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

Tomás I. Marina[a], Irene R. Schloss[a,b], Luciana Riccialdelli[a]

[a] *Centro Austral de Investigaciones Cientificas (CADIC-CONICET) Argentina*
[b] *Instituto Antartico Argentino (IAA) Argentina*

Abstract

The abstract goes here.

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

1. Introduction

Introduction to MPAs and MPA N-BB

Ecological importance of MPA N-BB to the region

Trophic ecology & keystone spp knowledge of B Burdwood

Why using a network approach

In the present work we present the first, detailed analysis of the food web for the MPA Namuncurá - Banco Burdwood 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 describe the species' role in such network framework.

2. Methodology

2.1. Study area

The MPA Namuncurá - Banco Burdwood is a shallow submarine plateau called Burdwood Bank (BB) located 150 km east of Isla de los Estados and 200 km south from Malvinas/Falkland Islands (Figure 1). It 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. The BB is surrounded by steep flanks of more than 3000 m depth through which strong currents circulate (Matano, Palma, & Combes, 2019; A. R. Piola & Gordon, 1989; Reta, 2014). 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, Baldoni, & Benavides, 1999; Matano et al., 2019). Physical features in the MPAN-BB are fairly stable, with salinity averaging 34 all year round and temperature ranging between 4 and 8ºC overall (Acha, Mianzan, Guerrero, Favero, & Bava, 2004; Guerrero et al., 1999; A. Piola & Falabella, 2009).

*Corresponding author
Email address: `tomasimarina@gmail.com` (Tomás I. Marina[a])

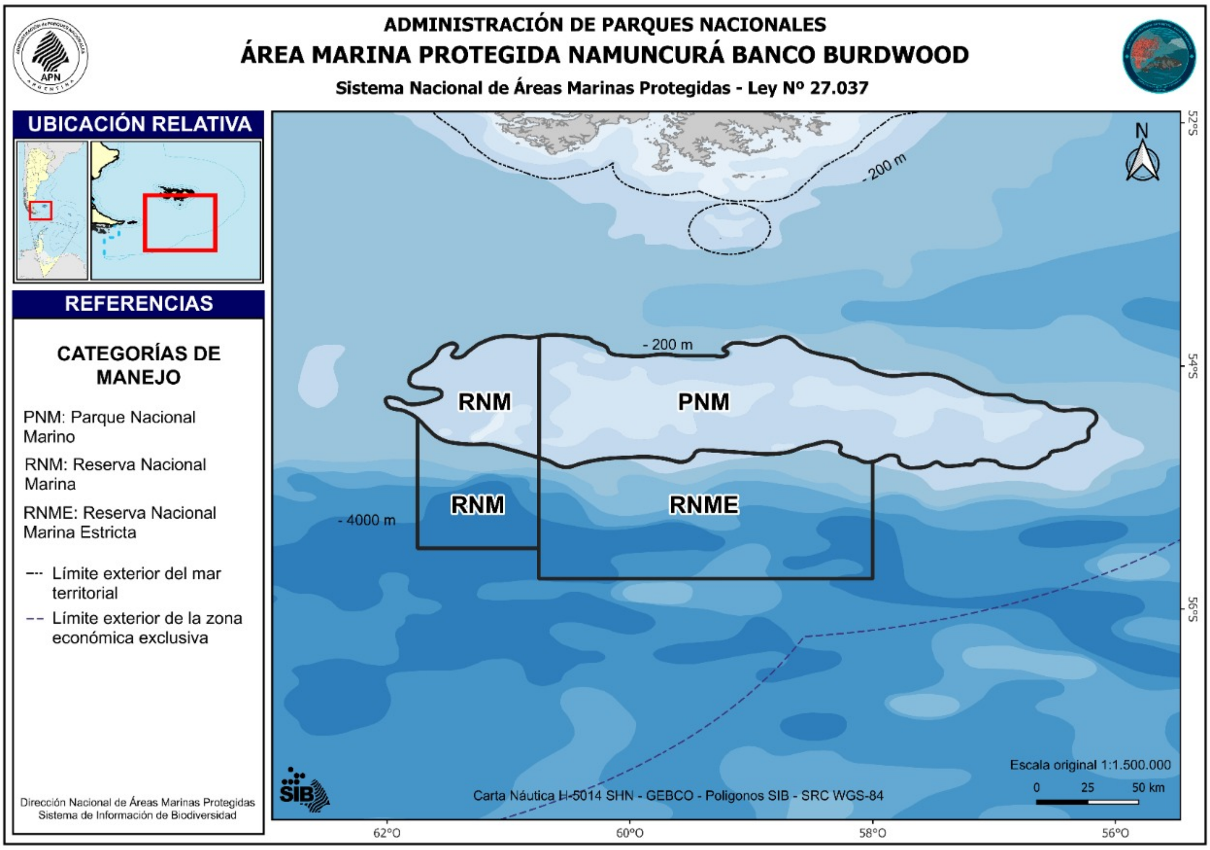

Figure 1: Map of the Marine Protected Area Namuncurá - Banco Burdwood. Taken from https://www.argentina.gob.ar/parquesnacionales/areasmarinas/namuncura-burdwood.

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 of the MPA Namuncurá-Banco Burdwood ecosystem. 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 MPA Namuncurá-Banco Burdwood, we followed the concept of trophic species, here defined as aggregated groups of taxa. In most cases we followed this when data on specific biological species were not available, but for some cases we collapsed species when taxa shared the same set of predators and prey (trophic similarity criteria). 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: 1) network, considering species and interactions of the whole network; and 2) species, considering interactions and species related to a particular species. The network-level analysis aims to characterize 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) shortest path length SPL. 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.) (Table 1). 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). We also studied the relationship between species trophic level and the other species properties by performing linear regression analyses. Thus, we considered the IS as the dependent variable and the given unweighted property 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 mean IS distribution with the species habitat. These 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.	It measures the probability of interactions; it 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
Shortest path length	Average shortest path length between all pairs of species.	A short path length imply a rapid spread of an impact (e.g. invasion, population fluctuation, local extinction) throughout the food web.	Watts & Strogatz 1998
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. Species with the same role are expected to have similar topological properties.	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, feeding on sources at different trophic levels. The food web showed a path length of 2.99, which implies that nearly three interactions are needed to connect any pair of species of the network (Table 1).

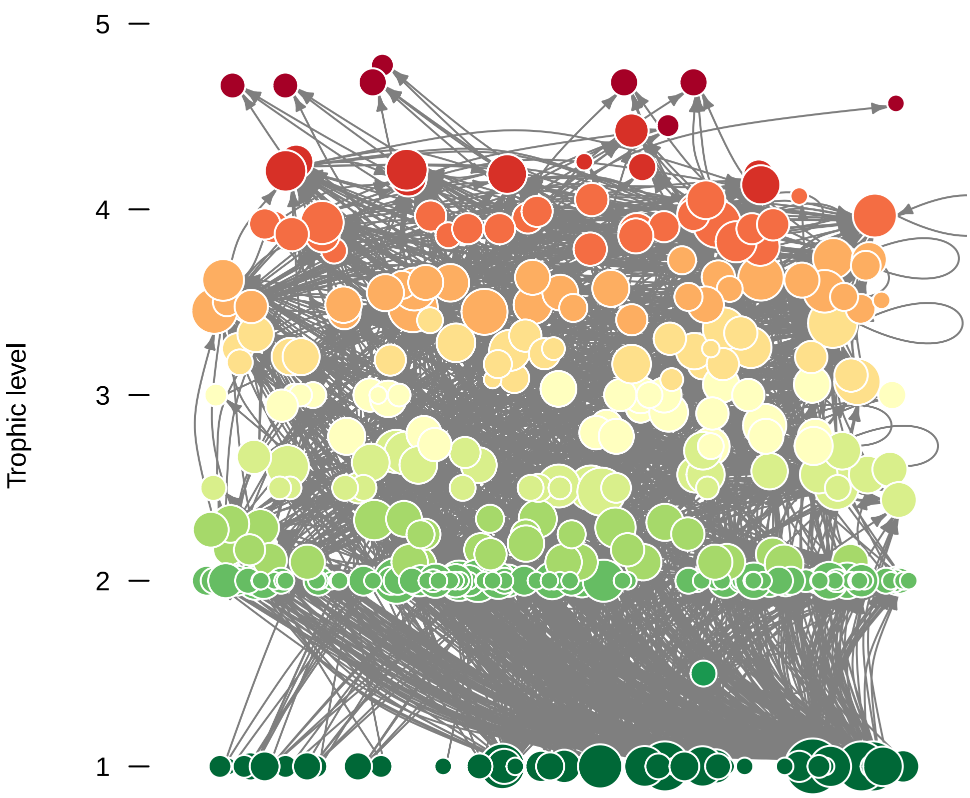

Figure 2: Graph of the food web for the MPA Namuncurá - Banco Burdwood. Circles represent species and arrows trophic interactions. Circle diameter is relative to the number of interactions. Colour gradient indicate the trophic level.

Table 2: Network-level properties of the MPA Namuncurá - Banco Burdwood food web. See table 1 for definitions and ecological relevance.

Species	Interactions	Density	Connectance	Omnivory	Path length
379	1778	4.69	0.01	0.48	2.99

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), *Bathyraja brachyurops* (Chondrichthyan, 30 prey), and *Bathyraja 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* (bentho-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).

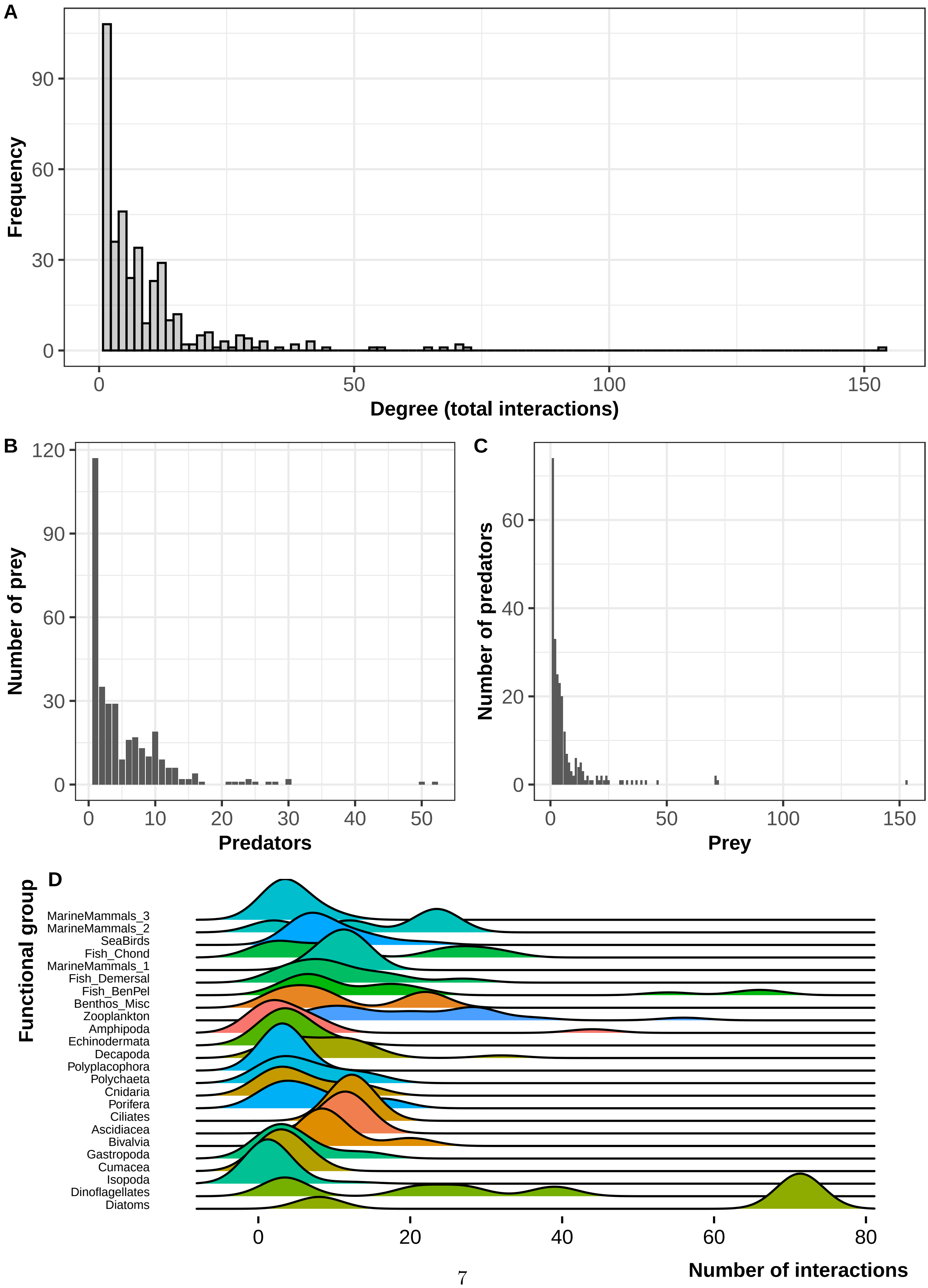

Figure 3: Degree distributions for the (A) food web, for (B) prey among predators, (C) predators among prey, and (D) for each functional group. Groups are vertically ordered by increasing trophic level; groups with less than 3 species were not plotted (e.g. pelagic fish).

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). In this regard, 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's noteworthy to highlight high-trophic level species with low values of trophic similarity: *Bathyraja 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's 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). These were 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's important to highlight species of 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.

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

4. Discussion

4.1. The MPA Namuncurá - Banco Burdwood food web

- The MPA Namuncurá - Banco Burdwood food web is one of the most highly-resolved networks of trophic interactions described for subpolar and polar regions. Compare network-level properties with other subpolar and polar food webs.

- The food web shows an asymmetry in the distribution of interactions at several levels: food web, functional group, prey and predators. In all of them interactions are concentrated in a few species. On one hand, this asymmetry indicates that most consumers have a narrow diet, and few present flexible diets (*Patagonotothen guntheri*, *P. ramsayi*, *Dissostichus eleginoides*, *Bathyraja brachyurops*, *B. griseocauda*). On the other hand few prey are consumed by many predators, meaning that there are dominant food sources from which most consumers depend on: detritus, diatoms (benthic, centric, pennate), and species of *Euphausia*.

4.2. Species' role

Our results state that certain species play particular roles in the structure of the food web.

- Betweenness. Species at mid-trophic levels (3-4) lie in more shortest paths between species than any other species: 'bridge' role. Implications for spread of perturbations like mercury (Fioramonti, Ribeiro Guevara, Becker, & Riccialdelli, 2022), microplastics (Cossi et al., 2021).

- Closeness. Low-trophic level species are relatively closer to other species in the food web. Apart from the most demanded food sources (i.e. detritus), which are logically closer to many species, unexpected consumers arise as important in this regard. Species of the zooplankton community like *Calanus* and *Euphausia* are crucial for the food web functioning, since they can affect others more quickly.

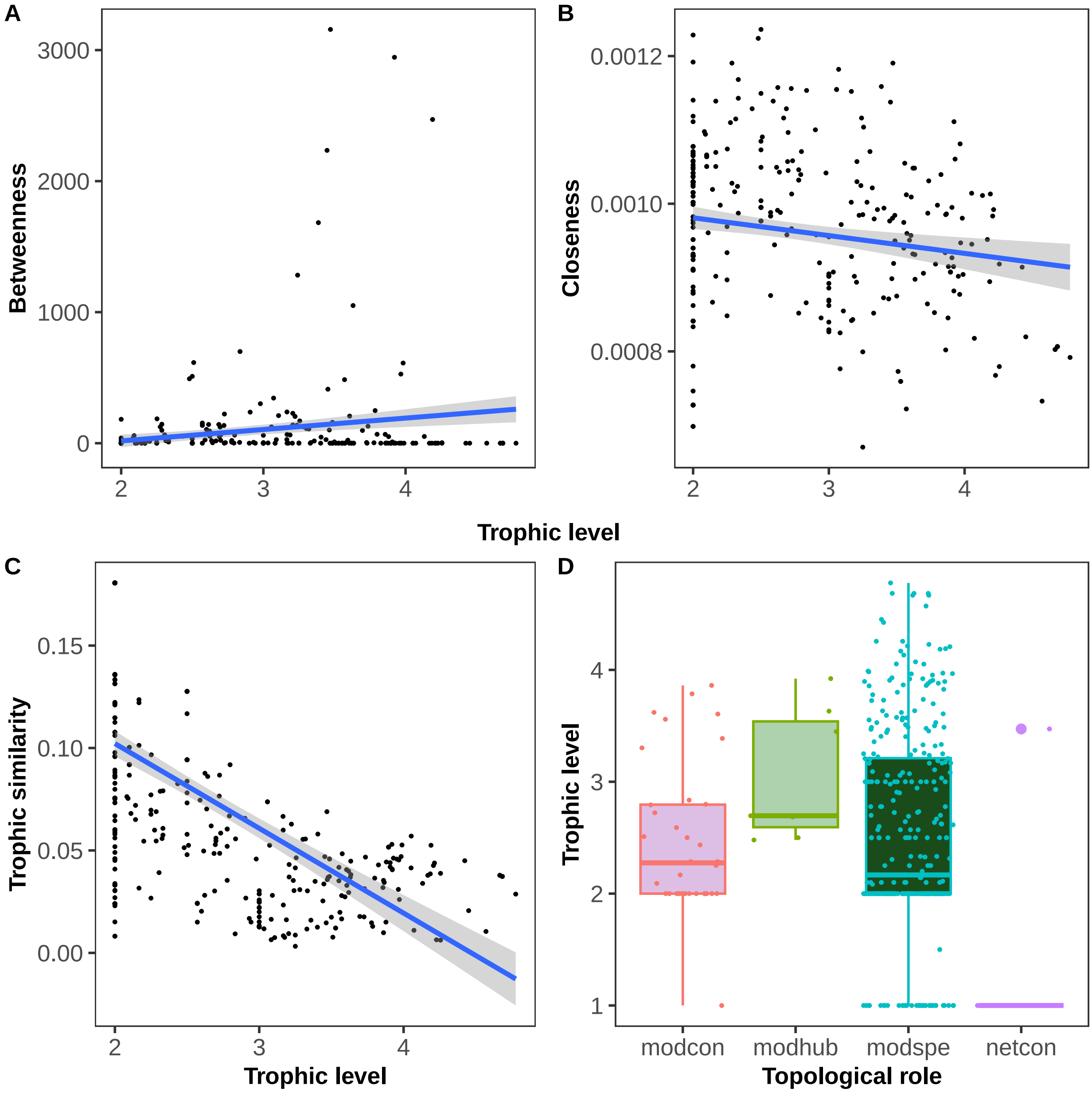

Figure 4: Species-level properties by trophic level: (A) betweenness, (B) closeness, (C) trophic similarity, and (D) topological role. Each point represents a species. Linear regressions for betweenness ($y = 72.48x - 111.98, R^2 = 0.04, p - value < 3.38e-05$), closeness ($y = 5.78e-06x - 9.37e-04, R^2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

- Trophic similarity. Species are more similar at low and mid-trophic levels (2-4). There is a functional redundancy at these levels of the food web. On the other hand, less trophic similarity at high TLs indicate uniqueness in terms of trophic role. This highlights the importance of top predators in the sense that they play a role that cannot be played by any other species.
- Topological role. Low and mid-trophic level species (TL = 1 - 3.86) are responsible for maintaining the connectivity of the food web (network connector and module connector). The functional groups represented are: Amphipoda, Bivalvia, Bryozoa, Cnidaria, Cumacea, Decapoda, Detritus, Diatoms, Echinodermata, Fish (bentho-pelagic, demersal, chondrichthyes), Foraminifera, Polychaeta, Porifera, Zooplankton. This shows that the structure of the food web depends on a diversity of species, which at the end comprise the ecosystem's diversity.
- Overall, low and mid-trophic level species arise as crucial in the structure of the MPA Namuncurá - Banco Burdwood food web, since they present the highest betweenness and closeness values, and the most important topological roles. This coincides with a recent study that suggest a wasp-waist trophic structure for the region (Riccialdelli et al., 2020). However, we also suggest that there exists functional redundancy at mid-trophic levels. Furthermore, our study points out species of high-trophic levels due to its uniqueness role.

4.3. Caveats and future perspectives

Caveats:

- Seasonal variation in predators' diet due to food source availability.
- Spatial variation of study area: Banco Burdwood west-east gradient.
- The lack of density or biomass data might have neglected well-known important species for the structure of the food web: *Sprattus fuegensis*.

Perspectives:

- Estimation of interaction strength to gain insights into food web stability and response to anthropogenic and environmental perturbations.
- Simulate perturbations on food web and target species: mercury transfer, microplastic pollution, fisheries.

5. Conclusion

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