

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

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Abstract

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Keywords: Food web, Complexity, Structure, Marine Protected Area, Southwest Atlantic

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 nearly 29,600,000 km², 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 (CBD, 2004). Despite this progress, recent reports have shown that effective 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 subAntarctic region, the level of protection is mainly associated to oceanic islands, such as South Georgia and the South Sandwich, Bouvet, Prince Edward, and Macquarie (IUCN & UNEP-WCMC, 2023). Interestingly, the case of the MPAs Namuncurá - Banco Burdwood I and II (MPA N-BB), which forms the focus of this work, is unique since they are associated to a submarine plateau and the southern adjacent deep slope region, respectively (Falabella, 2017). Added to this, such MPAs are part of a network of protected areas in the subAntarctic (jointly with MPA Yaganes), that contributes to protect and strengthen the functioning of this southern region to maintain global ocean health.

Many of these MPAs centre on the presence of particularly vulnerable, keystone, or charismatic species; the presence of large numbers (or proportions) of endemic species; and the presence of 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; L. Schejter et al., 2016). The benthic community is featured by a 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 m² (Commission for the Conservation of Antarctic Marine Living Resources, 2009). Also, it provides habitat to several small-sized species (López-Gappa et al., 2018; L. Schejter & Bremec, 2019; Sirito, 2019), and has an important role in the life history of fishes as a food source, refuge, or nursery area (Delpiani et al., 2020; García Alonso et al., 2018; Troccoli et al., 2020). The maintenance of this singular community is related to the oceanographic processes, including the circulation of the rich Malvinas (Falkland) current in the area (Guerrero et al., 1999; A. R. Piola & Gordon, 1989) and the upwelling and mixing phenomena (Matano et al., 2019). The input of nutrients coming from

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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 for the area (APN, 2022).

Recently, the identification of the most influential species has become a crucial task for conservation purposes in local and regional contexts to maintain ecosystem integrity and the supply of ecosystem services for the southwestern South Atlantic Ocean (Bergagna et al., 2020; Franco et al., 2020; Riccialdelli et al., 2020). In this regard, 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 is 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 than other subAntarctic areas, like the Atlantic coast of 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 characterised by an unexpected complexity 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 (APN, 2022; Guinder et al., 2020; L. Schejter et al., 2016, 2020), there is a need for a better understanding of species interactions’ complexity and structure. This aspect can be tackled by analysing one of the most-frequent relationships occurring 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, which represents 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 respond to environmental/anthropogenic changes (Cordone et al., 2018; Funes et al., 2022; Kortsch et al., 2015; Marina et al., 2023). Here it is worth mentioning that anthropogenic threats have been recently reported for the MPA N-BB region (Cossi et al., 2021; Fioramonti et al., 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 network framework.

2. Methodology

2.1. Study area

The MPAs Namuncurá - Banco Burdwood I and II, created by National Laws 26875 and 27490, comprise a shallow submarine plateau called Burdwood Bank (BB) and a deep slope that reaches 4000 m in depth, respectively (APN, 2023). They are located 150 km east of Isla de los Estados and 200 km south from Malvinas/Falkland Islands (Figure 1). The MPA Namuncurá - Banco Burdwood I comprises nearly 34,000 km² circumscribed by the 200 m isobath, between 54°–55°S and 56°–62°W, 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 8°C overall (Acha et al., 2004; Guerrero et al., 1999; A. 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; A. R. Piola & Gordon, 1989; Reta, 2014). Such deep slope form the basis of the MPA Namuncurá - Banco Burdwood II that protects about 32,000 km². Intense upwelling and mixing occur over it, entraining deep nutrient rich waters into the photic layer (Matano et al., 2019; A. 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 Namuncurá - Banco Burdwood I and II (references in APN, 2022), a joint management plan was recently proposed (APN, 2022). Three categories were defined according to the authorized activities: 1) Marine National Reserve (MNR), an area with the objective of conserving marine

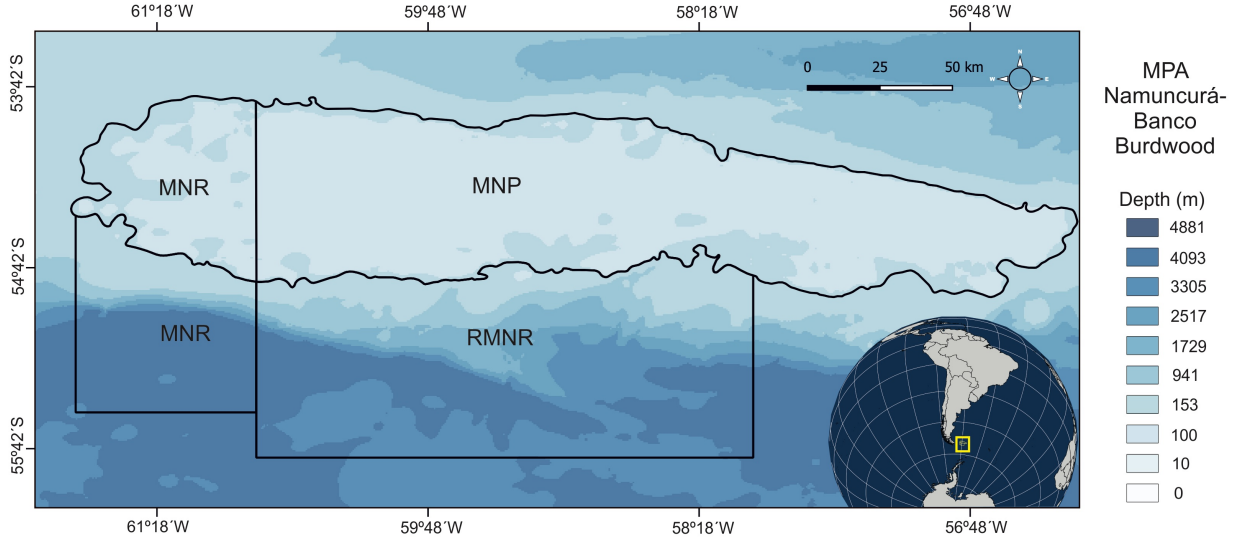


Figure 1: Map of the Marine Protected Areas Namuncurá - Banco Burdwood I (MNR and MNP, northern section) and II (MNR and SMNR, southern section). Acronyms indicate categories according to the management plan: MNR - Marine National Reserve, MNP - Marine National Park and RMNR - Restricted Marine National Reserve.

biodiversity, landscape quality and large-scale ecological processes, allowing scientific, educational, recreational uses and the sustainable use of one or more of its natural resources; 2) Marine National Park, an area with the objective of conserving marine biodiversity, landscape quality and large-scale ecological processes (MNP); and 3) Restricted Marine National Reserve (RMNR), an area of maximum permanent or temporary protection with the objective to preserve marine biodiversity and ecological processes in the long term, minimizing anthropogenic impact, and allowing scientific research and monitoring, as well as control and surveillance activities. Figure 1 shows the geographic location of these categories within MPAs Namuncurá - Banco Burdwood I and II.

2.2. Network construction

In order to build the network of predator-prey interactions we reviewed more than 150 references considering published articles, databases and doctoral theses. 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 expertise of the authors 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 preserves food web functional properties (Gauzens et al., 2013). Details about this can be found in Supplementary Material (Table S2).

With the gathered trophic data we constructed an interaction 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 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 Namuncurá - Banco Burdwood network of trophic interactions, hereafter 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 network of trophic interactions 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 properties of interest: characteristic path length (CPL) and clustering coefficient (CC). The CPL is defined as 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:

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

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-neighbor nodes of node i and the maximal possible number of such interactions (Newman, 2003). With the aim of testing whether the food web presented the small-world pattern, we compared the empirical values of CPL and CC with those resulted from 1000 randomly generated networks with the same size (S) and number of interactions (L), following the method proposed by Marina et al. (2018).

Also, we estimated the (7) degree distributions for the food web, for prey and predators, and for each functional group (e.g., Amphipoda, Ascidiacea, Bivalvia, Fish, Marine mammals, Sea birds, etc.). 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 refers to the fact that food webs tend to naturally organize in non-random, modular patterns (Grilli et al., 2016). Species can play different roles in this respect, according to the pattern of interactions they have 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 a general 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
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

Name	Definition	Implications	Reference
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
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 - Banco Burdwood food web consisted of 1778 predator-prey interactions and 379 species, where 93% of them were defined at the species taxonomical level (Figure 2, Table S2). The food web presented a link density of 4.69, meaning the average number of interactions per species, 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 was higher than the random networks (Table 2).

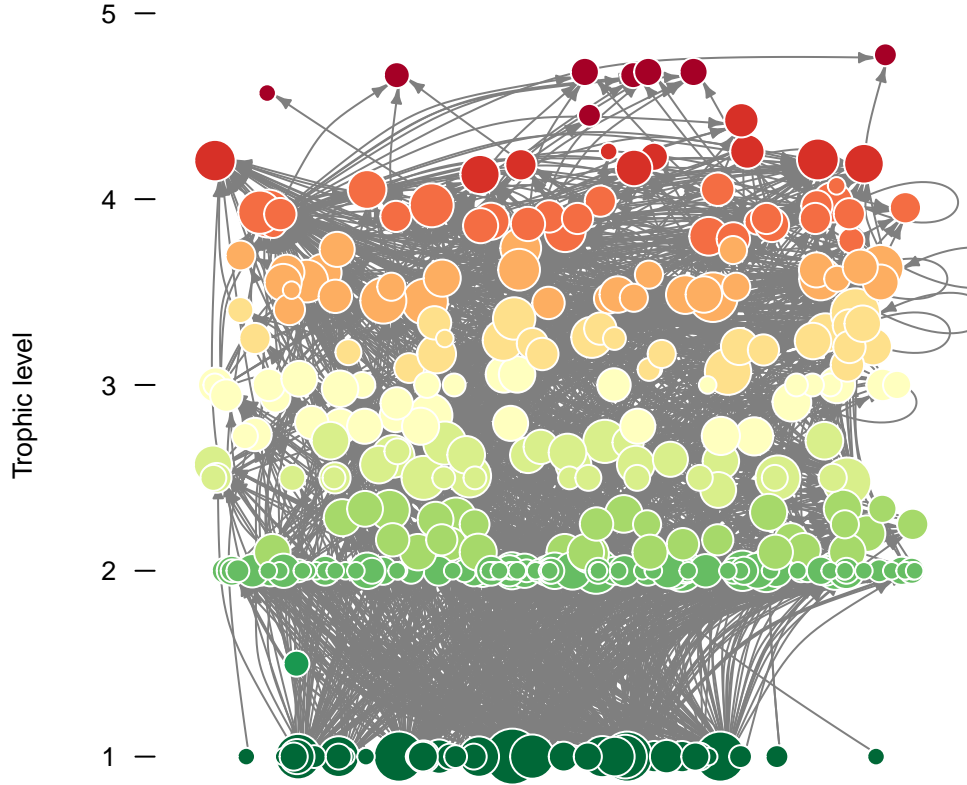


Figure 2: Graph of the food web for the MPA Namuncurá - Banco Burdwood. Circles represent species and arrows trophic interactions. Circle diameter is relative to the number of interactions. Colour gradient indicate the trophic level.

Table 2: Network-level properties of the MPA Namuncurá - Banco Burdwood 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
379	1778	4.69	0.01	0.48	2.99	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 the majority of them (Figure 3A). The distribution of prey among predators showed that most of the consumers fed on a low number of prey whereas few of them had multiple preys (Figure 3B). These were the top-five predators in number of prey: *Patagonotothen guntheri* (Notothenioid fish, 52 prey), *Patagonotothen ramsayi* (Notothenioid fish, 50 prey), *Dissostichus eleginoides* (Notothenioid fish, 30 prey), *Bathyraxa brachyurops* (Chondrichthyan, 30 prey), and *Bathyraxa griseocauda* (Chondrichthyan, 28 prey). Following the same distribution pattern, few prey presented multiple predators (Figure 3C). These were the top-five prey in number of predators: Detritus (Non-living, 153 predators), the three categories of Diatoms considered (benthic, centric and pennate, 72 predators on average), and species of the genus *Euphausia* (Zooplankton, 46 predators). Finally, taking into account the interactions within each functional group, again the majority of the interactions were concentrated in few species (Figure 3D). The most evident species were: *Themisto gaudichaudii* (Amphipoda), *Zygochlamys patagonica* (Bivalvia), *Aspidostoma giganteum* (Bryozoa), *Munida gregaria* (Decapoda), *Patagonotothen ramsayi* and *Patagonotothen guntheri* (benthic-pelagic fish), *Psychrolutes marmoratus* (demersal fish), and species of *Euphausia* (Zooplankton). Overall, there is an evident asymmetry in the distribution of interactions among species at different levels in the MPA Namuncurá - Banco Burdwood food web.

A list of the distribution of interactions per species is presented in Supplementary Material (Table S3).

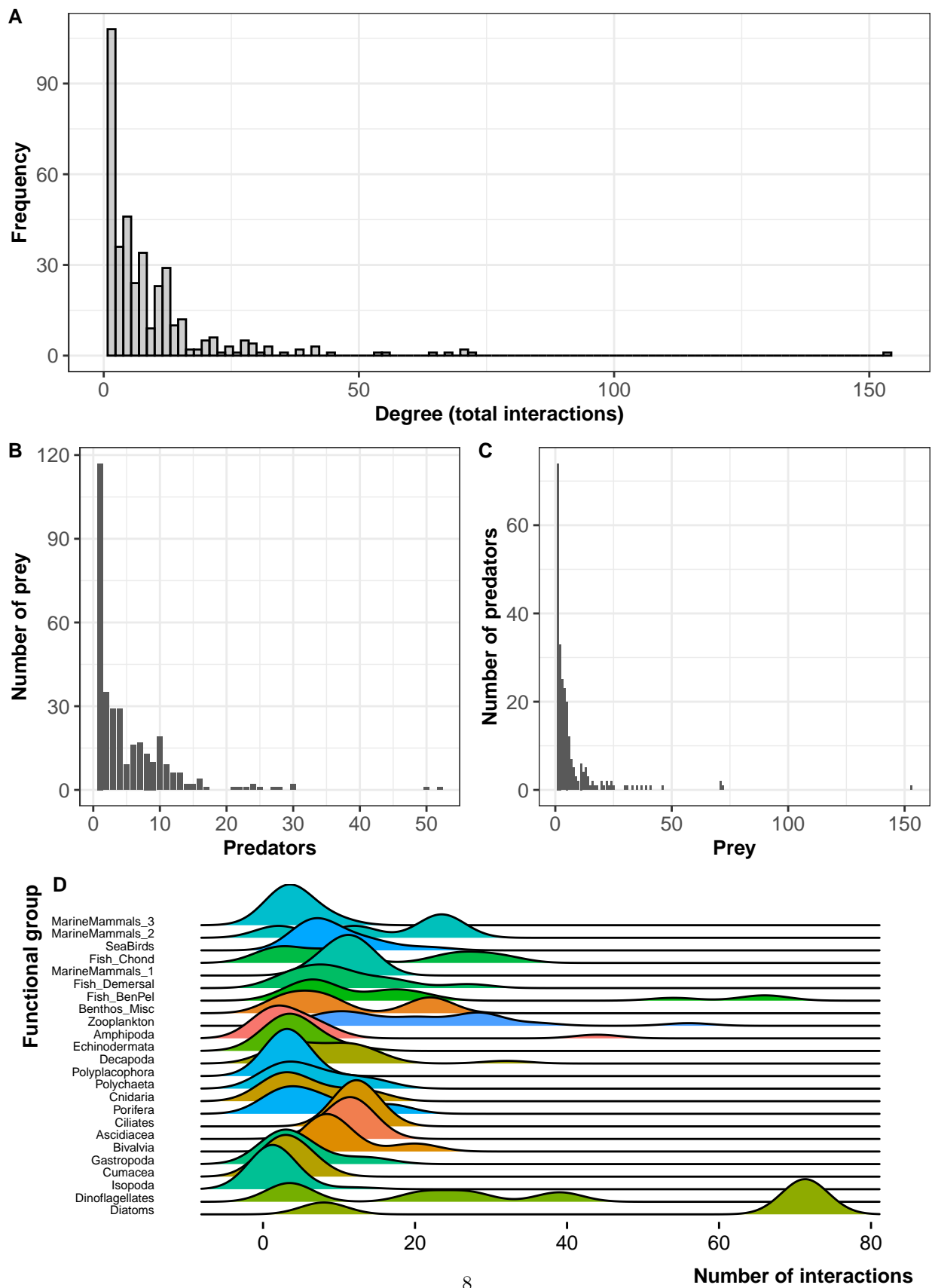


Figure 3: Degree distributions for the (A) food web, for (B) prey among predators, (C) predators among prey, and (D) for each functional group. Groups are vertically ordered by increasing trophic level; groups with less than 3 species were not plotted (e.g., pelagic fish).

3.2. Species-level properties

The majority of the species of the food web were consumers, 336 out of 379; the rest were primary producers, such as diatoms (phytoplankton), and non-living food sources like detritus and necromass.

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 high-trophic level species with low values of trophic similarity: *Bathyrāja macloviana* and *Squalus acanthias* (Chondrichthyans), *Diplopteraster clarki* and *Pteraster sp* (echinoderms), *Phalacrocorax atriceps* and *Eudyptes chrysocome* (sea birds), and *Lagenorhynchus cruciger* and *Mesoplodon bowdoini* (marine mammals) (Table S3).

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

It is noteworthy that the highest values of betweenness were shown by species of mid-TLs (3-4), 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*, *Dissostichus eleginoides*, *Salilota australis* (fishes), *Doryteuthis gahi* (Cephalopoda), and *Patagonotothen guntheri* (Notothenioid fish) (Table S3).

Taking into account the topological role, 'module specialist' species were the most frequent and presented a wide TL range (1 - 4.77); 'module hub' was constrained to mid-TL species (2.48 - 3.92); 'module connector' from low to mid-TLs (1 - 3.86); and 'network connector', the least frequent, had all of its species in $TL = 1$, except for one with $TL = 3.47$ (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: 40 species (5 network connectors + 35 module connectors) from 20 different functional groups with a TL range = 1 - 3.86. The following were the 5 species with a network connector role: Detritus, Diatoms (benthic, centric and pennate), and *Patagonotothen ramsayi*. The 35 species with a module connector role represent these functional groups: Amphipoda, Bivalvia, Brachiopoda, Bryozoa, Cnidaria, Cumacea, Decapoda, Detritus, Diatoms, Dinoflagellates, Echinodermata, Fish (benthic-pelagic, demersal, chondrichthyans), Foraminifera, Polychaeta, Porifera, Pycnogonida, Sea birds, 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 - Banco Burdwood ecosystem

The food web of the MPA Namuncurá - Banco Burdwood 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 a marine protected area worldwide. 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/or 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 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 robustness. In this sense, empirical analyses support the notion that highly-connected ecological networks are robust against

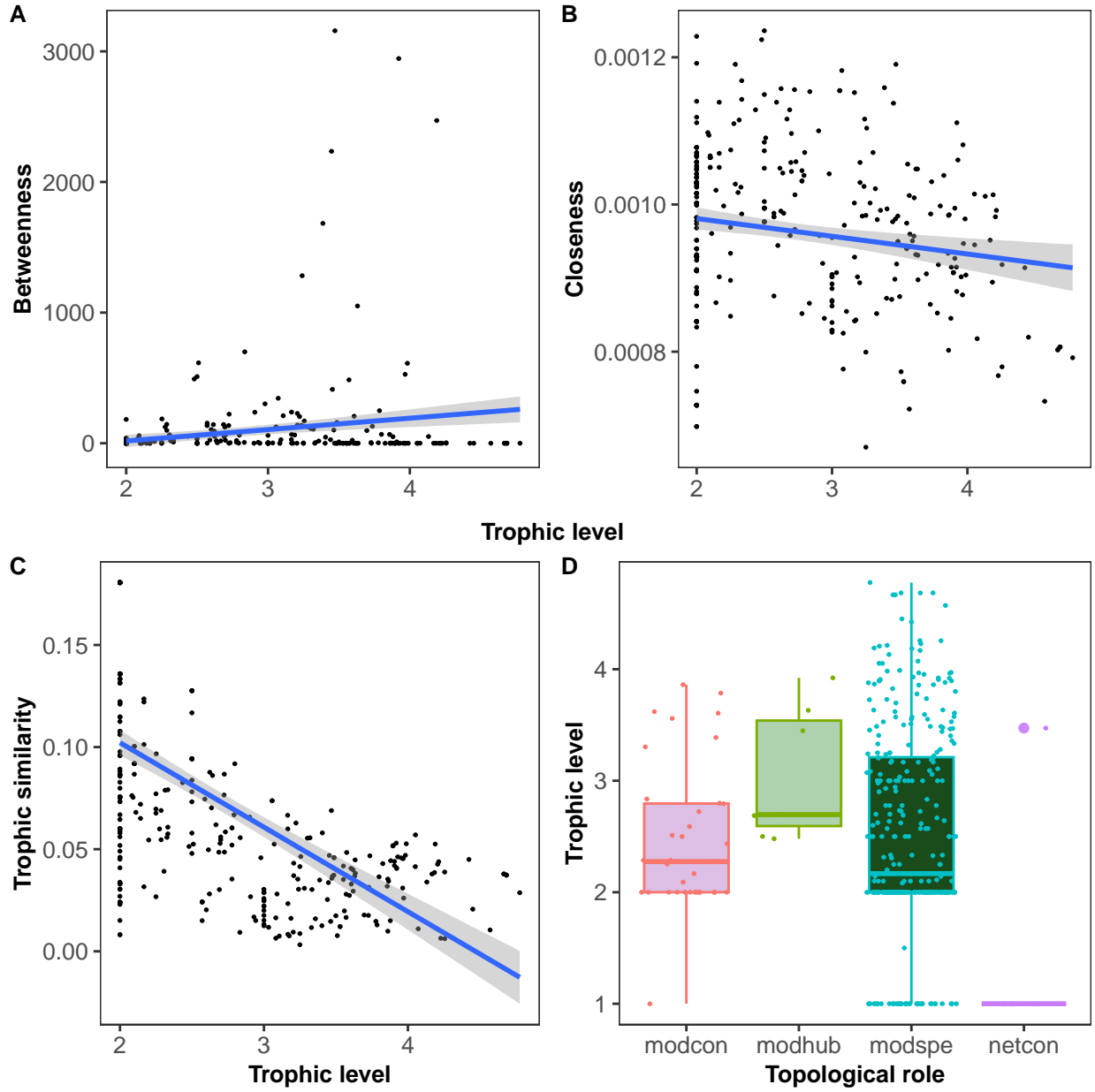


Figure 4: Species-level properties by trophic level: (A) betweenness, (B) closeness, (C) trophic similarity, and (D) topological role. Each point represents a species. Linear regressions for betweenness ($y = 72.48x - 111.98$, $R^2 = 0.04$, $p\text{-value} < 3.38e-05$), closeness ($y = 5.78e-06x - 9.37e-04$, $R^2 = -0.0005$, $p\text{-value} = 0.37$) and trophic similarity ($y = -0.01x - 0.11$, $R^2 = 0.07$, $p\text{-value} = 6.76e-08$). Note that for A, B and C panels only species with TLs equal or greater than 2 were considered.

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 - Banco Burdwood (0.01) is one of the lowest reported so far for these regions; five times lower than that of Beagle Channel, an adjacent area (Rodríguez et al., 2022).

The degree distribution or the distribution of number of interactions per species is the core for 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 is a pattern that we have 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 intentional attacks: 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 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., 2018). However, the food web of the MPA N-BB does display a small-world pattern, characterizing a network with short path length and high clustering coefficient. Consequences of the small-world pattern in food webs are 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 and, at the same time, a more potentially adaptive dynamics in 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 between them (Heer et al., 2020; Kortsch et al., 2019). Overall, a small-world topology provides ecological networks with a 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 primary loss of species (Borrvall et al., 2000). This is based in the fact that omnivores are species able to adapt faster and at a wider 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 on 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).

To resume, the food web of the MPA Namuncurá - Banco Burdwood presents a combination of network properties that make it unique in terms of network resolution, complexity, and structural pattern. All this suggest that the ecosystem might be fragile to external perturbations targeting high connected species. However, structural properties might provide resilience and resistance with the final outcome of a rearrange structure maintaining their functions.

4.2. Dominant consumers and food sources

The degree distribution allows to identify 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 the majority of the consumers in the food web of the MPA N-BB has a narrow diet or are specialists, while few present a broad diet. The most evident generalist species are *Patagonotothen guntheri*, *P. ramsayi*, *Dissostichus eleginoides*, *Bathyrāja brachyurops*, and *B. griseocauda*, 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 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 Arctic regions (Arkhipkin & Laptikhovsky, 2013; Kortsch et al., 2019). The importance of these particular generalist species also arises since they feed on 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, few 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 (L. Schejter et al., 2016). 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 (Raya Rey, 2022; Ricciardelli, 2022).

4.3. Species' role related to their trophic level

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

Closeness and betweenness are defined as "meso-scale" 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 others 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 notothen *Patagonotothen guntheri*, and the Patagonian longfin squid *Doryteuthis gahi* should be considered as relevant energy transfers for 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 (Ricciardelli et al., 2020).

Ecosystems with a pronounced 'wasp-waist' structure are suggested to present a high trophic redundancy, since a large proportion of species would show similar trophic habits (Cury et al., 2000). The significant negative relationship we found between trophic similarity and trophic level enhances the hypothesis of functional redundancy at low and mid-TL species compared to higher TL species for the MPA N-BB food web (Ricciardelli et al., 2020). At the same time, our results highlight the uniqueness in terms of trophic role for high-TL predators. Here, not only the expected pelagic animals such as marine mammals and sea birds arise as relevant, but also benthic vertebrate (chondrichthyans *Bathyraja macloviana* and *Squalus acanthias*) and invertebrate species (echinoderms *Diploptaster 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.

Species' role can be also assessed in a module-based context, 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). 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 (Ricciardelli et al., 2020). But most importantly, our results broadens 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 it is the diversity of species (benthic and pelagic) what maintains the connectivity of the food web, therefore contributing to the trophic structure and ecosystem’s stability.

5. Conclusion

We compiled information on the species and trophic diversity of the Marine Protected Area Namuncurá - Banco Burdwood, generating an unprecedented well-resolved network of trophic interactions for a subAntarctic ecosystem. Particular properties at the network level might reflect ecosystem’s vulnerability to perturbations of highly-connected species, with a rearrange structure maintaining their functions due to its potential resilience and resistance.

We identified several species as important in terms of different aspects of trophic structure and functioning, and response to perturbations (i.e. environmental/anthropogenic changes). On one hand, we suggest that generalist species, mostly fishes, play a crucial role in the ecosystem’s benthic-pelagic coupling process. At the same time, we propose that other species rather than the longtail southern cod *Patagonotothen ramsayi* and the Fuegian sprat *Sprattus fuegensis* should be considered as relevant energy transfers for the ecosystem. Finally, we argue that it is the diversity of species, representing the benthic and pelagic habitats, what maintains the connectivity of the food web against perturbations, therefore contributing to the structure and stability of the ecosystem.

6. Acknowledgements

We are indebted to all those experts of the working group ‘Banco Burdwood / Área Protegida Namuncurá’ who humbly provided their knowledge to enhance the quality of the present research. 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. XX of the MPA Namuncurá (Law 26875).

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