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

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25 Abstract: The total area of the world ocean designated under marine protection has increased
26 recently. Most Marine Protected Areas (MPAs) target vulnerable, keystone, charismatic and/
27 or endemic species. In the sub-Antarctic, ocean protection is associated to oceanic islands,
28 except for MPAs Namuncurá - Burdwood Bank I and II (MPA N-BB, ~53º–55ºS and ~56º–
29 62ºW), which are associated to a submarine plateau and its southern adjacent deep slope,
30 respectively. Here, we present the first analysis of the network of predator-prey interactions
31 for the MPA N-BB. We applied a network approach to characterise the complexity and
32 structure of the food web, and identify the species' role in such a framework. The MPA N-BB
33 food web consisted of 1788 interactions and 379 species, with a connectance of 0.01. Almost
34 half of the consumers were omnivores (0.48), and the network displayed a small-world
35 pattern. These suggest that the ecosystem might be vulnerable to perturbations targeting
36 highly connected species, although other properties might provide resilience and resistance,
37 resulting in a rearranged structure that preserves its original functions. Several species arose
38 as important in terms of different aspects of trophic structure and functioning, and response to
39 perturbations. Generalist species, mainly fishes, play a crucial role in the ecosystem's bentho-
40 pelagic coupling and should be considered as relevant energy transfers for the ecosystem. We
41 argue that the diversity of species, including both the benthic and pelagic habitats, is

42   responsible for securing the connectivity within the food web against perturbations, therefore
43   contributing to the structure and stability of the ecosystem.

44   Keywords: Food web; Complexity; Structure; Burdwood Bank; Southwest Atlantic.

45 1.   INTRODUCTION

46 The evidence of benefits provided by Marine Protected Areas (MPAs) as well as the urgent

47 need for ocean protection have driven an unprecedented increase in the number of MPAs

48 worldwide in recent years (Roberts et al. 2017, Sala et al. 2018). Globally, the total area of

49 the world ocean designated under marine protection adds up to approximately 29,600,000

50 km^2, distributed across nearly 18,444 MPAs and covering 8.16% of the ocean's surface

51 (IUCN 2023), and therefore approaching the 10% goal of the Convention of Biological

52 Diversity (Secretariat of the Convention on Biological Diversity 2004). Despite this progress,

53 recent reports have shown that actual protection has been overestimated because it includes

54 areas that are not yet effectively protected (only declared) as well as areas that allow

55 significant extractive activities (Sala et al. 2018).

56 In the sub-Antarctic region, the level of ocean protection is mainly associated to oceanic

57 islands, such as the South Georgias and South Sandwich, Bouvet, Prince Edward, and

58 Macquarie islands (IUCN 2023). Interestingly, the case of the MPAs Namuncurá - Burdwood

59 Bank I and II (MPA N-BB, ~53º–55ºS ~56º–62ºW), which is the focus of this work, is unique

60 since these MPAs are associated to a submarine plateau and its southern adjacent deep slope

61 region, respectively (Falabella 2017, Schejter et al. 2020). In addition, such MPAs are part of

62 a network of protected areas in the sub-Antarctic area (jointly with MPA Yaganes) that aims

63 to protect this southern region in order to contribute to global ocean health.

64 Many of these MPAs focus on the presence of particularly vulnerable, keystone, or

65 charismatic species, large numbers (or proportions) of endemic species, and/or high

66 biodiversity across taxonomic levels (Hogg et al. 2016). Indeed, the MPA N-BB was created

67 to protect a potentially sensitive and biodiverse benthic habitat that was only barely known

68 (Schejter et al. 2016, Falabella 2017). The benthic community is featured by high biomass of

69 vulnerable and fragile species (mainly Porifera, Bryozoa and Cnidaria) that considered with

70   their environment meet the characteristics of vulnerable marine ecosystems (Schejter &

71   Albano 2021), here defined as sites that present densities of Indicator Taxa of > 10 kg per

72   1200 m^2^ (CCAMLR 2009). Also, the benthic realm provides habitat to several small-sized

73   species (Lopez-Gappa et al. 2018, Martin Sirito 2019, Schejter & Bremec 2019), and has an

74   important role in the life history of fishes as a food source, refuge and nursery area (García

75   Alonso et al 2018, Vazquez et al 2018, Delpiani et al. 2020, Troccoli et al. 2020, Covatti Ale

76   et al. 2022, Fischer et al. 2022, Matusevich et al. 2023). The maintenance of this singular

77   community is related to local and regional oceanographic processes, including the circulation

78   of the rich Malvinas (Falkland) current in the area (Piola & Gordon 1989, Guerrero et al.

79   1999) and the upwelling and mixing phenomena (Matano et al. 2019). The input of nutrients

80   from the Malvinas (Falkland) current also supports a diverse plankton community (Guinder et

81   al. 2020).

82   Overall, 811 benthic and plankton species have been identified for the MPA N-BB

83   ecosystem, where 349 were reported for the first time in the area in recent years (APN 2022).

84   Identifying the main species involved in the maintenance of ecosystem services and health as

85   well as for management and conservation is essential. Recently, the structure of the

86   southwestern South Atlantic Ocean has been proposed to be under a 'wasp-waist' control,

87   meaning that the structure and dynamics of the ecosystem are regulated primarily by mid-

88   trophic level species (e.g., fishes, crustaceans) (Padovani et al. 2012, Saporiti et al. 2015,

89   Riccialdelli et al. 2020). In particular, the ecosystem of the MPA N-BB shows a more

90   pronounced 'wasp-waist' structure, meaning a shorter food chain and a greater trophic overlap

91   and redundancy, than other sub-Antarctic areas, such as the continental shelf off Tierra del

92   Fuego. The Fuegian sprat *Sprattus fuegensis* and longtail southern cod *Patagonotothen*

93   *ramsayi* are considered the most plausible 'wasp-waist' species (Riccialdelli et al. 2020).

94   High-latitude marine ecosystems, such as the MPA N-BB, are complex systems in terms of

95   biodiversity and ecological interactions (Day et al. 2013, Kortsch et al. 2019, Cordone et al.

96   2020, Trathan et al. 2021). Although there is a robust knowledge about the complexity

97   considering the richness of the benthic and plankton communities in the MPA N-BB

98   ecosystem (Schejter et al. 2016, Guinder et al. 2020, Schejter et al. 2020, APN 2022), a better

99   understanding of species interactions' complexity and structure is needed.

100   This aspect can be tackled by analysing one of the most frequent relationships between

101   species: the predator-prey interaction (Bascompte2009). The sum of predator-prey or trophic

102   interactions of a particular region is referred to as a food web, representing the roadmap for

103   matter and energy flow in an ecosystem.

104   In recent years, network approaches have been successfully applied to study complex high-

105   latitude marine ecosystems, improving our knowledge on structure, functioning, and response

106   to environmental/anthropogenic changes (Kortsch et al. 2015, Cordone et al. 2018, Funes et

107   al. 2022, Marina et al. 2023). Among anthropogenic threats, it is worth mentioning that

108   contaminants like mercury and microplastics have been recently reported as important threats

109   to the MPA N-BB region (Cossi et al. 2021, Di Mauro et al. 2022, Fioramonti et al. 2022);

110   also fishing vessels are allowed to operate in the western section of the MPA N-BB (i.e.

111   Marine National Reserve category), altering the stocks of commercially important fish

112   species (Martinez et al. 2021, APN 2022). Moreover, there is a potential hazard related to the

113   effects of offshore activities (exploration and exploitation) to the west of the MPA N-BB

114   (APN 2022).

115   In the present work, we present the first detailed analysis of the network of predator-prey

116   interactions, hereafter food web, for the MPA N-BB ecosystem. For this, we applied a

117   network approach to a highly resolved food web. The objective was twofold: characterise the

118   food web in terms of complexity and structure, and identify the species' role in the network.

119 2.   MATERIALS & METHODS

120 ## 2.1. STUDY AREA

121 The MPAs Namuncurá - Burdwood Bank I and II, created by National Laws 26.875 in 2013

122 and 27.490 in 2017, comprise a shallow submarine plateau called Burdwood Bank (BB) and a

123 deep slope that reaches 4000 m in depth, N-BB I and N-BB II, respectively (Tombesi et al.

124 2020, APN 2022) (Figure 1). They are located 150 km east of Isla de los Estados and 200 km

125 south of Malvinas/Falkland Islands.

126 The MPA N-BB I comprises nearly 28,900 km^2 circumscribed by the 200 m isobath,

127 between ~54º–55ºS and ~56º–62ºW, with a slight slope extended nearly 370 km east–west.

128 Physical features in the BB are fairly stable, with salinity averaging 34 all year round and

129 temperature ranging between 4 and 8ºC (Guerrero et al. 1999, Acha et al. 2004, Piola &

130 Falabella 2009). The BB is surrounded by steep flanks of up to 4000 m depth through which

131 strong currents circulate (Piola & Gordon 1989, Reta 2014, Matano et al. 2019). The N-BB II

132 includes such a deep slope, protecting about 32,000 km^2 (~55º-56ºS, ~58º-62ºW). Intense

133 upwelling and mixing occur in relation with the slope, entraining deep nutrient-rich waters

134 into the photic layer (Piola & Falabella 2009, Matano et al. 2019) and resulting in a fairly

135 homogeneous water column both spatially and temporally (Glorioso & Flather 1995,

136 Guerrero et al. 1999, Matano et al. 2019).

137 Given the evidence collected during several research cruises about the oceanographic and

138 ecological processes connecting MPAs N-BB I and II (references in APN 2022), a joint

139 management plan was recently proposed (APN 2022). This is why the study area of the

140 present work includes both MPAs.

141 ## 2.2. NETWORK CONSTRUCTION

142 In order to build the network of predator-prey interactions, we reviewed more than 170

143 references considering published articles, Ph.D. theses, public databases, and reports

144 belonging to 16 research cruises conducted in the MPAs N-BB I and II during 2014-2019. It

145   is noteworthy that the sampling effort was greater in the MPA N-BB I. Furthermore, we took

146   into account personal communications from experts belonging to the working group of the

147   study area (https://www.pampazul.gob.ar/tag/banco-burdwood/). The diversity of the authors'

148   expertise contributing to the present study was a key factor in enhancing the quality of the

149   network, and inherently improved the network representation. A list of the references used to

150   build the network is presented in Supplementary Material (Table S1).

151   Due to a lack of trophic data resolution for some species inhabiting the study area, we

152   followed the concept of trophic species, here defined as follows: taxa collapsed into a single

153   node in the network. In most cases, we followed this concept when specific data on species,

154   in the taxonomic sense, were not available. In some cases, we collapsed species when taxa

155   shared the same set of predators and prey (trophic similarity, Martinez 1991), one of the

156   aggregation methods that better preserve food web functional properties (Gauzens et al.

157   2013). In addition, for endemic species (e.g. bryozoan *Burdwoodipora paguricola*) and other

158   species with no trophic studies so far, we inferred their feeding interactions applying a

159   conservative approach that assumes that the set of prey and predators are at some point

160   preserved in time. In those cases we gathered information from upper taxonomic levels (i.e.

161   Genus, Family, Order, Class, Phylum) as a good proxy variable (Morales-Castilla et al. 2015,

162   Pomeranz et al. 2019). Details about this can be found in Supplementary Material (Table S2).

163   Furthermore, we considered non-living food sources, such as detritus and necromass, as prey

164   species in the food web context.

165   With the gathered trophic data, we constructed a matrix of pairwise interactions; a value of 1

166   or 0 was assigned to each element a_{ij} of the matrix depending on whether the j-species preyed

167   or not on the i-species. Then we transformed such a matrix into an oriented graph with L

168   trophic interactions between S nodes or species. The orientation or direction of the graph

169   follows the flow of energy and matter in the network, from prey to predator.

170   2.3. NETWORK ANALYSIS

171   We analysed the MPA N-BB network of trophic interactions, or food web, at two levels: A)

172   network, considering species and interactions of the whole network; and B) species,

173   considering interactions and species related to a particular species (Table 1).

174   The network-level analysis aims to characterise the food web in terms of complexity and

175   structure. For this, we calculated several network properties commonly used to describe

176   empirical food webs (Pascual & Dunne 2005): (1) number of species S; (2) number of

177   interactions or links L; (3) link density L/S; (4) connectance L/S^2; (5) omnivory Omn; and (6)

178   small-world pattern. In order to explore the small-world phenomenon, we analysed the

179   characteristic path length (CPL) and the clustering coefficient (CC). The CPL is the average

180   shortest path length between all pairs of nodes (Watts & Strogatz 1998). Here, CPL was

181   calculated as the average number of nodes in the shortest path $CPL_{Min}(i,j)$ between all pairs of

182   nodes $S(i,j)$ in a network averaged over $S(S-1)/2$ nodes:

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

183   The CC quantifies the local interconnectedness of the network and it is defined as the fraction

184   of the number of existing links between neighbours of node i among all possible links

185   between these neighbours. In this study, the CC was determined as the average of the

186   individual clustering coefficients CC_i of all the nodes in the network. Individual CC_i were

187   determined as follows:

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

188   where E_i is the effective number of interactions between K_i nearest-neighbour nodes of node i

189   and the maximal possible number of such interactions (Newman 2003).

190   To test whether the food web presented the small-world pattern, we compared the empirical

191   values of *CPL* and *CC* with those resulting from 1000 randomly generated networks with the

192   same size (*S*) and number of interactions (*L*), following the method proposed by Marina et al.

193   2018b.

194   Also, we estimated the (7) degree distributions for the food web, prey and predators, and each

195   functional group (e.g., Amphipoda, Ascidiacea, Bivalvia, fish, marine mammals, seabirds,

196   among others). The prey and predator distributions indicate the frequency of prey among

197   predators, and vice versa; the functional group's degree shows the distribution of interactions

198   within groups.

199   The species-level analysis aims to describe the species' role in the food web. For this, we

200   considered the following properties: betweenness Btw, closeness Cl, trophic similarity TS,

201   topological role TR, and trophic level TL (Table 1). Topological roles refer to the fact that

202   food webs tend to naturally organize in non-random, modular patterns, where modules are

203   defined as a group of species that interact more frequently among themselves than with

204   species that are not members of the module (Guimerà & Nunes Amaral 2005). Species can

205   play different roles in this respect, according to the pattern of interactions within their own

206   module and/or across modules. We computed the topological role for each species, classified

207   as module hub, species with a relatively high number of interactions, but most within its own

208   module; module specialist, species with relatively few interactions and most within its own

209   module; module connector, species with relatively few interactions mainly between modules;

210   and network connector, species with high connectivity between and within modules (Guimerà

211   & Nunes Amaral 2005).

212   We also studied the relationship between species TL and the other species properties by

213   performing linear regression analyses. Thus, we considered the TL as the dependent variable

214   and the given property (i.e. betweenness, closeness, trophic similarity) as the independent

215   variable and obtained the coefficients (slope and intercept) for the linear model. Models were

216   fitted using the least squares approach. We also explored the topological role categories with

217   the species TL. These species-level properties provide an appropriate description of species'

218   role in empirical complex food webs (Cirtwill et al. 2018).

219   All network analyses and graphs were performed in R version 4.2.2 (R Core Team 2022),

220   mainly using 'igraph' (Csardi & Nepusz 2006) and 'multiweb' (Saravia 2022) packages. The

221   source code and data are available at https://github.com/TomasMarina/Banco-Burdwood.

222 3.   RESULTS
223 3.1. NETWORK-LEVEL PROPERTIES

224   In terms of complexity, the MPA Namuncurá - Burdwood Bank food web consisted of 1788

225   predator-prey interactions and 379 species, where 93% of them were defined at the species

226   taxonomical level (Figure 2, Table S2). The food web presented a link density (e.g., the

227   average number of interactions per species) of 4.72, and a connectance of 0.01. Almost half

228   of the consumers were omnivores (0.48), feeding on sources at different trophic levels. The

229   food web displayed a small-world pattern, meaning that the path length was lower and the

230   clustering coefficient higher than the random networks (Table 2).

231   The degree distribution of the food web showed an asymmetric frequency in the number of

232   interactions, where most of the species had a relatively low number of interactions and few

233   species concentrated most of them (Figure 3A). The distribution of prey among predators

234   showed that most consumers fed on a low number of prey whereas few had multiple prey

235   (Figure 3B). The top-five predators in number of prey were: yellowfin notothen

236   *Patagonotothen guntheri* (Notothenioid fish, 50 prey), rock cod *Patagonotothen ramsayi*

237   (Notothenioid fish, 49 prey), broad nose skate *Bathyraja brachyurops* (Chondrichthyan, 33

238   prey), Patagonian toothfish *Dissostichus eleginoides* (Notothenioid fish, 30 prey), and

239   graytail skate *Bathyraja griseocauda* (Chondrichthyan, 28 prey). Following the same

240   distribution pattern, few prey presented multiple predators (Figure 3C). The top-five prey (or

241 food sources) in number of predators were: Detritus (Non-living, 153 predators), the three

242 categories of Diatoms considered (benthic, centric and pennate, 72.5 predators on average),

243 and species of the genus *Euphausia* (Zooplankton, 46 predators). Finally, taking into account

244 the interactions within each functional group, most interactions were concentrated in a few

245 species (Figure 3D). The most evident species were: *Doryteuthis gahi* (Cephalopoda),

246 *Grimothea (=Munida) gregaria* (Decapoda), *P. ramsayi*, *P. guntheri* and *D. eleginoides*

247 (bentho-pelagic fish), *Sprattus fuegensis* and *Micromesistius australis* (pelagic fish), and

248 species of Euphausia and *Themisto gaudichaudii* (Zooplankton). Overall, there is an evident

249 asymmetry in the distribution of interactions among species at different levels in the MPA N-

250 BB food web.

251 A list of the distribution of interactions per species is presented in Supplementary Material

252 (Table S3).

253 3.2. SPECIES-LEVEL PROPERTIES

254 We found different relationships between the species trophic level (TL) and the rest of the

255 analysed species-level properties (Figure 4A-D). The most evident significant relationship

256 was with trophic similarity, i.e. the higher the species' TL, the lower the trophic similarity or

257 the higher the uniqueness in terms of trophic role (Figure 4C). Here it is noteworthy to

258 highlight those high-trophic level species (TL > 3.1) with low values of trophic similarity:

259 *Bathyraja macloviana* and *Squalus acanthias* (Chondrichthyans), *Diplopteraster clarki* and

260 *Pteraster sp.* (echinoderms), *Daption capense* and *Eudyptes chrysocome* (seabirds), Ziphiidae

261 and *Lagenorhynchus cruciger* (marine mammals) (Table S3).

262 We also found a significant negative relationship between TL and closeness, however less

263 evident, meaning that low-TL species are relatively closer to any other species in the food

264 web (Figure 4B). Detritus, species of genera *Calanus* and *Euphausia*, and Foraminifera, all

265 with TL < 3, registered the highest closeness values (Table S3). Notably, species of mid-TLs

266   (3-4.2) showed the highest values of betweenness, meaning that those species participated in

267   the highest number of shortest paths between species (Figure 4A). The following are the

268   species with the highest values (descending order): *P. ramsayi*, *Salilota australis*, *D.*

269   *eleginoides* (fishes)*, D. gahi* (Cephalopoda)*,* and *P. guntheri* (Notothenioid fish) (Table S3).

270   Considering the topological role, 'module specialist' species were the most frequent and

271   presented a wide TL range (1 - 4.78), as well as 'module hub' species (TL = 1 - 3.92); 'module

272   connector' was constrained to mid-TLs (2 - 3.86); and 'network connector', was represented

273   by only one trophic species: detritus (Figure 4D, see Figure S2 for species' topological roles

274   in a food web graph framework). Here it is important to highlight the two latter topological

275   roles because they are responsible for linking modules and maintaining the connectivity of

276   the food web: 42 species (1 network connector + 41 module connectors) from 19 different

277   functional groups with a TL range = 1 - 3.86. The 41 species with a module connector role

278   represented these functional groups: Amphipoda, Bivalvia, Brachiopoda, Bryozoa, Hydrozoa

279   (as 'Cnidaria_benthic'), Copepoda, Cumacea, Decapoda, Echinodermata, fish (bentho-pelagic

280   and demersal Osteichthyes, and Chondrychthyes), Foraminifera, Polychaeta, Porifera,

281   Pycnogonida (as 'Benthos_Misc') and zooplankton (see Supplementary Material Table S3 for

282   the identity of the species).

283   An exhaustive list of the species-level properties is presented in Supplementary Material

284   (Table S3).

285 4.   DISCUSSION
286 4.1. COMPLEXITY AND STRUCTURE OF THE FOOD WEB

287   The food web of the MPA N-BB ecosystem analysed in this study is one of the most highly-

288   resolved networks of trophic interactions ever studied, not only for a high-latitude open-

289   ocean ecosystem but also for any marine protected area worldwide to our knowledge. It is of

290   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 positives) (Martinez 1993, Gauzens et al. 2013).

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. 2018a). In particular, food webs from high-latitude regions tend to exhibit a connectance closer to the minimum (between 0.01 and 0.05) (Santana et al. 2013, Kortsch et al. 2015, Rodríguez et al. 2022). 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 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 be much lower than that of Beagle Channel (0.05), an adjacent coastal area (Rodríguez 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

316 al. 2002a, Montoya & Solé 2003, Stouffer et al. 2005), and has received great attention in

317 complex networks in general (Albert & Barabási 2002, Newman2003). The degree

318 distribution affects the resilience of complex food webs against random failures and pressure

319 on a particular component of the web: food webs showing right-skewed distributions, like the

320 one described in this study, are more vulnerable to the removal of the most connected species

321 or hubs, with the potential of producing secondary extinctions and a catastrophic

322 fragmentation of the network (Albert et al. 2000, Dunne et al. 2002b, Eklöf & Ebenman

323 2006).

324 It is suggested that the small-world pattern, i.e., a network with short path length and high

325 clustering coefficient, is not frequent in complex marine food webs, mainly due to a low

326 clustering coefficient compared to random networks (Dunne et al. 2002c, Marina et al.

327 2018b). However, the food web of the MPA N-BB does display a small-world pattern.

328 Consequences of this could be of great importance in recognizing species evolutionary paths

329 and the vulnerability to perturbations (Montoya & Solé 2002). On the one hand, a short path

330 length implies a rapid spread of an impact (e.g., contaminant, population fluctuation, local

331 extinction) throughout the network but, at the same time, more potentially adaptive dynamics

332 in the face of external perturbations (Montoya & Solé 2002, Williams et al. 2002). On the

333 other hand, a high clustering coefficient indicates the formation of subnetworks composed

334 only by the neighbours of particular species. This translates into a greater resistance of the

335 network due to the confinement of perturbations mainly within subnetworks and not

336 spreading between them (Kortsch et al. 2019, Heer et al. 2020]. Overall, a small-world

337 topology provides ecological networks with greater resilience and resistance (Bornatowski et

338 al. 2017, Dormann et al. 2017).

339 Omnivory acts as a buffer to changes as the ecosystem presents alternative energy pathways

340 in the face of perturbations, i.e., reducing the risk of cascading extinctions following the

341   primary loss of species (Borrvall et al. 2000). Omnivores are species able to adapt faster and

342   to a broader range of environmental conditions by changing their foraging habits to feed on

343   the most abundant prey (Fagan 1997). Furthermore, omnivory can be analysed from the

344   interaction point of view: theoretical studies have identified omnivorous interactions as a

345   possible candidate for a keystone interaction, sensu Kadoya et al. 2018, highlighting the

346   importance of omnivory in stabilizing food web dynamics (McCann & Hastings 1997, Neutel

347   et al. 2002). The high proportion of omnivory in the food web of the MPA N-BB suggests

348   that the network might be robust to variations in prey abundances, which could increase food

349   web's persistence and stability (Stouffer & Bascompte 2010).

350   In summary, the food web of the MPA N-BB presents a combination of network properties

351   that makes it unique in terms of network resolution, complexity, and structural pattern. All

352   this suggests that the food web might be fragile to external perturbations targeting highly

353   connected species, which in turn coincides to be commercially exploited species as fishes

354   (Laptikhovsky et al. 2013, Martínez et al. 2015, Winter & Arkhipkin 2023). However,

355   structural properties might provide resilience and resistance with the final outcome of a

356   rearranged structure maintaining its functions.

357   4.2. DOMINANT CONSUMERS AND FOOD SOURCES

358   The degree distribution allows identifying important species, such as potential keystone

359   species (i.e. highly connected) (Solé & Montoya 2001, Dunne et al. 2002b),

360   generalist/specialist species, and dominant food sources (Kondoh et al. 2010).

361   We have identified that most of the consumers in the food web of the MPA N-BB either have

362   a narrow diet or are specialists, while few present a broad or generalist diet. The most evident

363   generalist species are *Patagonotothen guntheri* (Covatti Ale et al. 2022), *Patagonotothen*

364   *ramsayi* (Fischer et al. 2022), juveniles of *Dissostichus eleginoides* (Troccoli et al. 2020),

365   *Bathyraja brachyurops* (Belleggia et al. 2008), and *Bathyraja griseocauda* (Bellegia et al.

366   2014), with more than 25 potential prey. Since these species present mid-trophic positions in

367   the food web (with the exception of adults of *D. eleginoides* that are top predators), acting as

368   predator and prey, they might be important links between lower and higher trophic levels.

369   This result is in agreement with the sole analysis, using stable isotopes, that exists so far for

370   the trophic structure of the MPA N-BB (Riccialdelli et al. 2020), and resembles other high-

371   latitude marine systems of the Southwest Atlantic and Antarctic regions (Arkhipkin &

372   Laptikhovsky 2013, Marina et al. 2018a). The importance of these particular generalist

373   species also arises since they feed in the benthic and pelagic habitats (Troccoli et al. 2020,

374   Covatti Ale et al. 2022, Fischer et al. 2022), linking these realms and contributing to the

375   vertical carbon flow.

376   On the other hand, a low number of prey are consumed by many predators in the food web of

377   the MPA N-BB. This suggests that there are dominant food sources on which most

378   consumers depend and from where the ecosystem energy is being transferred to the upper

379   trophic levels. The most demanded source we identified in this study (i.e. detritus) supports

380   the abundant benthic community of filter-feeders (Schejter et al. 2016), components of the

381   animal forest (Schejter et al. 2020), likely feeding on detritus that is constantly resuspended

382   from the bottom (Martin & Flores-Melo 2021). Furthermore, we found that the second and

383   third-most consumed prey were diatoms and species of *Euphausia*, respectively, which are

384   essential sources for the diverse zooplankton community (Spinelli et al. 2020), mid-TL

385   consumers like the Fuegian sprat *Sprattus fuegensis* (Padovani et al. 2021) and *P. ramsayi*

386   (Fischer et al. 2022), and top predators such as the black-browed and grey-headed albatrosses

387   (*Thalassarche melanophris* and *Thalassarche chrysostoma*, respectively) (Catry et al. 2004),

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

389   2018).

390   4.3. SPECIES' ROLE RELATED TO THEIR TROPHIC LEVEL

391   Describing species' roles in food webs provides a toolbox to assess the significance of

392   species in terms of community's functioning and overall stability (Thebault & Fontaine 2010,

393   Cirtwill et al. 2018). We used a range of descriptors to characterise the dynamic and

394   multifaceted nature of the species forming the MPA N-BB food web.

395   Closeness and betweenness are defined as "mesoscale" properties because they consider

396   direct and indirect interactions, therefore describing the focal species' ability to influence the

397   rest of the species of the food web (Lai et al. 2012). Closeness quantifies how many steps

398   away species i is from all other species in the food web, and is proportional to how rapidly

399   the indirect effects of the focal species can spread to other species in the network (Scotti &

400   Jordán 2010). In the food web of the MPA N-BB, low-TL consumers arise as important in

401   this regard: species of the zooplankton community, *Calanus* and *Euphausia*, *Zygochlamys*

402   *patagonica* (Bivalvia), and Brachiopoda. Any perturbation affecting these species, such as the

403   recently confirmed contaminants mercury (Fioramonti et al. 2022) and microplastics (Cossi et

404   al. 2021, Di Mauro et al. 2022), should be of concern since it might reach many other species

405   in the food web. Otherwise, betweenness measures the number of shortest paths between

406   species, providing information on the importance of species as "bridges" for energy transfer:

407   a species with high betweenness takes part in more food chains and therefore affects more

408   energy flows (Scotti & Jordán 2010). We have identified the longtail southern cod *P. ramsayi*

409   as the most important species in this sense. Moreover, in light of our analysis, other species

410   like the Patagonian toothfish *D. eleginoides* (juveniles), the Patagonian cod *Salilota australis*,

411   the yellowfin notothenioid *P. guntheri*, and the Patagonian longfin squid *Doryteuthis gahi*

412   should be considered as relevant in the energy transfer in the ecosystem. All these species

413   have a mid-trophic position in the food web, supporting the 'wasp-waist' control hypothesis

414   for the MPA N-BB (Riccialdelli et al. 2020).

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

416   redundancy, since many species would show similar trophic habits (Cury et al. 2000). The

417   significant negative relationship between trophic similarity and trophic level enhances the

418   hypothesis of functional similarity at low and mid-TL species compared to higher TL species

419   for the MPA N-BB food web (Riccialdelli et al. 2020). At the same time, our results highlight

420   the uniqueness in terms of the trophic role of high-TL predators. Here, not only the expected

421   pelagic animals such as marine mammals and seabirds arise as relevant, but also demersal

422   vertebrate (chondrichthyans *Bathyraja macloviana* and *Squalus acanthias*) and benthic

423   invertebrate species (echinoderms *Diplopteraster clarki* and *Pteraster sp.*) are noteworthy.

424   The role that such species play in the MPA N-BB ecosystem is unique and perturbations on

425   them might result in unprecedented changes at the trophic structure and functioning level. In

426   this regard, we should mention the potential threat of the fisheries operating in the western

427   section of the MPA N-BB, where this activity is allowed and mostly focuses on the

428   Patagonian toothfish *D. eleginoides* and the southern blue whiting *Micromesistius australis*

429   (Martínez et al. 2015). Although the fishing effort is concentrated outside the limits of the

430   MPA N-BB, the impact on the MPA ecosystem should not be neglected (Martínez et al.

431   2021).

432   Species' role can also be assessed in a module-based context. Among the varying numbers of

433   topological roles in which species can be divided, two are remarkable: 'module connector'

434   and 'network connector'. Here, our results point out that there are several species, belonging

435   to a wide range of trophic positions (1 to 3.86) and representing 17 different functional

436   groups, that should be considered as influential species for the connectivity of the food web.

437   Thus, we propose that the diversity of species (benthic and pelagic) maintains the

438   connectivity of the food web, therefore contributing to the trophic structure and ecosystem's

439   stability.

440   4.4. CAVEATS AND FUTURE PERSPECTIVE

441   The food web studied in the present work might be more representative of the shallow

442   ecosystem of the submarine plateau called Burdwood Bank, on which most of the research

443   was focused as the MPA N-BB I was first created. This is related to the sampling effort that

444   was conducted during the research cruises in the former MPA compared to the MPA N-BB II

445   (i.e. deep flanks to the south). As a consequence, most of the data we used to build the

446   network come from studies performed in the MPA N-BB I. Despite this fact, we decided to

447   build the food web considering both MPAs due to the tight oceanographic and ecological

448   connection that exists among them (APN 2022 and references therein).

449   It's important to note that we did not consider quantitative data (i.e. abundance, biomass) to

450   assess the species' role in the food web. Although there exists such data for some species

451   (Schejter & Albano 2021), it would not be possible to include it in the food web framework

452   described here due to a taxonomical resolution mismatch. In this regard, we should mention

453   the case of *Zygochlamys patagonica* (Bivalvia) and Brachiopoda that are highlighted by our

454   species-level analyses though they have been found in low abundances in the area (Schejter

455   & Albano 2021).

456   Some species of sessile suspension feeders in high-latitude marine ecosystems, such as

457   sponges, ascidians and octocorals, avoid predation by producing secondary metabolites that

458   function as a chemical defense (Núñez-Pons et al. 2010, Moles et al. 2015, Prieto et al. 2022).

459   Although this was not yet recorded at the MPA N-BB, there are a few studies that reported it

460   in other locations in species that inhabit the MPA N-BB (Rojo de Almeida et al. 2010).

461   The MPA N-BB I presents complex oceanographic conditions that generate an internal

462   spatial heterogeneity, mainly along its longitudinal axis (Matano et al. 2019). So far this

463   heterogeneity has been reflected in phytoplankton and zooplankton communities (Bértola et

464   al. 2018, García Alonso et al. 2020, Spinelli et al. 2020), and in fish assemblages (Delpiani et

465   al. 2020). Moreover, seasonal variations also occur in some physical and biological aspects of

466   the MPA N-BB I (García Alonso et al. 2018, Matano et al. 2019). Considering both MPAs

467   (N-BB I and II), a seasonal variation in the community composition of marine mammals and

468   seabirds was recorded recently (Dellabianca et al. 2023). The spatial and seasonal variations

469   in the plankton community might affect the energy and matter flow to higher levels of the

470   food web. This has been recently studied in the vicinity of the MPA N-BB I, in the Beagle

471   Channel, where a differential energy flow pattern of the plankton community has been

472   recognised in two micro-basins of the Channel separated by a sill, each with different

473   physicochemical properties (Giesecke et al. 2021), nutrient concentration (Latorre et al. 2023)

474   as well as in the dominant component of the plankton community (Bruno et al. 2023, Presta

475   et al. 2023). Although we were aware of the above, we decided to characterise a food web

476   representing the whole MPA N-BB I year round since this is the first study of its type in the

477   area.

478   Taking into account the mentioned caveats, and with the aim of improving the knowledge

479   regarding the structure, functioning and stability of the MPA N-BB, we suggest that the

480   future perspectives should: 1) incorporate spatial heterogeneity among MPA N-BB I and II

481   (Schejter & Albano 2021), which might lead to distinct food web properties in terms of

482   structure and functioning (Kortsch et al. 2019, Cordone et al. 2020); 2) include species traits,

483   like body size and mass, since they are known to be important drivers in predator-prey

484   interactions (Brose et al. 2019); 3) simulate the anthropogenic impacts already present in the

485   MPA N-BB ecosystem (e.g. microplastics, mercury) (Cossi et al. 2021, Di Mauro et al. 2022,

486   Fioramonti et al. 2022) as perturbations within the framework of the described complex food

487   web; and 4) estimate the interaction strength of each predator-prey relationship in the food

488   web considering species and interaction traits (i.e. body size, body mass, interaction

489   dimensionality), and species density data (Nilsson & McCann 2016, Pawar et al. 2012).

490 5.   CONCLUSION

491   We compiled information on the species and trophic diversity of the oceanic Marine

492   Protected Area Namuncurá - Burdwood Bank, generating an unprecedented, well-resolved

493   network of trophic interactions for a sub-Antarctic ecosystem, identifying the complexity and

494   structure of the system, and the main species role in a network framework. Particular

495   properties at the network level allowed us to identify the ecosystem's vulnerability and

496   potential response to perturbations in the presence of highly-connected species, with a

497   rearranged structure maintaining their functions due to its potential resilience and resistance.

498   We identified several species as important regarding different aspects of trophic structure and

499   functioning, and response to perturbations (i.e. environmental/anthropogenic changes). On

500   the one hand, we suggest that generalist species, mainly fishes, play a crucial role in the

501   ecosystem's bentho-pelagic coupling process. At the same time, we propose that other species

502   besides the longtail southern cod *Patagonotothen ramsayi* and the Fueguian sprat *Sprattus*

503   *fuegensis* should be considered relevant energy transfers for the ecosystem. Finally, we argue

504   that it is the diversity of species, representing the benthic and pelagic habitats, that maintains

505   the connectivity of the food web against perturbations, therefore contributing to the structure

506   and stability of the ecosystem.

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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. 2002a
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. 2002a
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	The removal of a species with high closeness will affect the most other	Freeman 1978, Lai et al. 2012

	given species.	species in the food web.	
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.	Guimerà & Nunes Amaral 2005

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.

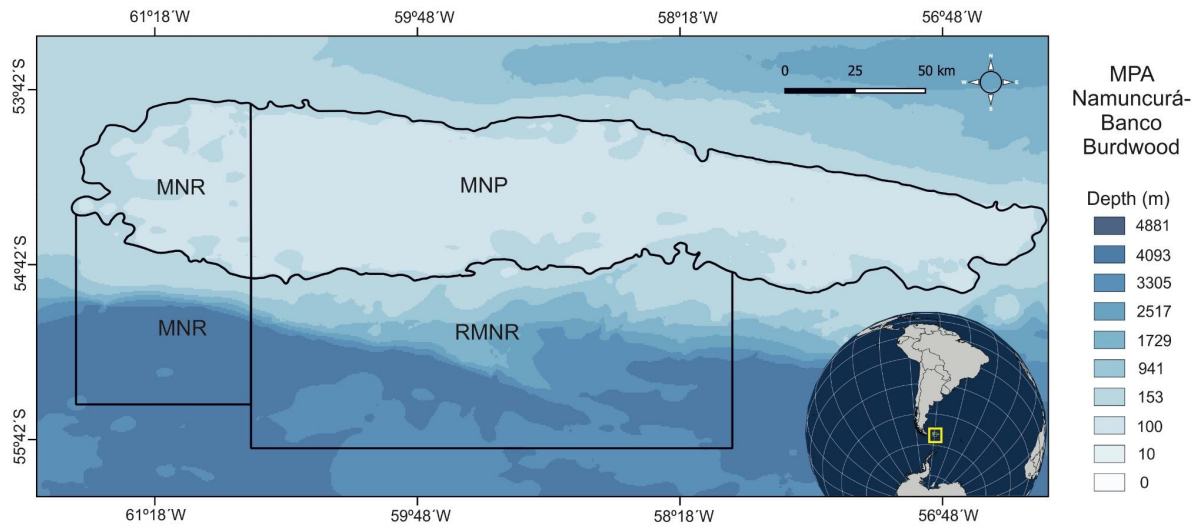| Species	Interactions	Density	Connectance	Omnivory	CPL	CC	SW
379	1788	4.72	0.01	0.48	2.99	0.08	TRUE

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.
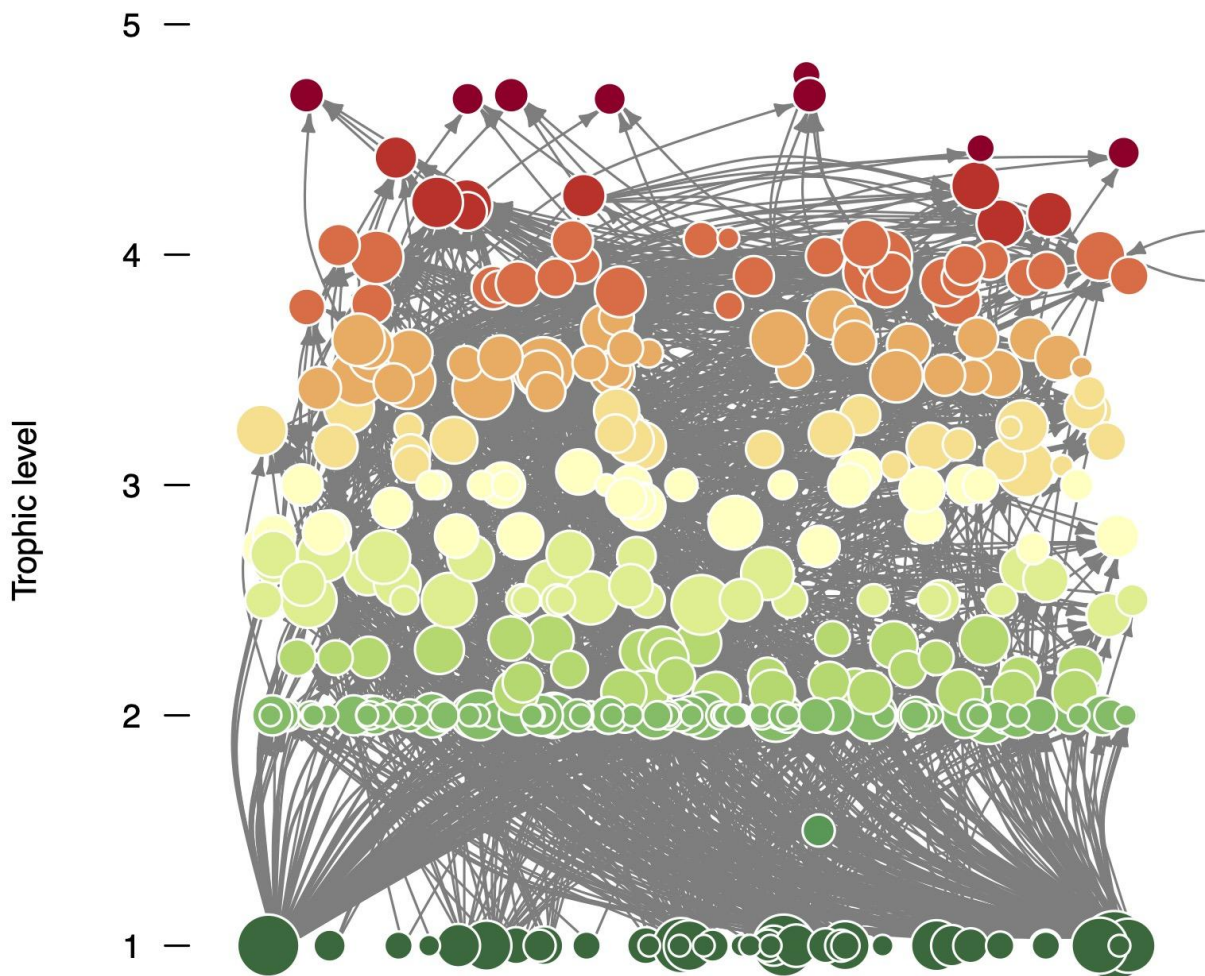

Figure 2: Graph of the food web for the MPA Namuncurá - Burdwood Bank. Circles represent species and arrows trophic interactions. Circle diameter is relative to the number of interactions. Colour gradient indicates the trophic level.
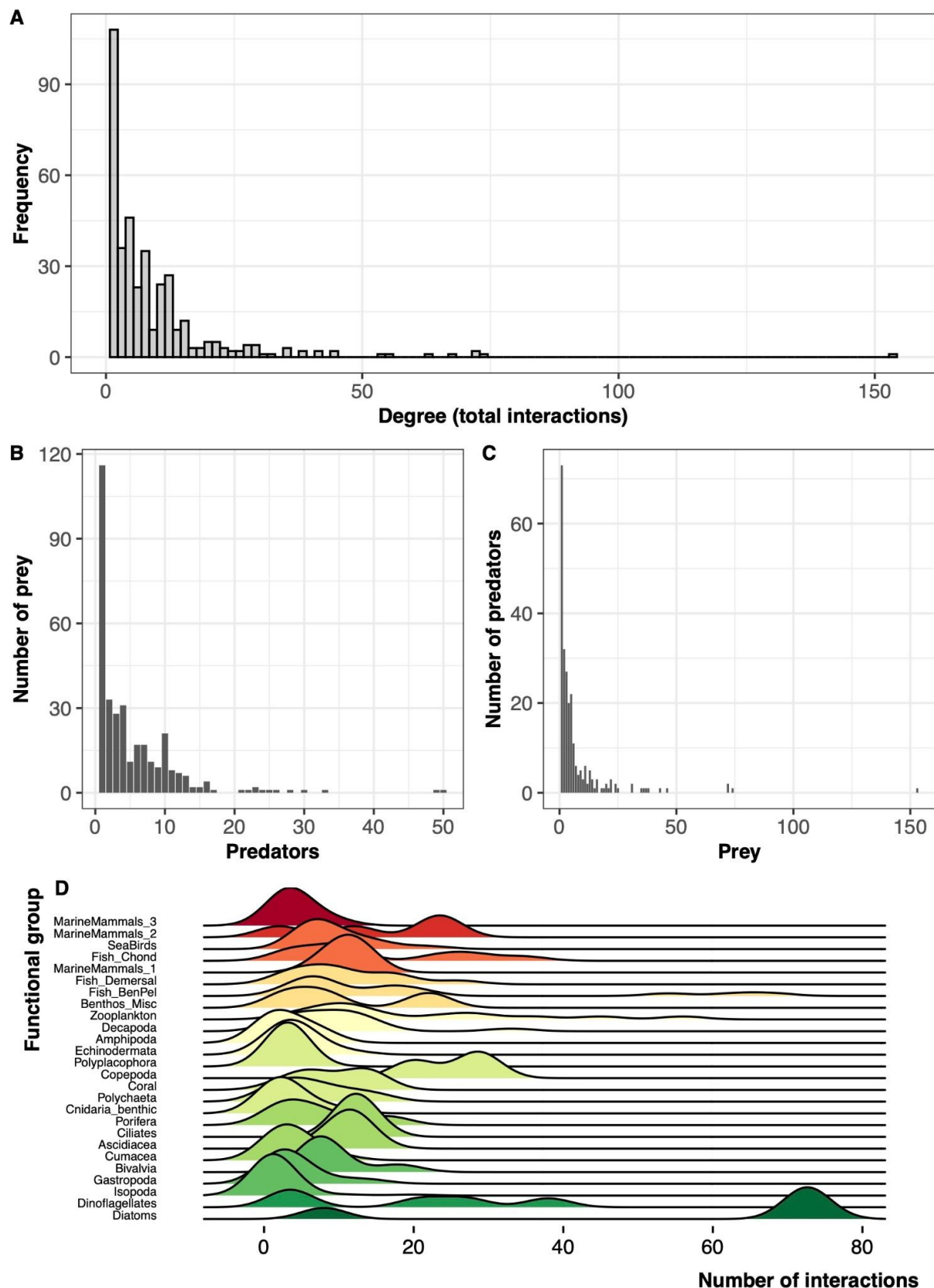
Figure 3: Degree distributions for the (A) food web, for (B) prey among predators, (C) predators among prey, and (D) for each functional group. Groups are vertically ordered by increasing trophic level (following coloration of figure 2); groups with less than 3 species

were not plotted (e.g., pelagic fish). All functional groups and the species that comprise them are shown in Supplementary Material (Table S3).
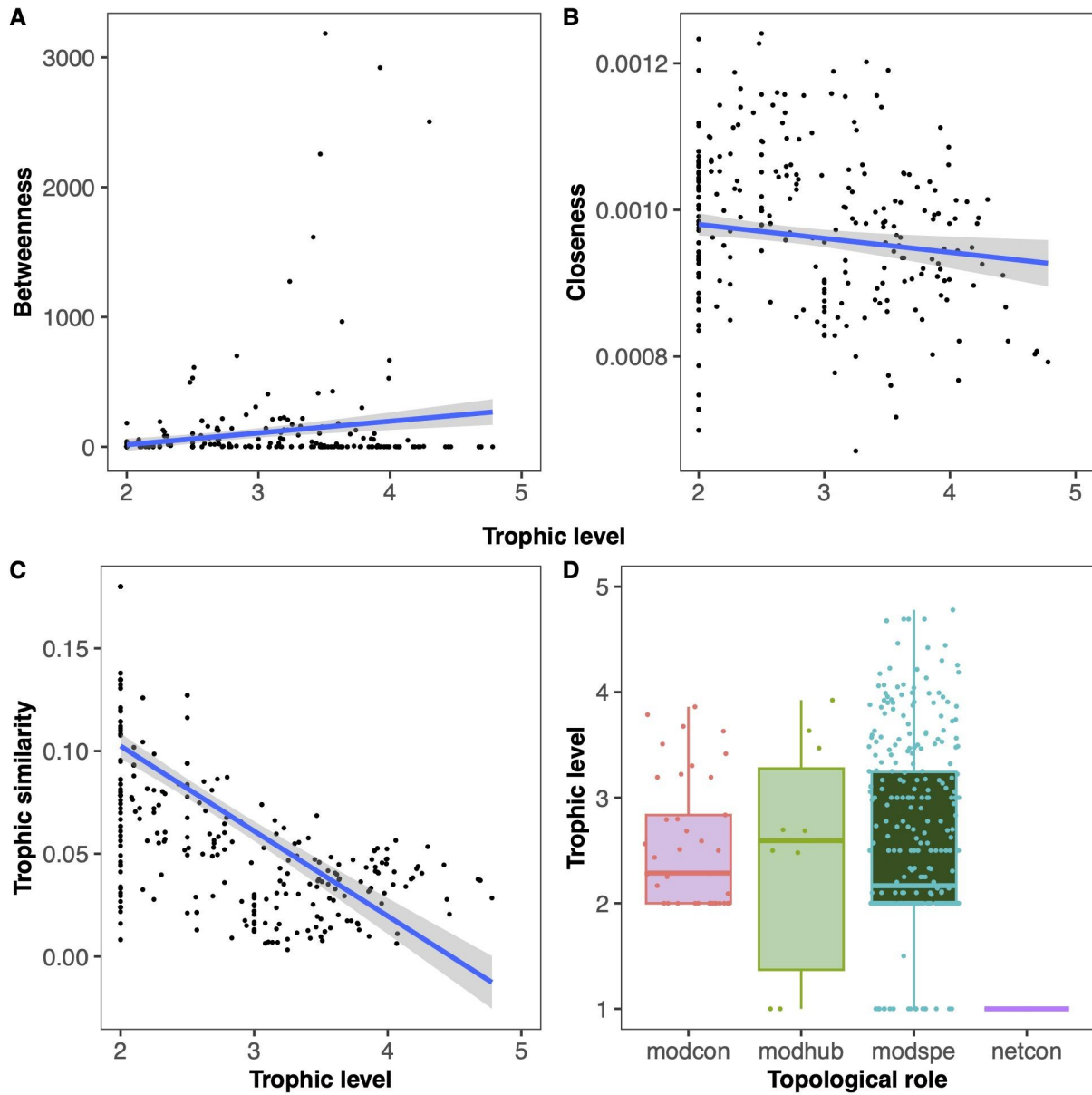

Figure 4: Species-level properties by trophic level: (A) betweenness, (B) closeness, (C) trophic similarity, and (D) topological role. Each point represents a species. Linear regressions for betweenness (y = 74.97x − 117.35, R^2 = 0.05, p − value < 0.01), closeness (y = 9.33e − 06x − 9.31e − 4, R^2 = 0.003, p − value = 0.15) and trophic similarity (y = −0.02x + 0.11, R^2 = 0.07, p − value < 0.01). Note that for panels A, B and C only species with TLs equal or greater than 2 were considered.