The complex network of trophic interactions in a subAntarctic oceanic Marine Protected Area

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Abstract

Globally, the total area of the world ocean designated under marine protection has increased in the recent decades. The majority of these Marine Protected Areas (MPAs) focus on the presence of particularly vulnerable, keystone, or charismatic species, large numbers of endemic species, and/or high biodiversity across taxonomic levels. In the sub-Antarctic region, the level of ocean protection is mainly associated to oceanic islands, except for the MPAs Namuncurá - Burdwood Bank I and II (MPA N-BB, 53º–55ºS and 56º–62ºW, respectively), which are associated to a submarine plateau and its southern adjacent deep slope region, respectively. Here, we present the first detailed analysis of the network of predator-prey interactions (food web) for the MPA N-BB ecosystem. We applied a network approach to characterise the food web in terms of complexity and structure, and identifying the species' role in such a framework. In terms of complexity, the MPA N-BB food web consisted of 1780 predator-prey interactions and 375 species, with a link density of 4.75 and a connectance of 0.01. In terms of structure, almost half of the consumers were omnivores (0.48), and the network displayed a small-world pattern. These findings suggest that the ecosystem might be vulnerable to external perturbations targeting highly connected species, although structural properties might provide resilience and resistance, resulting in a rearranged structure that preserves its original functions. Furthermore, we identified several species as important in terms of different aspects of trophic structure and functioning, and response to perturbations. We suggest that generalist species, mainly fishes, play a crucial role in the ecosystem's bentho-pelagic coupling process and that other species, besides the longtail southern cod *Patagonotothen ramsayi* and the Fueguian sprat *Sprattus fuegensis*, should be considered as relevant energy transfers for the ecosystem. Finally, we argue that the diversity of species, including both the benthic and pelagic habitats, is responsible for seccuring the connectivity within the food web against perturbations, therefore contributing to the structure and stability of the ecosystem.

Keywords: Food web, Complexity, Structure, Burdwood Bank, Southwest Atlantic

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1. Introduction

The evidence of benefits provided by Marine Protected Areas (MPAs) as well as the urgent need for ocean protection have driven an unprecedented increase in the number of MPAs worldwide in recent years (Roberts et al., 2017; Sala et al., 2018). Globally, the total area of the world ocean designated under marine protection adds up to approximately 29,600,000 km^2, distributed across nearly 18,444 MPAs and covering 8.16% of the ocean's surface (IUCN & UNEP-WCMC, 2023), and therefore approaching the 10% goal of the Convention of Biological Diversity (Secretariat of the convention on biological diversity, 2004). Despite this progress, recent reports have shown that actual protection has been overestimated because it includes areas that are not yet effectively protected (only declared) as well as areas that allow significant extractive activities (Sala et al., 2018).

In the sub-Antarctic region, the level of ocean protection is mainly associated to oceanic islands, such as the South Georgia and South Sandwich, Bouvet, Prince Edward, and Macquarie islands (IUCN & UNEP-WCMC, 2023). Interestingly, the case of the MPAs Namuncurá - Burdwood Bank I and II (MPA N-BB, 53º–55ºS 56º–62ºW), which is the focus of this work, is unique since these MPAs are associated to a submarine plateau and its southern adjacent deep slope region, respectively (Falabella, 2017). 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 and strengthen the functioning of this southern region to maintain global ocean health.

Many of these MPAs focus on the presence of particularly vulnerable, keystone, or charismatic species, large numbers (or proportions) of endemic species, and/or high biodiversity across taxonomic levels (Hogg et al., 2016). Indeed, the MPA N-BB was created to protect a sensitive and biodiverse benthic habitat that was barely known (Falabella, 2017; Schejter et al., 2016). The benthic community is featured by high biomass of vulnerable and fragile species (mainly Porifera and Cnidaria) that meet the characteristics of vulnerable marine ecosystems (Schejter & Albano, 2021), here defined as sites that present taxa with a minimum biomass of 10 kg per 1200 m^2 (Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), 2009). Also, it provides habitat to several small-sized species (López-Gappa et al., 2018; Martin Sirito, 2019; Schejter & Bremec, 2019), and has an important role in the life history of fishes as a food source, refuge and nursery area (Covatti Ale et al., 2022; Delpiani et al., 2020; Fischer et al., 2022; Florencia et al., 2023; García Alonso et al., 2018; Troccoli et al., 2020; Vazquez et al., 2018). The maintenance of this singular community is related to local and regional oceanographic processes, including the circulation of the rich Malvinas (Falkland) current in the area (Guerrero et al., 1999; Piola & Gordon, 1989) and the upwelling and mixing phenomena (Matano et al., 2019). The input of nutrients from the Malvinas (Falkland) current also supports a diverse plankton community (Guinder et al., 2020). Overall, 811 benthic and plankton species have been identified for the MPA N-BB ecosystem, where 349 were reported for the first time in the area in recent years (Administración de Parques Nacionales, 2022). However, identifying the main species involved in the maintenance of ecosystem services and health as well as for management and conservation is essential.

Recently, the structure of the southwestern South Atlantic Ocean has been proposed 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; Riccialdelli et al., 2020; Saporiti et al., 2015). In particular, the ecosystem of the MPA N-BB shows a more pronounced 'wasp-waist' structure, meaning a shorter food-chain length and a greater trophic overlap and redundancy, than other sub-Antarctic areas, such as the continental shelf off Tierra del Fuego. The Fuegian sprat *Sprattus fuegensis* and longtail southern cod *Patagonotothen ramsayi* are considered the most plausible 'wasp-waist' species (Riccialdelli et al., 2020).

High-latitude marine ecosystems, such as the MPA N-BB, are considered complex systems in terms of biodiversity and ecological interactions (Cordone et al., 2020; Day et al., 2013; Kortsch et al., 2019; Trathan et al., 2021). Although there is a robust knowledge about the complexity considering the richness of the benthic and plankton communities in the MPA N-BB ecosystem (Administración de Parques Nacionales, 2022; Guinder et al., 2020; Schejter et al., 2016, 2020), a better understanding of species interactions' complexity and structure is needed. This aspect can be tackled by analysing one of the most frequent relationships between species: the predator-prey interaction (Bascompte, 2009). The sum of predator-prey or trophic interactions of a particular region is referred to as a food web, representing the roadmap for matter and

energy flow in an ecosystem. In recent years, 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 (Cordone et al., 2018; Funes et al., 2022; Kortsch et al., 2015; Marina et al., 2023). Among anthropogenic threats, it is worth mentioning that contaminants like mercury and microplastics have been recently reported as important threats to the MPA N-BB region (Cossi et al., 2021; Di Mauro et al., 2022; Fioramonti et al., 2022); also 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 (Administración de Parques Nacionales, 2022; Martínez et al., 2021). Moreover, there is a potential hazard related to the effects of offshore activities (exploration and explotation) to the west of the MPA N-BB (Administración de Parques Nacionales, 2022).

In the present 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 network approach to a highly resolved food web. The objective was twofold: characterise the food web in terms of complexity and structure, and identify the species' role in such a network framework.

2. Methodology

2.1. Study area

The MPAs Namuncurá - Burdwood Bank I and II, created by National Laws 26.875 in 2013 and 27.490 in 2017, comprise a shallow submarine plateau called Burdwood Bank (BB) and a deep slope that reaches 4000 m in depth, N-BB I and N-BB II, respectively (Administración de Parques Nacionales, 2022; Tombesi et al., 2020) (Figure 1). They are located 150 km east of Isla de los Estados and 200 km south of Malvinas/Falkland Islands. The MPA N-BB I comprises nearly 34,000 km^2 circumscribed by the 200 m isobath, between 54º–55ºS and 56º–62ºW, with a slight slope extended nearly 370 km east–west. Physical features in the BB are fairly stable, with salinity averaging 34 all year round and temperature ranging between 4 and 8ºC (Acha et al., 2004; Guerrero et al., 1999; Piola & Falabella, 2009). The BB is surrounded by steep flanks of up to 4000 m depth through which strong currents circulate (Matano et al., 2019; Piola & Gordon, 1989; Reta, 2014). The N-BB II includes such a deep slope, protecting about 32,000 km^2. Intense upwelling and mixing occur over it, entraining deep nutrient-rich waters into the photic layer (Matano et al., 2019; Piola & Falabella, 2009) and resulting in a fairly homogeneous water column both spatially and temporally (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 reviewed more than 150 references considering published articles, Ph.D. theses, public databases, and reports belonging to 16 research cruises conducted in the MPAs N-BB I and II during 2014-2019. It is noteworthy that the sampling effort was greater in the MPA N-BB I. Furthermore, we took into account personal communications from experts belonging to the working group of the study area (https://www.pampazul.gob.ar/tag/banco-burdwood/). 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 Supplementary Material (Table S1).

Due to a lack of trophic data resolution for some species inhabiting the study area, we followed the concept of trophic species, here defined as aggregated groups of taxa. In most cases, we followed it 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
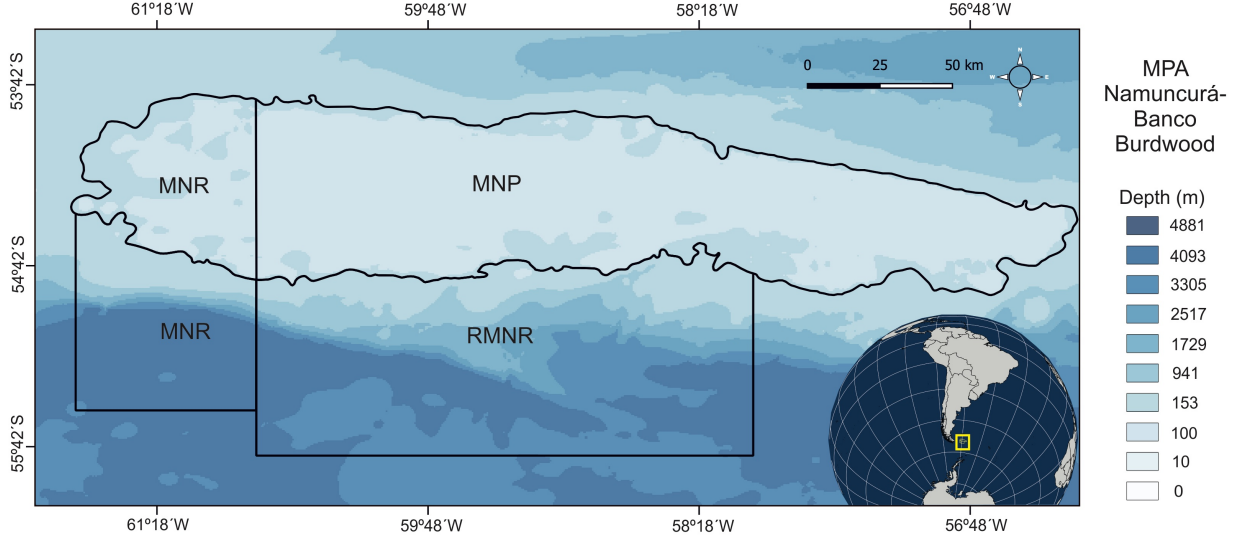
Figure 1: Marine Protected Areas Namuncurá - Burdwood Bank I (MNR and MNP, northern section) and II (MNR and SMNR, southern section). Acronyms indicate categories according to the management plan: MNR - Marine National Reserve, MNP - Marine National Park and RMNR - Restricted Marine National Reserve.

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 taxonomic 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 Supplementary Material (Table S2).

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 the j-species preyed or not on the i-species. Then we transformed such a matrix into an oriented graph with L trophic interactions between S nodes or species. The orientation or direction of 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 two levels: A) network, considering species and interactions of the whole network; and B) species, considering interactions and species related to a particular 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 Omn; 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). Here, CPL was calculated as the average number of nodes in the shortest path $CPL_{Min}(i, j)$ between all pairs of nodes $S(i, j)$ in a network averaged over $S(S - 1)/2$ nodes:

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

The CC quantifies the local interconnectedness of the network and it 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 the nodes in the network. Individual CC_i were determined as follows:

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

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 the method proposed by Marina, Saravia, et al. (2018).

Also, we estimated the (7) 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 viceversa; the functional group's degree 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: (1) betweenness Btw; (2) closeness Cl; (3) trophic similarity TS; (4) topological role TR; and (5) trophic level TL (Table 1). Topological roles refer to the fact that food webs tend to naturally organize 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). 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 modules; and network connector, species with high connectivity between and within modules (Guimerà & Nunes Amaral, 2005).

We also studied the relationship between species TL and the other species properties by performing linear regression analyses. Thus, we considered the TL as the dependent variable and the given property (i.e. betweenness, closeness, trophic similarity) as the independent variable and obtained the coefficients (slope and intercept) for the linear model. Models were fitted using the least squares approach. We also explored the topological role categories with the species TL. These species-level properties provide an appropriate description of species' role in empirical complex food webs (Cirtwill et al., 2018).

All network analyses and graphs were performed in R version 4.2.2 (Team, 2022), mainly using 'igraph' (Csardi & Nepusz, 2006) and 'multiweb' (Saravia, 2022) packages. The source code and data are available at https://github.com/TomasMarina/Banco-Burdwood.

Table 1: List of 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.	It represents the 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.	It represents the number of pathways along which matter and energy can flow.	Dunne et al. 2002

Name	Definition	Implications	Reference
Link density	Ratio of interactions to species in a food web	It represents the average number of interactions per species; informs about how connected species are in the food-web.	Dunne et al. 2002
Connectance	Proportion of potential links among species that are actually realized. Range = 0 - 1.	It 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 strength of the interactions are distributed.	Martinez 1992
Degree distribution	Frequency of trophic species that have k or more interactions.	It suggests on the vulnerability of complex food webs against random failures and intentional attacks (i.e. species extinctions).	Albert & Barabási 2002
Omnivory	Species feeding on prey from more than one trophic level.	It influences food web's stability; intermediate levels of omnivory may stabilize it and may diffuse top-down effects thus reduce the probability of trophic cascades.	McCann & Hastings 1997
Small-world pattern	A 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 going 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.	The removal of a species with high closeness will affect the most other species in the food web.	Freeman 1978, Lai et al. 2012

Name	Definition	Implications	Reference
Trophic similarity	Trophic overlap based on shared and unique resources (prey) and consumers (predators).	It measures one of the most important aspects of species' niches, the trophic niche, and functional aspects of biodiversity.	Martinez 1992
Topological role	Species role 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.	Guimera & Nunes Amaral 2005

3. Results

3.1. Network-level properties

In terms of complexity, the MPA Namuncurá - Burdwood Bank food web (N-BB I and II) consisted of 1780 predator-prey interactions and 375 species, where 93% of them were defined at the species taxonomical level (Figure 2, Table S2). The food web presented a link density (e.g., the average number of interactions per species) of 4.75, and a connectance of 0.01. Almost half of the consumers were omnivores (0.48), 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).
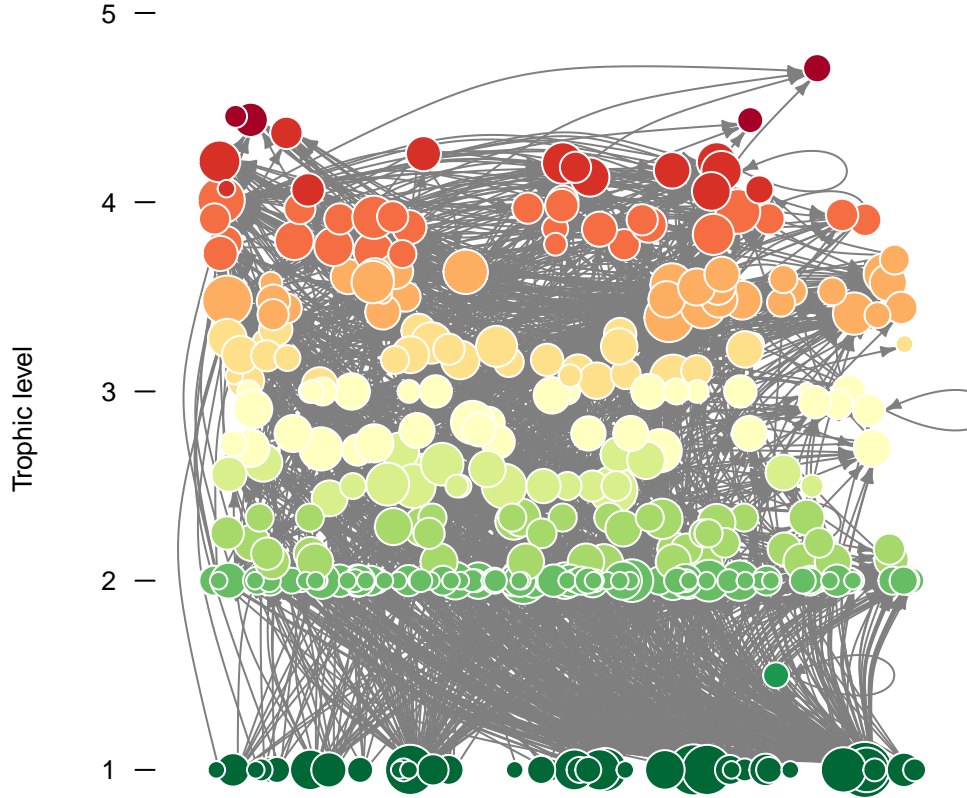
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Figure 2: Graph of the food web for the MPA Namuncurá - Burdwood Bank. Circles represent species and arrows trophic interactions. Circle diameter is relative to the number of interactions. Colour gradient indicates the trophic level.

Table 2: Network-level properties of the MPA Namuncurá - Burdwood Bank food web. CPL: Characteristic Path Length; CC: Clustering Coefficient; SW: Small-World pattern. See table 1 for definitions and ecological relevance.

Species	Interactions	Density	Connectance	Omnivory	CPL	CC	SW
375	1780	4.75	0.01	0.48	2.96	0.08	True

The degree distribution of the food web showed an asymmetric frequency in the number of interactions, where most of the species had a relatively low number of interactions and few species concentrated most of them (Figure 3A). The distribution of prey among predators showed that most consumers fed on a low number of prey whereas few had multiple prey (Figure 3B). The top-five predators in number of prey were: yellowfin notothen *Patagonotothen guntheri* (Notothenioid fish, 50 prey), rock cod *Patagonotothen ramsayi* (Notothenioid fish, 49 prey), broad nose skate *Bathyraja brachyurops* (Chondrichthyan, 33 prey), Patagonian toothfish *Dissostichus eleginoides* (Notothenioid fish, 30 prey), and graytail skate *Bathyraja griseocauda* (Chondrichthyan, 28 prey). Following the same distribution pattern, few prey presented multiple predators (Figure 3C). The top-five prey in number of predators were: Detritus (Non-living, 155 predators), the three categories of Diatoms considered (benthic, centric and pennate, 75 predators on average), and species of the genus *Euphausia* (Zooplankton, 47 predators). Finally, taking into account the interactions within each functional group, most interactions were concentrated in a few species (Figure 3D). The most evident species were: *Doryteuthis gahi* (Cephalopoda), *Grimothea gregaria* (Decapoda), *Patagonotothen ramsayi*, *Patagonotothen guntheri* and *Dissostichus eleginoides* (bentho-pelagic 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 in

the MPA N-BB food web.

A list of the distribution of interactions per species is presented in Supplementary Material (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 (Figure 4A-D). The most evident significant relationship was with trophic similarity, i.e. the higher the species' TL, the lower the trophic similarity or the higher the uniqueness in terms of trophic role (Figure 4C). Here it is noteworthy to highlight those high-trophic level species (TL > 3.1) with low values of trophic similarity: *Bathyraja macloviana* and *Squalus acanthias* (Chondrichthyans), *Diplopteraster clarki* and *Pteraster sp* (echinoderms), *Daption capense* and *Eudyptes chrysocome* (seabirds), Ziphiidae and *Lagenorhynchus cruciger* (marine mammals) (Table S3).

We also found a significant negative relationship between TL and closeness, however less evident, meaning that low-TL species are relatively closer to any other species in the food web (Figure 4B). Detritus, species of genera *Calanus* and *Euphausia*, and Foraminifera, all with TL < 3, registered the highest closeness values (Table S3).

Notably, species of mid-TLs (3-4.2) showed the highest values of betweenness, meaning that those species participated in the highest number of shortest paths between species (Figure 4A). The following are the species with the highest values: *Patagonotothen ramsayi*, *Salilota australis*, *Dissostichus eleginoides* (fishes), *Doryteuthis gahi* (Cephalopoda), and *Patagonotothen guntheri* (Notothenioid fish) (Table S3).

Considering the topological role, 'module specialist' species were the most frequent and presented a wide TL range (1 - 4.7), as well as 'module hub' species (TL = 1 - 4); 'module connector' was constrained to mid-TLs (2 - 3.86); and 'network connector', the least frequent, had all of its species in low-TLs (1 - 2), except for one with TL = 3.48 (Figure 4D, see Figure S2 for species' topological roles in a food web graph framework). Here it is important to highlight the two latter topological roles because they are responsible for linking modules and maintaining the connectivity of the food web: 41 species (4 network connectors + 37 module connectors) from 19 different functional groups with a TL range = 1 - 3.86. The following were the four species with a network connector role: detritus, benthic diatoms, Foraminifera and *Patagonotothen ramsayi*. The 37 species with a module connector role represented these functional groups: Amphipoda, Bivalvia, Brachiopoda, Bryozoa, Hydrozoa (as 'Cnidaria_benthic'), Copepoda, Cumacea, Decapoda, diatoms, Echinodermata, fish (bentho-pelagic and demersal Osteichthyes, and Chondrychthyes), Polychaeta, Porifera, Pycnogonida (as 'Benthos_Misc') and zooplankton (see Supplementary Material Table S3 for the identity of the species).

An exhaustive list of the species-level properties is presented in Supplementary Material (Table S3).

4. Discussion

4.1. The food web of the MPA Namuncurá - Burdwood Bank 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 marine 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 the aggregation of species might mask food web properties and produce type II errors (false positive) (Gauzens et al., 2013; Martinez, 1993).

Food web connectance is a feature that resumes 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 - 0.27 (Marina, Saravia, et al., 2018). In particular, food webs from high-latitude regions tend to exhibit a connectance closer to the minimum (between 0.01 and 0.05) (Kortsch et al., 2015; Rodriguez et al., 2022; Santana et al., 2013). Whether food webs display a low or a high connectance helps to better comprehend ecosystem's synthetic properties like
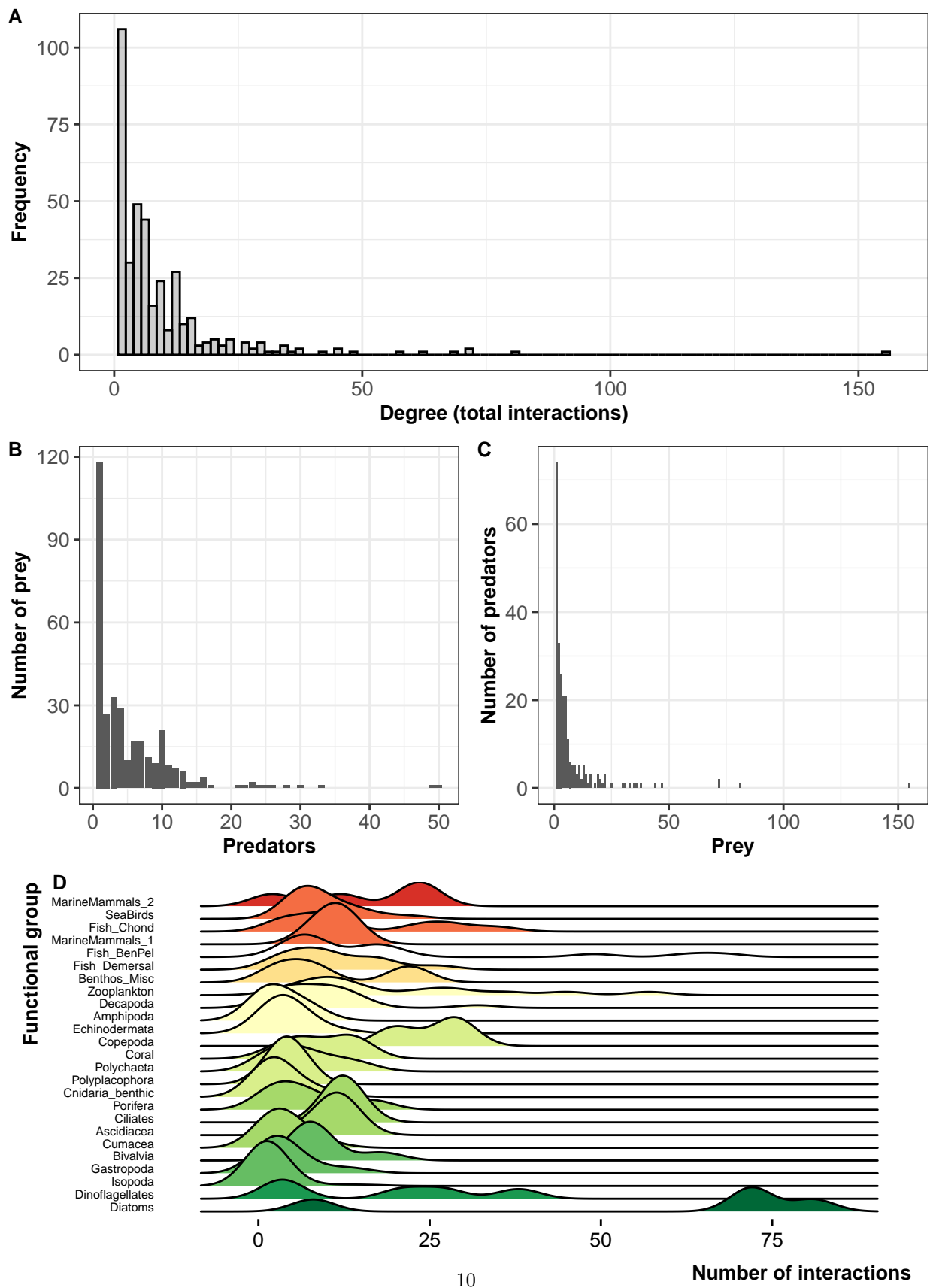
Figure 3: Degree distributions for the (A) food web, for (B) prey among predators, (C) predators among prey, and (D) for each functional group. Groups are vertically ordered by increasing trophic level (following coloration of figure 2); groups with less than 3 species were not plotted (e.g., pelagic fish). All functional groups and the species that comprise them are shown in Supplementary Material (Table S3).
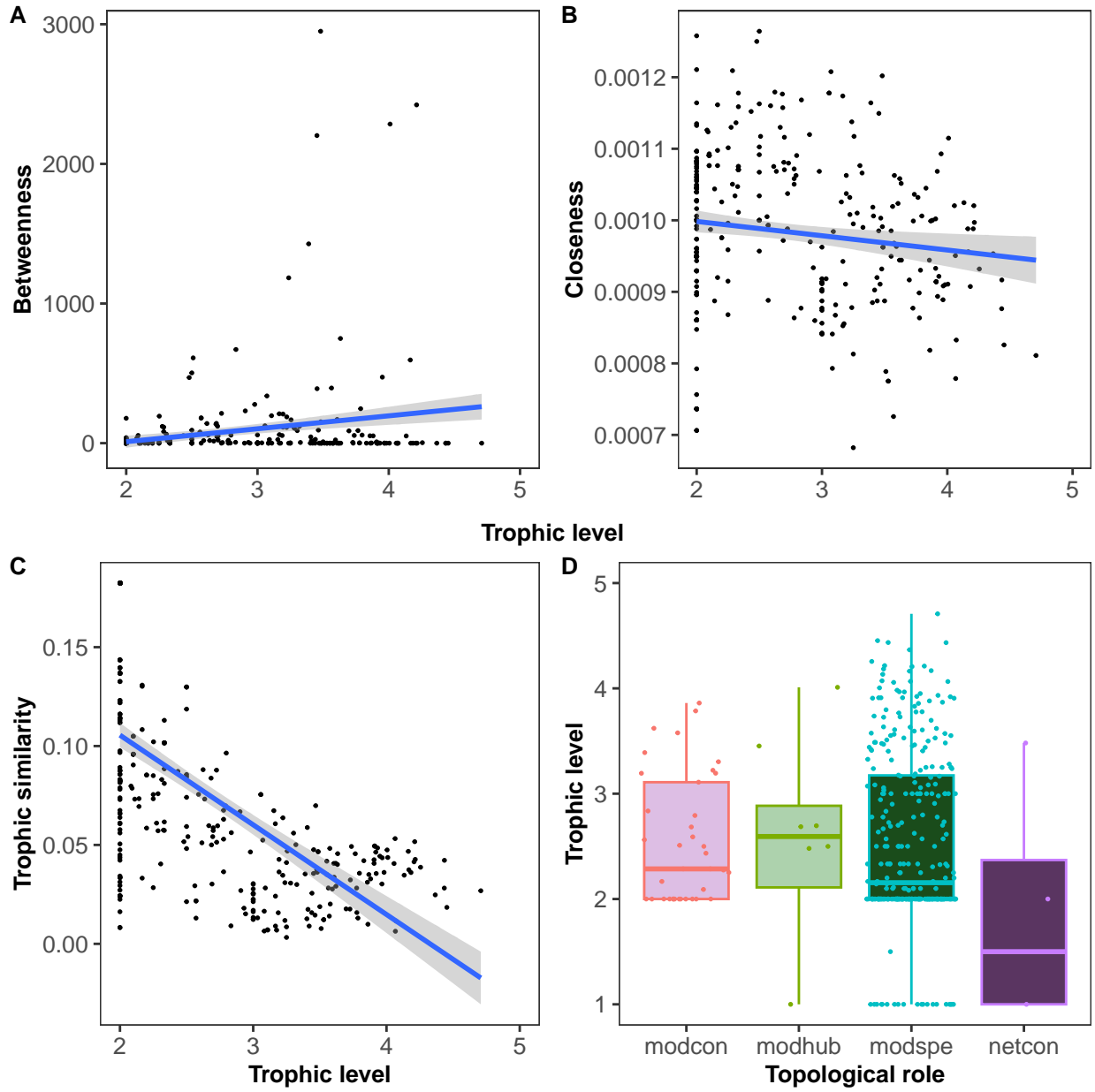
Figure 4: Species-level properties by trophic level: (A) betweenness, (B) closeness, (C) trophic similarity, and (D) topological role. Each point represents a species. Linear regressions for betweenness ($y = 74.96x - 121.71, R^2 = 0.05, p-value < 0.01$), closeness ($y = 1.01e - 05x - 9.48e - 4, R^2 = 0.003, p-value = 0.14$) and trophic similarity ($y = -0.02x + 0.11, R^2 = 0.08, p-value < 0.01$). Note that for panels A, B and C only species with TLs equal or greater than 2 were considered.

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robustness. In this sense, empirical analyses support the notion that highly-connected ecological networks are robust against external perturbations such as the introduction of new (e.g., invasive) species (Smith-Ramesh et al., 2017) as well as species removal (e.g., local extinction) (Dunne et al., 2002b; Montoya & Solé, 2003). The connectance of the food web of the MPA Namuncurá - Burdwood Bank (0.01) is one of the lowest reported so far for these regions; in particular, it appears to much lower than that of Beagle Channel (0.05), an adjacent coastal area (Rodriguez et al., 2022).

The degree distribution, the distribution of the number of interactions per species, is 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 for 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 of 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, Saravia, et al., 2018). 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 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 by 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 (Heer et al., 2020; Kortsch et al., 2019). 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). Omnivores are species able to adapt faster and to a broader range of environmental conditions by changing their foraging habits 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 a possible candidate for a keystone interaction, 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's 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 ecosystem might be fragile to external perturbations targeting highly connected species, which in turn coincides to be commercial exploited species as fishes (Martínez et al., 2015). However, structural properties might 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 identifying important species, such as potential keystone species (Dunne et al., 2002b; Solé & Montoya, 2001), 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 diet. The most evident generalist species are *Patagonotothen guntheri* (Covatti Ale et al., 2022), *P. ramsayi* (Fischer et al., 2022), *Dissostichus eleginoides* (Troccoli et al., 2020), *Bathyraja brachyurops* (Belleggia et al., 2008), and *B. griseocauda* (Bellegia et al., 2014), with more than 25 potential prey. Since these species present mid-trophic positions in the food web (3-4), acting as predator 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 (Riccialdelli et al., 2020), and resembles other high-latitude marine systems of the Southwest Atlantic and Antarctic regions (Arkhipkin & Laptikhovsky, 2013; Marina, Salinas, et al., 2018). The importance of these particular generalist species also arises since they feed in the benthic and pelagic habitats (Covatti Ale et al., 2022; Fischer et al., 2022; Troccoli et al., 2020), linking these realms and contributing to the 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 from which most consumers depend on and from where the ecosystem energy is being transferred to the upper trophic levels. The most demanded source we identified in this study (i.e. detritus) supports the abundant benthic community of filter-feeders (Schejter et al., 2016), 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 the black-browed and grey-headed albatrosses (*Thalassarche melanophris* and *Thalassarche chrysostoma*, respectively) (Catry et al., 2004), and baleen whales (species of the genera Balaenoptera and Eubalaena) (Valenzuela et al., 2018).

4.3. Species' role related to their trophic level

Describing species' roles in food webs provides a toolbox to assess the significance of species in terms of community's functioning and overall stability (Cirtwill et al., 2018; Thébault & Fontaine, 2010). We used a range of descriptors to characterise the dynamic and multifaceted nature of the species forming the MPA N-BB food web.

Closeness and betweenness are defined as "mesoscale" properties because they consider direct and indirect interactions, therefore describing the focal species' ability to influence the rest of the species of the food web (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). In the food web of the MPA N-BB, low-TL consumers arise as important in this regard: species of the zooplankton community, *Calanus* and *Euphausia*, 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) for the area, 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*, the Patagonian cod *Salilota australis*, the yellowfin notothenioid *Patagonotothen guntheri*, and the Patagonian longfin squid *Doryteuthis gahi* should be considered as relevant in the energy transfer in the ecosystem. All these species have a mid-trophic position in the food web, supporting the 'wasp-waist' control hypothesis for the MPA N-BB (Riccialdelli et al., 2020).

Ecosystems with a pronounced 'wasp-waist' structure are suggested to present a high trophic redundancy, since many species would show similar trophic habits (Cury et al., 2000). The significant negative relationship between trophic similarity and trophic level enhances the hypothesis of functional similarity at low and mid-TL species compared to higher TL species for the MPA N-BB food web (Riccialdelli et al., 2020). At the same time, our results highlight the uniqueness in terms of the trophic role of high-TL predators. Here, not only the expected pelagic animals such as marine mammals and seabirds arise as relevant, but also demersal

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vertebrate (chondrichthyans *Bathyraja macloviana* and *Squalus acanthias*) and benthic invertebrate species (echinoderms *Diplopteraster clarki* and *Pteraster sp*) 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 the 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).

Species' role can also be assessed in a module-based context. Among the varying numbers of topological roles in which species can be divided, two are remarkable: 'module connector' and 'network connector'. Here again, the longtail southern cod *Patagonotothen ramsayi* is emphasized as an influential species for the connectivity of the food web, which agrees with the suggested 'wasp-waist' control for the MPA N-BB ecosystem (Riccialdelli et al., 2020). But most importantly, our results broaden this issue by pointing out that there are other species, belonging to a wide range of trophic positions (1 to 3.86) and representing 20 different functional groups, that should be considered. 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's 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 that was conducted 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 among them (Administración de Parques Nacionales, 2022 and references therein).

It's important to mark that we did not consider quantitative data (i.e. abundance, biomass) to assess the species' role in the food web. Although there exists such data for some species (Schejter & Albano, 2021), it would not be possible to include it 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) that is highlighted by our species-level analyses though it has been found in low abundances in the area (Schejter & Albano, 2021).

Some species of sessile suspension feeders in high-latitude marine ecosystems, such as sponges, ascidians and octocorals, avoid predation by producing secondary metabolites that function as a chemical defense (Moles et al., 2015; Núñez-Pons et al., 2010; Prieto et al., 2022). Although this was not yet recorded at the MPA N-BB, there are a few studies that reported it in other locations in species that inhabit the MPA N-BB (Rojo de Almeida et al., 2010).

The MPA N-BB I presents complex oceanographic conditions that generate an internal spatial heterogeneity, mainly along its longitudinal axis (Matano et al., 2019). So 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), a 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 has been recognised in two micro-basins of the Channel separated by a sill, each with different physicochemical properties (Giesecke et al., 2021), nutrient concentration (Latorre et al., 2023) as well as in the dominant component 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.

Taking into account the mentioned caveats, and with the aim of improving the knowledge regarding the structure, functioning and stability of the MPA N-BB, we suggest that the future perspectives should: 1) incorporate spatial heterogeneity among MPA N-BB I and II (Schejter & Albano, 2021), which might lead to distinct food web properties in terms of structure and functioning (Cordone et al., 2020; Kortsch et al., 2019); 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. body size, body mass, interaction dimensionality), and species density data (Nilsson & McCann, 2016; Pawar et al., 2012).

5. Conclusion

We compiled information on the species and trophic diversity of the Marine Protected Area Namuncurá - Burdwood Bank, generating an unprecedented, well-resolved network of trophic interactions for a sub-Antarctic ecosystem, identifying the complexity and structure of the system, and the main species role in a network framework. Particular properties at the network level allowed us to identify the ecosystem's 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 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 ecosystem's bentho-pelagic coupling process. At the same time, we propose that other species besides the longtail southern cod *Patagonotothen ramsayi* and the Fueguian sprat *Sprattus fuegensis* should be considered relevant energy transfers for the ecosystem. Finally, we argue that it is the diversity of species, representing the benthic and pelagic habitats, that maintains the connectivity of the food web against perturbations, therefore contributing to the structure and stability of the ecosystem.

6. Acknowledgements

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