoya JM, Solé RV (2003) Topological properties of food webs: from real data to community assembly models. *Oikos* 102:614–622
- ✦ Morales-Castilla I, Matias MG, Gravel D, Araújo MB (2015) Inferring biotic interactions from proxies. *Trends Ecol Evol* 30:347–356
- ✦ Neutel AM, Heesterbeek JAP, de Ruiter PC (2002) Stability in real food webs: weak links in long loops. *Science* 296: 1120–1123
- ✦ Newman MEJ (2003) The structure and function of complex networks. *SIAM Rev* 45:167–256
- ✦ Nilsson KA, McCann KS (2016) Interaction strength revisited clarifying the role of energy flux for food web stability. *Theor Ecol* 9:59–71
- ✦ Padovani LN, Viñas MD, Sánchez F, Mianzan H (2012) Amphipod-supported food web: *Themisto gaudichaudii*, a key food resource for fishes in the southern Patagonian Shelf. *J Sea Res* 67:85–90
- Padovani LN, Álvarez N, Fariás A (2021) Alimentación de la sardina fueguina (*Sprattus fuegensis*) en la región patagónica austral durante la Época reproductiva. Tech Rep. Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata
- Pascual M, Dunne JA (2005) Ecological networks: linking structure to dynamics in food webs. Oxford University Press, New York, NY
- ✦ Pawar S, Dell AI, Savage VM (2012) Dimensionality of consumer search space drives trophic interaction strengths. *Nature* 486:485–489
- Piola AR, Falabella V (2009) El mar Patagónico. In: Falabella V, Campagna C, Croxall J (eds) Atlas del Mar Patagónico: especies y espacios. Wildlife Conservation Society & BirdLife International, Ciudad Autónoma de Buenos Aires, p 54–57
- ✦ Piola AR, Gordon AL (1989) Intermediate waters in the southwest South Atlantic. *Deep-Sea Res A Oceanogr Res Pap* 36:1–16
- ✦ Poisot T, Gravel D (2014) When is an ecological network complex? Connectance drives degree distribution and emerging network properties. *PeerJ* 2:e251
- ✦ Pomeranz JPF, Thompson RM, Poisot T, Harding JS (2019) Inferring predator–prey interactions in food webs. *Methods Ecol Evol* 10:356–367
- ✦ Presta ML, Riccialdelli L, Bruno DO, Castro LR and others (2023) Mesozooplankton community structure and trophic relationships in an austral high-latitude ecosystem (Beagle Channel): the role of bottom-up and top-down forces during springtime. *J Mar Syst* 240:103881
- ✦ Riccialdelli L, Newsome SD, Fogel ML, Goodall RNP (2010) Isotopic assessment of prey and habitat preferences of a cetacean community in the southwestern South Atlantic Ocean. *Mar Ecol Prog Ser* 418:235–248
- ✦ Riccialdelli L, Becker YA, Fioramonti NE, Torres M, Bruno DO, Raya Rey A, Fernández DA (2020) Trophic structure of southern marine ecosystems: a comparative isotopic analysis from the Beagle Channel to the oceanic Burdwood Bank area under a wasp-waist assumption. *Mar Ecol Prog Ser* 655:1–27
- ✦ Roberts CM, O'Leary BC, McCauley DJ, Cury PM and others (2017) Marine reserves can mitigate and promote adaptation to climate change. *Proc Natl Acad Sci USA* 114:6167–6175
- ✦ Rodríguez ID, Marina TI, Schloss IR, Saravia LA (2022) Marine food webs are more complex but less stable in sub-Antarctic (Beagle Channel, Argentina) than in Antarctic (Potter Cove, Antarctic Peninsula) regions. *Mar Environ Res* 174:105561
- ✦ Sala E, Lubchenko J, Grorud-Colvert K, Novelli C, Roberts C, Sumaila UR (2018) Assessing real progress towards effective ocean protection. *Mar Policy* 91:11–13
- ✦ Saporiti F, Bearhop S, Vales DG, Silva L and others (2015) Latitudinal changes in the structure of marine food webs in the Southwestern Atlantic Ocean. *Mar Ecol Prog Ser* 538:23–34
- ✦ Saravia LA (2022) multiweb: ecological network analyses including multiplex networks. R package version 0.6.9. <https://github.com/lasaravia/multiweb>
- ✦ Schejter L, Albano M (2021) Benthic communities at the marine protected area Namuncurá/Burdwood bank, SW Atlantic Ocean: detection of vulnerable marine ecosystems and contributions to the assessment of the rezoning process. *Polar Biol* 44:2023–2037
- ✦ Schejter L, Bremec CS (2019) Stony corals (Anthozoa: Scleractinia) of Burdwood Bank and neighbouring areas, SW Atlantic Ocean. *Sci Mar* 83:247–260
- ✦ Schejter L, Rimondino C, Chiesa I, Díaz de Astarloa JM and others (2016) Namuncurá Marine Protected Area: an oceanic hot spot of benthic biodiversity at Burdwood Bank, Argentina. *Polar Biol* 39:2373–2386

- ✦ Schejter L, Genzano G, Gaitán E, Perez CD, Bremec CS (2020) Benthic communities in the Southwest Atlantic Ocean: conservation value of animal forests at the Burdwood Bank slope. *Aquat Conserv* 30:426–439
- ✦ Scotti M, Jordán F (2010) Relationships between centrality indices and trophic levels in food webs. *Community Ecol* 11:59–67
- ✦ Secretariat of the Convention on Biological Diversity (2004) Technical advice on the establishment and management of a national system of marine and coastal protected areas. Tech Ser 13. <https://www.cbd.int/doc/publications/cbd-ts-13.pdf>
- ✦ Smith-Ramesh LM, Moore AC, Schmitz OJ (2017) Global synthesis suggests that food web connectance correlates to invasion resistance. *Glob Change Biol* 23:465–473
- ✦ Solé RV, Montoya M (2001) Complexity and fragility in ecological networks. *Proc R Soc B* 268:2039–2045
- ✦ Spinelli ML, Malits A, García Alonso VA, Martín J, Capitanio FL (2020) Spatial gradients of spring zooplankton assemblages at the open ocean sub-Antarctic Namuncurá Marine Protected Area/Burdwood Bank, SW Atlantic Ocean. *J Mar Syst* 210:103398
- ✦ Stouffer DB, Bascompte J (2010) Understanding food-web persistence from local to global scales. *Ecol Lett* 13:154–161
- ✦ Stouffer DB, Camacho J, Guimerà R, Ng CA, Nunes Amaral LA (2005) Quantitative patterns in the structure of model and empirical food webs. *Ecology* 86:1301–1311
- R Development Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Thébault E, Fontaine C (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329:853–856
- ✦ Tilman D (1996) Biodiversity: population versus ecosystem stability. *Ecology* 77:350–363
- Tombesi ML, Rabuffetti F, Lovrich GA (2020) Las Áreas marinas protegidas en la Argentina. *Lupa Col Fueguina Divulg Cient* 16:2–7
- ✦ Troccoli GH, Aguilar E, Martínez PA, Belleggia M (2020) The diet of the Patagonian toothfish *Dissostichus eleginoides*, a deep-sea top predator off Southwest Atlantic Ocean. *Polar Biol* 43:1595–1604
- ✦ Valenzuela LO, Rowntree VJ, Sironi M, Seger J (2018) Stable isotopes ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$, $\delta^{34}\text{S}$) in skin reveal diverse food sources used by southern right whales *Eubalaena australis*. *Mar Ecol Prog Ser* 603:243–255
- ✦ Vazquez DM, Belleggia M, Schejter L, Mabrugaña E (2018) Avoiding being dragged away: finding egg cases of *Schroederichthys bivius* (Chondrichthyes: Scyliorhinidae) associated with benthic invertebrates. *J Fish Biol* 92:248–253
- ✦ Watts DJ, Strogatz SH (1998) Collective dynamics of 'small-world' networks. *Nature* 393:440–442
- ✦ Williams RJ, Berlow EL, Dunne JA, Barabási AL, Martinez ND (2002) Two degrees of separation in complex food webs. *Proc Natl Acad Sci USA* 99:12913–12916
- ✦ Winter A, Arkhipkin A (2023) Opportunistic survey analyses reveal a recent decline of skate (Rajiformes) biomass in Falkland Islands waters. *Fishes* 8:24

Editorial responsibility: Deborah K. Steinberg,
Gloucester Point, Virginia, USA
Reviewed by: 3 anonymous referees

Submitted: July 18, 2023
Accepted: April 19, 2024
Proofs received from author(s): May 14, 2024