

1 **The food web of Potter Cove (Antarctica): complexity, structure and function**

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22 **Abstract**

23 Knowledge of the food web structure and complexity are central to better understand ecosystem
24 functioning. A food-web approach includes both species and energy flows among them,
25 providing a natural framework for characterizing species' ecological roles and the mechanisms
26 through which biodiversity influences ecosystem dynamics. Here we present for the first time a
27 high-resolution food web for a marine ecosystem at Potter Cove (northern Antarctic Peninsula).
28 Eleven food web properties were analyzed in order to document network complexity, structure
29 and topology. We found a low linkage density (3.4), connectance (0.04) and omnivory
30 percentage (45), as well as a short path length (1.8) and a low clustering coefficient (0.08).
31 Furthermore, relating the structure of the food web to its dynamics, an exponential degree
32 distribution (in- and out-links) was found. This suggests that the Potter Cove food web may be
33 vulnerable if the most connected species became locally extinct. For two of the three more
34 connected functional groups, competition overlap graphs imply high trophic interaction between
35 demersal fish and niche specialization according to feeding strategies in amphipods. On the other
36 hand, the prey overlap graph shows also that multiple energy pathways of carbon flux exist
37 across benthic and pelagic habitats in the Potter Cove ecosystem. Although alternative food
38 sources might add robustness to the web, network properties (low linkage density, connectance
39 and omnivory) suggest fragility and potential trophic cascade effects.

40 **Key words:** Ecological networks; Structure; Degree distribution; Marine ecosystem;
41 Antarctica.

42

43 **1. Introduction**

44 Food web (FW) characterization is essential to understanding ecology as a way to describe and
45 quantify the complexity of ecosystems by identifying the trophic interactions among species
46 (Bascompte 2009). The framework of ecological network analysis could also be used to quantify
47 the effects of the environment and how indirect effects of such interactions influence overall
48 ecosystem properties (Brose and Dunne 2009).

49 Since the early 2000s, ecological networks from marine systems have received more attention
50 answering an emphatical call of Raffaelli (2000) for more research on marine webs. In this sense,
51 indices derived from Ecological Network Analysis (ENA), a system-oriented methodology to
52 analyze within system interactions (Fath et al. 2007), have been used to investigate trophic
53 interactions in marine ecosystems (Baird et al. 2007, Ulanowicz 2011, Wuff et al. 2012,
54 Heymans et al. 2014). Among marine webs, polar FWs recently began to be considered in the
55 frame of FW theory (e.g. Jacob et al. 2006, Bodini et al. 2009, de Santana et al. 2013). Moreover,
56 some conclusions on the effects of global warming on Arctic and Antarctic marine FWs have
57 been proposed (de Santana et al. 2013, Kortsch et al. 2015).

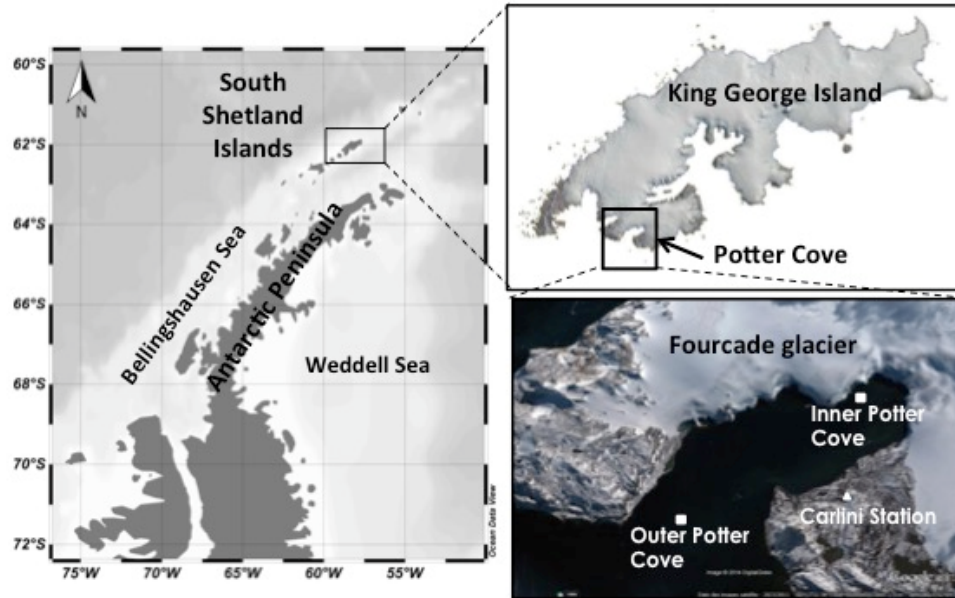
58 Potter Cove is an Antarctic fjord that suffers from the impact of the high rate of warming
59 occurring in Western Antarctic Peninsula (Quartino et al. 2013, Deregibus et al. 2016). The
60 abundant and rich epibenthic fauna has been changing under the influence of considerable
61 sediment inputs and other effects derived from ice melting (Pasotti et al. 2015a, Sahade et al.
62 2015). The way in which network properties can be modified under climate change is in general,
63 poorly known (Petchey et al. 2010, Walther 2010, Woodward et al. 2010). To understand the
64 community-level consequences of the rapid polar warming, Wirta et al. (2015) suggested that we
65 should turn from analyses of populations, population pairs, and isolated predator–prey couplings

66 to considering all the species interacting within communities. If species affected by perturbations
67 possess key functional roles in the FW, then the potential higher order, indirect effects of those
68 perturbations on the entire FW structure can be dramatic (Kortsch et al. 2015). Knowing that
69 climate change effects are already occurring in Potter Cove ecosystem and that ecosystems
70 respond to perturbations as a whole, a network approach could contribute to a better
71 understanding of changes in the ecosystem's synthetic properties like resilience or stability. A
72 representative roadmap of trophic interactions of Potter Cove will allow testing for the impact of
73 ongoing climate change effects (e.g. glacier retreat, loss of ice shelves, increment of
74 sedimentation input) which might be transmitted throughout the entire ecosystem.
75 Although FW studies use binary webs that indicate the presence of a trophic interaction but do
76 not provide any information on the frequency of the interaction or the rate of biomass flow
77 through the interaction, overlap graphs (e.g. competition and common-enemy graphs), can
78 provide information about indirect interaction strength between predators and prey, respectively.
79 Indirect effects in predator and prey assemblages can also be studied by evaluating these graphs.
80 The strength of predator-predator and prey-prey indirect interactions is extremely difficult to
81 measure but, if they prove generally prevalent, they could be a major driver of community
82 dynamics and ecosystem functioning (Woodward et al. 2005). The analysis of the degree
83 distribution of links in the overlap graphs, omitted in most FW studies, might be very useful to
84 identify, based on the competition graph, generalist and specialist predators, and to evaluate
85 energy pathways in the common-enemy graph.
86 In the current work, we present the first, detailed analysis of the FW for the Potter Cove
87 ecosystem (South Shetland Islands, Antarctica). The objectives of this study were to: 1) analyze
88 the complexity and structure of the ecological network in the context of the most-studied marine

89 FWs; and 2) examine its degree distribution and overlap graphs in order to gain insight into the
90 ecosystem dynamics and functioning.

91 **2. Methods**

92 Potter Cove is a 4 km long and 2.5 km wide Antarctic fjord located at 25 de Mayo/King George
93 Island (62°14'S, 58°40'W, South Shetland Islands) (Fig. 1). A shallow sill (< 30 m) separates its
94 inner and outer areas. The inner cove is characterized by soft sediments and by a shallower depth
95 than the outer cove (< 50 m); in the outer cove the bottom is mainly rocky and with average
96 depths of 100 m. Potter Cove is adjacent to Maxwell Bay, which connects to the Bransfield
97 Strait. Water circulation in Potter Cove is strongly influenced by the general circulation of
98 Maxwell Bay (Roese and Drabble 1998). A cyclonic circulation has been identified, with
99 efficient water renewal in the northern sector, where water from Maxwell Bay enters the Cove.
100 Freshwater input varies both seasonally and inter-annually and carries important amounts of
101 suspended sediments. Two main creeks discharge into the Cove, the Matias and the Potter
102 creeks. They exhibit different regimes, the first being snowy and lacustrine, the latter snowy and
103 glacial (Varela 1998). Drainage ranged between 0.03 and 0.11 m³ s⁻¹ in the Matias Creek and
104 from 0.08 to 3.8 m³ s⁻¹ in Potter Creek (Varela 1998). Suspended sediment discharges ranged
105 between 0.04 and 15 kg m⁻³ (average = 0.14 kg m³), which correlate with air temperature. These
106 characteristics are consistent with data from other glaciomarine environments in Antarctic
107 coastal waters (Leventer and Dunbar 1985).



108 Fig. 1. Map of Potter Cove and its location on Isla 25 de Mayo/King George Island.

109 2.1. Food web assembly

110 We constructed the FW of Potter Cove ecosystem primarily based on information about species
111 living in that system and their feeding habits from studies within the framework of an
112 international research cooperation between Argentina and Germany initiated in 1994 and
113 ongoing for more than 20 years (Wiencke et al. 1998, 2008).

114 We collected information on feeding links by a thorough literature search (> 500 papers and
115 reports revised). To assemble the network we only considered trophic interactions confirmed by
116 gut content studies and/or field observation. Furthermore, direct observations of researchers from
117 field sampling campaigns in the Cove (e.g. divers when collecting benthic samples) were also
118 taken into account. Laboratory experimental studies, where feeding selectivity, palatability or
119 behavior was tested, were not included in this study as we consider the trophic links proved from
120 experiments are not as robust as the ones gathered from the field data. Investigations using
121 biomarkers (i.e. stable isotopes and fatty acids) were not considered since trophic interactions are

122 established by sampling few individuals ($n \approx 10-100$) and studied prey-predator relationships are
123 usually between trophic species widely aggregated. Further details on the trophic links included
124 in the present study (references and methods used to confirm a link) are presented in the
125 electronic supplementary material (Appendix A).

126 Trophospecies, here defined as aggregated groups of taxa, were only considered when data on
127 specific biological species were not available (lack of data resolution) or when taxa shared the
128 same set of predators and prey within the FW (trophic similarity criteria). We have not
129 considered top vertebrate predators (e.g. penguins, seals, whales), as they only sporadically enter
130 the Cove to feed. In addition, pelagic fish (typically taken by Antarctic penguins and pinnipeds)
131 were not considered due to paucity of occurrence (Barrera-Oro and Casaux 2008).

132 The diversity of the expertise of the authors contributing to the present study was a key factor in
133 generating the quality of the FW, and inherently improved the network representation of the
134 Potter Cove ecosystem.

135 2.2. Network analysis

136 An interaction matrix of pairwise interactions was constructed; a value of 1 or 0 was assigned to
137 each element a_{ij} of the matrix depending on whether the j -species preyed or not on the i -species.

138 The FW is an oriented graph with L trophic links between S nodes or species. The FW graph was
139 drawn from the interaction matrix using Visone software version 2.9.2 (Brandes and Wagner
140 2004).

141 Several network properties that are commonly used to describe complexity and structure in FWs
142 were calculated (Dunne et al. 2002b, de Santana et al. 2013): (1) number of species, S ; (2) total
143 number of interactions or trophic links, L ; (3) number of interactions per species or linkage

144 density, L/S ; (4) connectance or trophic links divided by total number of possible interactions,
145 $C=L/S^2$; percentage of (5) top species (species with prey but without predators), (6) intermediate
146 species (species with prey and predators), (7) basal species (species with predators/consumers
147 but without prey); and (8) percentage of omnivores (species eating prey from more than one
148 trophic level).
149 Trophic levels (TL) of species were calculated using the short-weighted TL formula of Williams
150 and Martinez (2004). Short-weighted trophic level is defined as the average of the shortest TL
151 and prey-averaged TL . Shortest TL of a consumer in a food web is equal to 1 + the shortest chain
152 length from this consumer to any basal species (Williams and Martinez 2004). Prey averaged TL
153 is equal to 1 + the mean TL of all consumer's trophic resources, calculated as

$$TL_j = 1 + \sum_{i=1}^S l_{ij} \frac{TL_i}{n_j}$$

154 where TL_j is the trophic level of species j ; S is the total number of species in the food web; l_{ij} is
155 the connection matrix with S rows and S columns, in which for column j and row i , l_{ij} is 1 if
156 species j consumes species i and 0 if not; and n_j is the number of prey species in the diet of
157 species j . Therefore, Short-weighted TL yields a minimum estimate of TL and assumes a value of
158 1.0 for basal species (Williams and Martinez 2004). We considered the mean TL of the web as
159 the average of all species' TL .
160 Two secondary graphs, the competition graph and the common-enemy graph, were constructed.
161 The first one, also known as predator overlap graph, connects predators that share one or more
162 prey, while the latter is drawn by connecting prey species sharing one or more predators (Pimm
163 et al. 1991). Predator overlap graph results were discussed considering dietary data on each
164 predator species involved. To examine a plausible organization in predator and prey species, we
165 separately studied the degree distribution of links $P(k)$ for each overlap graph. Links in predator

166 distribution represent the number of prey, while in prey distribution it depicts number of
167 predators. Graphs were plotted using Visone software (version 2.9.2).

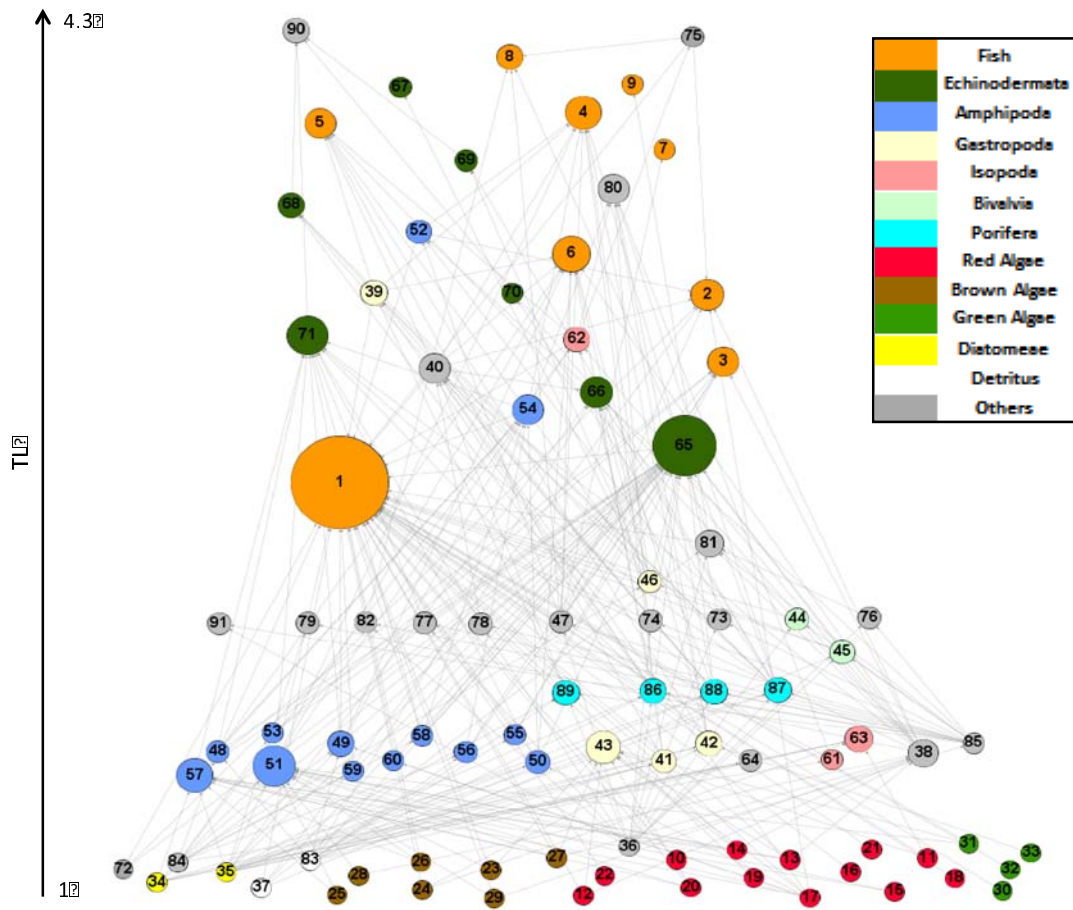
168 We also studied the topology of the FW by measuring three more properties: (9) characteristic
169 path length (ChPath), or the average shortest path length between all pairs of species, (10)
170 clustering coefficient (CC), or the average fraction of pairs of species connected to the same
171 species that are also connected to each other, and (11) degree distribution, or the fraction of
172 trophic species $P(k)$ that have k or more trophic links (both predator and prey links) (Albert and
173 Barabási 2002). Trophic links were treated as undirected when calculating path length and
174 clustering because effects can propagate through the web in either direction, through changes to
175 both predator and prey species (Watts and Strogatz 1998).

176 Results of these properties and the ones aforementioned for Potter Cove FW were compared
177 among other marine webs that were chosen considering different criteria: size ($S > 25$), temporal
178 era (fourth era, see Link et al. 2005) and quality data (i.e. FWs built upon stable isotopes were
179 excluded).

180 Degree distributions of the total FW and of the mentioned overlap graphs were examined and
181 fitted using nonlinear regression analysis (Xiao et al. 2011). Model selection was performed by
182 computing the Akaike Information Criterion corrected for small sample size (AICc) (Burnham
183 and Anderson 2002, Xiao et al. 2010). R package *nls* (Nonlinear Least Squares) was used to
184 make power-law and exponential fitting (R Core Team 2016).

185 3. Results

186 The Potter Cove FW (Fig. 2) includes 91 species, composed of 71 biological species, 17
187 trophospecies (i.e., merging two or more taxonomic species by trophic similarity) and 3 non-
188 living nodes (i.e. fresh detritus, aged detritus and necromass).



189 Fig. 2. Graphic representation of Potter Cove FW with the trophic level (TL) on the vertical scale
190 and node width proportional to the total degree (in- and out-). Node colors are by functional
191 group. Network was plotted with Visone (version 2.9.2). See electronic supplementary material
192 (Appendix B) for exhaustive lists of trophic species, their trophic level, degree (in- and out-
193 links), functional and taxonomic group affiliation (e.g. algae, phytoplankton, zooplankton, fish,
194 amphipods).

195 Algae (24 species) comprise red (13 spp.), brown (7 spp.) and green algae (4 spp.). The next
196 trophic levels consist of 13 amphipod species, 3 isopod species, 4 sponge species (one

197 aggregated node: *Stylocordyla borealis* and *Mycale acerata*), 5 gastropod species, 2 bivalve
198 species, 7 echinoderm species, and 9 demersal fish species. See electronic supplementary
199 material (Appendix B) for exhaustive lists of taxa, their trophic level, degree (in- and out-links),
200 functional and taxonomic group affiliation (e.g. algae, phytoplankton, zooplankton, fish,
201 amphipods).

202 The first thing to note about Potter Cove FW is that most of the species (47%) were at
203 intermediate levels, implying that they act as predators and prey depending on the trophic
204 interaction they are involved in. Moreover, as shown in Fig. 2 some species are far more
205 connected (9 species with degree > 15) than others, according to the total number of trophic
206 interactions they have (e.g. fish and echinoderms).

207 The main properties of the network complexity for Potter Cove FW included 307 total
208 interactions and a linkage density of 3.4. As a consequence, a connectance of 0.04 was reported
209 (Table 1).

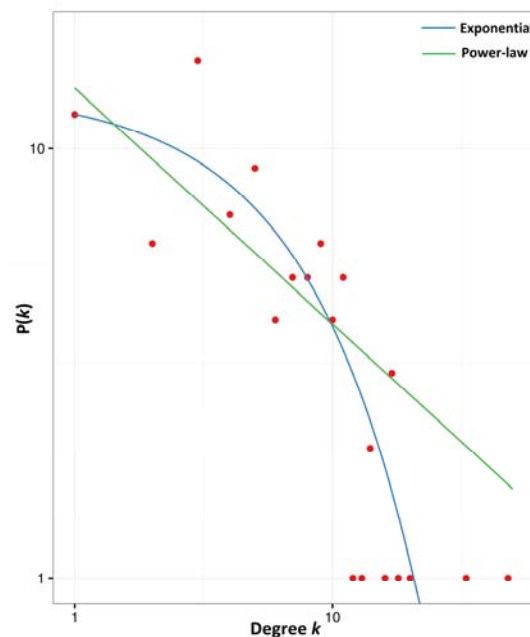
210 Table 1. Properties of network complexity and structure for Potter Cove FW. S = number of
211 trophic species, L/S = linkage density, C = connectance (L/S^2), T = % top species, I = %
212 intermediate species, B = % basal species, Omn = percentage of omnivorous, TL = mean trophic
213 level, ChPath = characteristic path length, CC = clustering coefficient.

Food web	S	L/S	C	T	I	B	Omn	TL	ChPath	CC
Potter Cove	91	3.4	0.04	19	47	34	45	2.1	1.8	0.08

214 Although intermediate species outnumbered top and basal species, comprising more than half of
215 the species in the FW, the basal species were also numerous (Table 1). In addition, almost half of
216 the species were omnivorous (45%), similar to the percentage observed in intermediate species.
217 The mean trophic level (TL) for Potter Cove FW was 2.1, which was supported by the relatively
218 high proportion of basal species that tend to lower the average.

219 Network topological properties, characteristic path length (ChPath) and clustering coefficient
220 (CC) were 1.8 and 0.08, respectively.

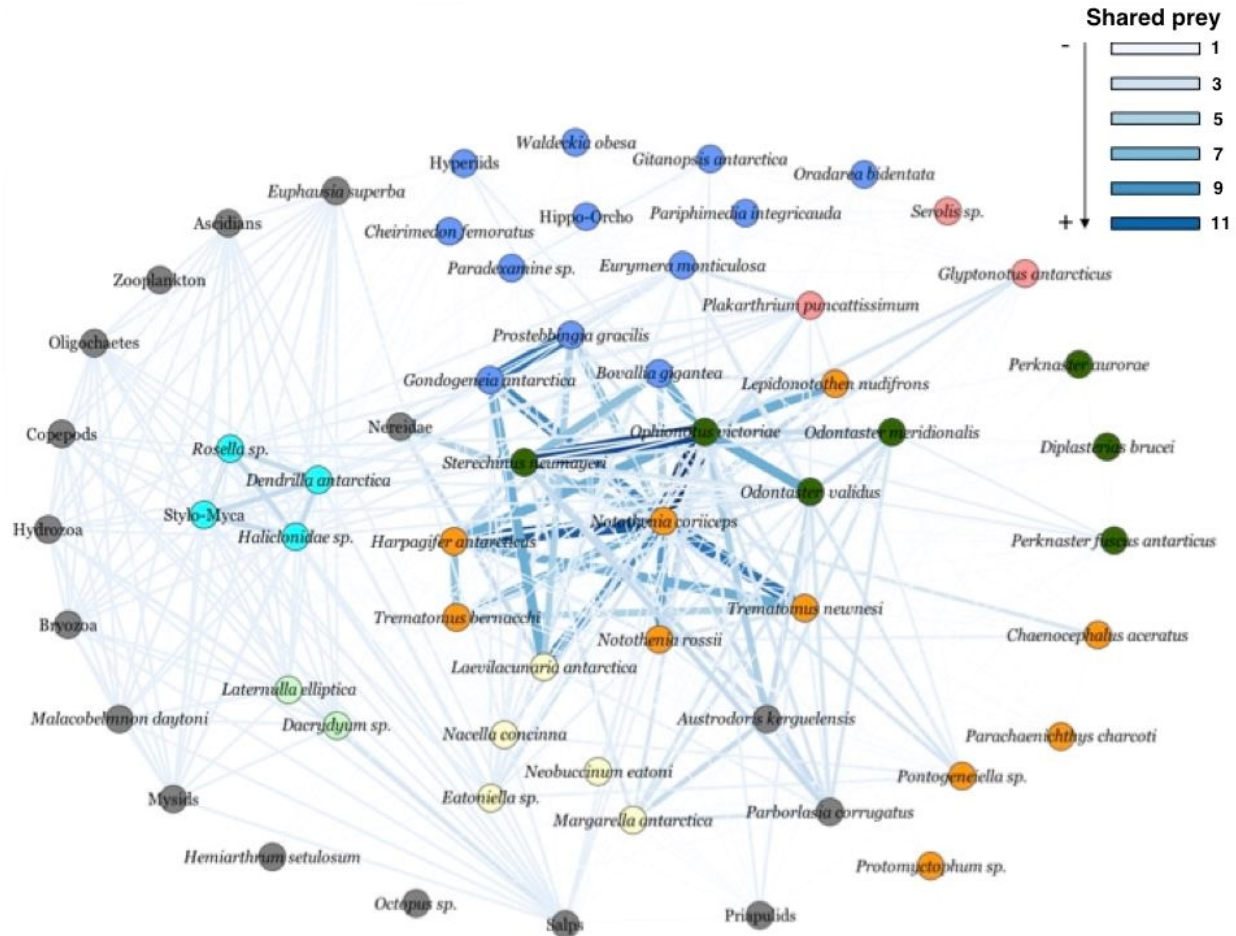
221 The degree distribution for the Potter Cove FW (Fig. 3) showed that the exponential model best
222 fitted the data, according to nonlinear regression and AICc analyses (Table 2). The three species
223 with the highest degree were: *Notothenia coriiceps* (fish, 48 links), *Ophionotus victoriae*
224 (echinoderm, 33 links) and *Gondogeneia antarctica* (amphipod, 20 links).



225 Fig. 3. Log-log degree distribution of links $P(k)$ for Potter Cove FW. Two candidate models are
226 shown. Best fit is the exponential model.

227 The competition graph derived from Potter Cove FW is highly connected. It includes 60 species
228 and 478 indirect interactions (Fig. 4) and shows that several pairs of predators share many prey.

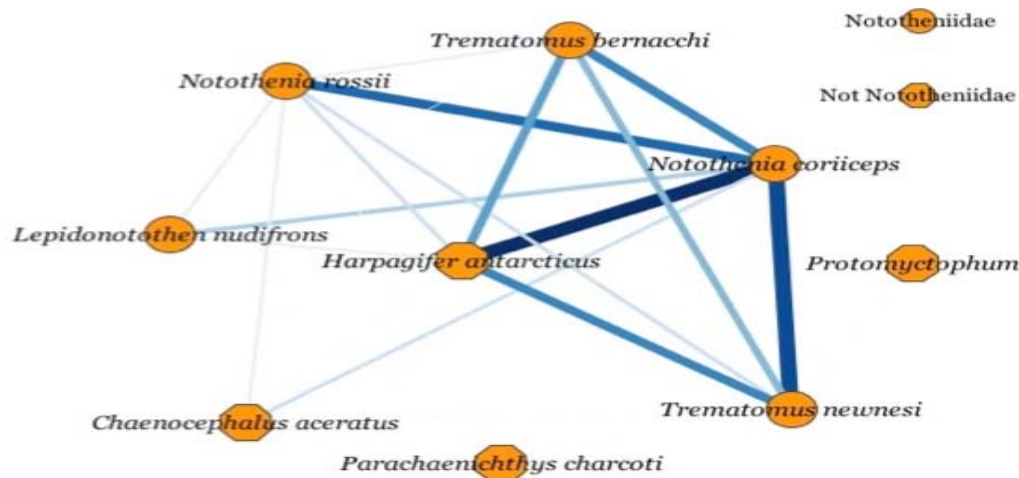
229 For instance, all trophic species of sponges form a more connected group than with the rest of the
230 prey species. Furthermore, some species of echinoderms, amphipods and demersal fish are
231 intensively competing for common food sources (see link width and color, Fig. 4).



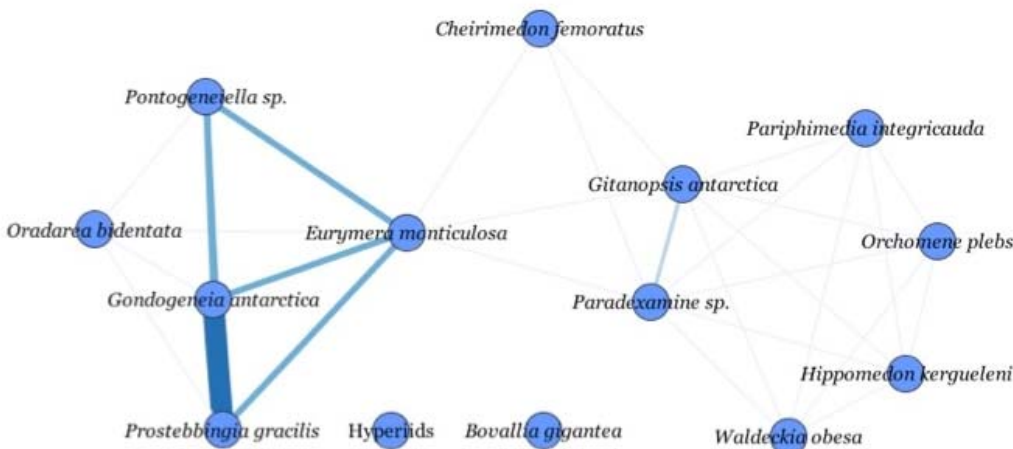
232 Fig. 4. Competition graph for the Potter Cove FW. Node colors (as in Fig. 2): functional groups.
233 Link width and colors: number of shared prey.

234 To study these potential species interactions, specific competition graphs for the latter two
235 functional groups were built (Fig. 5). The fish overlap graph includes 9 biological species and 28
236 competitive interactions. It is worthy to note that two species, *Notothenia coriiceps* and
237 *Harpagifer antarcticus*, presented highly overlapping diets. Moreover, *N. coriiceps* shares many
238 of the same prey species, which may or may not involve any competition (Fig. 5 a). On the other
239 hand, the amphipod overlap graph suggested low resource overlap among species. However,
240 *Gondogeneia antarctica* and *Prostebbingia gracilis* have many prey in common (Fig. 5 b).

(a)



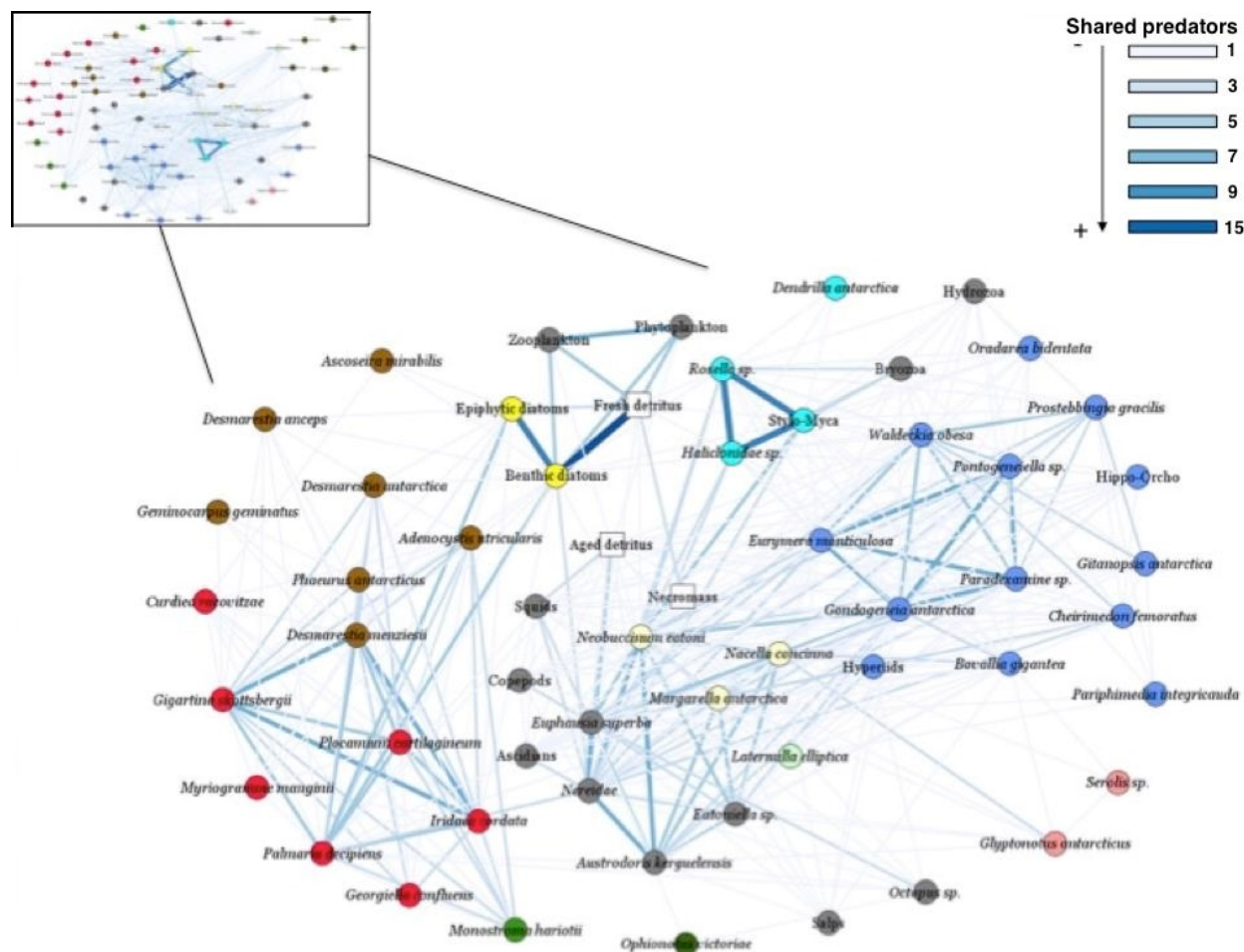
(b)



241 Fig. 5. Competition graphs for (a) demersal fish and (b) amphipod functional groups. Link width
 242 and colors: number of shared prey (see Fig. 4).

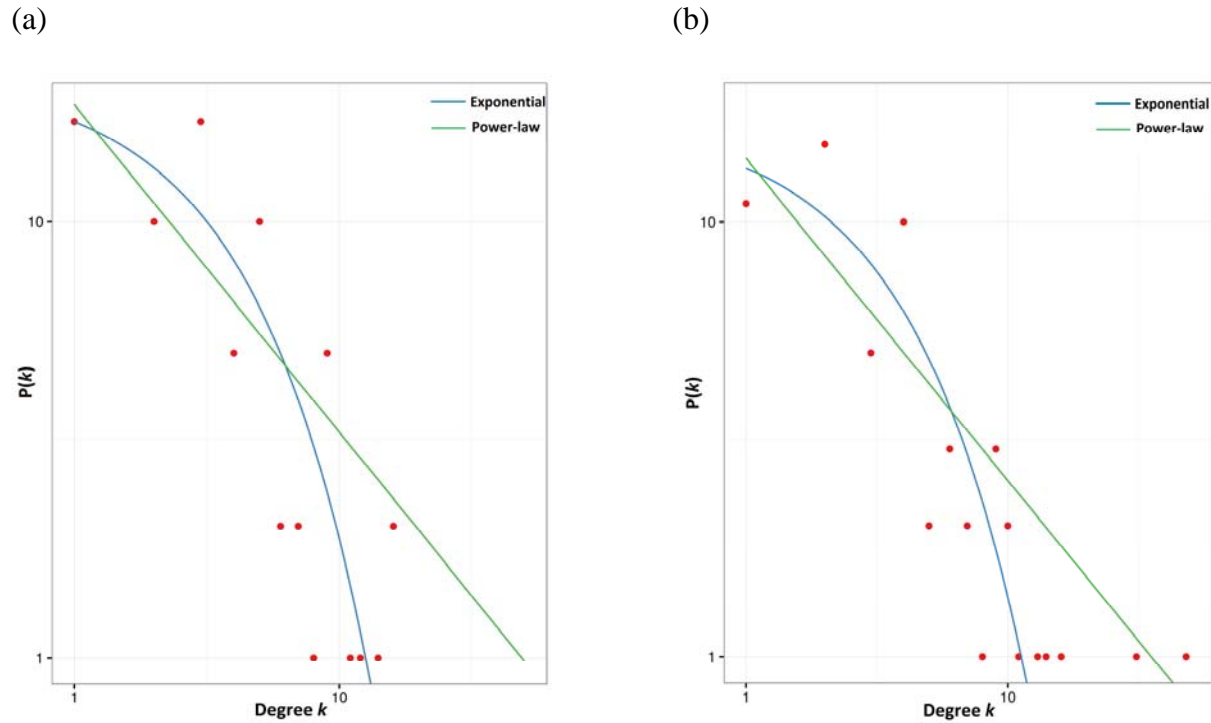
243 The common-enemy graph shows a hyperconnected structure, where the majority of the species
 244 are connected. It contained 74 prey species and 1497 indirect interactions (Fig. 6, up-left). Most
 245 of the species are connected due to having only one predator in common. In order to elucidate
 246 groups of species having stronger indirect interactions, we eliminated links with value 1. This
 247 new graph (Fig. 6, large network) showed groups of species connected by strong interactions:

248 sponges (except for *Dendrilla antarctica*), benthic diatoms – fresh detritus, benthic diatoms –
249 epiphytic diatoms, zooplankton – phytoplankton, some species of amphipods (i.e. *Gondogeneia*
250 *antarctica* – *Paradexamine* sp. – *Prostebbingia* sp. – *Eurymera meticulosa*), and several red and
251 brown algae (*Gigartina skottsbergii* – *Desmarestia menziesii* – *Iridaea cordata*) (Fig. 6).



252 Fig. 6. Common-enemy graph for Potter Cove FW. Original graph in left upper corner. Large
253 network shows prey species that share more than one predator. Node colors (as in Fig. 2):
254 functional groups. Link width and colors: number of shared predators.

255 Degree distribution of links in the competition and common-enemy graphs (Fig. 7) fit best to an
256 exponential model (Table 2).



257 Fig. 7. Log-log degree distribution of links $P(k)$ for (a) the competition and (b) common-enemy
258 graphs. Best fit is the exponential model for both distributions.
259

260 Comparison between the Potter Cove FW and other marine webs showed that linkage density
261 (L/S) and connectance (C) were lower in the Potter Cove web. The proportions of top and basal
262 species were relatively high, whereas the percentage of omnivory was the second lowest among
263 all webs that were compared. While the characteristic path length in Potter Cove FW was similar
264 to the rest of the FWs, the clustering coefficient was one order of magnitude lower (Table 3).

265 Table 2. Model fit of exponential and power-law models for degree distributions of total FW (in-
 266 and out-links), competition (only predators) and common-enemy (only prey) overlap graphs.
 267 AICc and AIC_Δ are the Akaike corrected for small sample size and delta values for each
 268 candidate model. * Indicates best-fit model.

	Model	AICc	AIC_Δ
Total FW	Exponential *	94.90	0.000
	Power-law	101.70	6.756
Competition graph	Exponential *	72.56	0.000
	Power-law	76.31	3.751
Common-enemy graph	Exponential *	76.16	0.000
	Power-law	82.00	5.839

269 Table 3. Comparison of network properties between Potter Cove and other marine FWs. S =
 270 number of trophic species, L/S = linkage density, C = connectance (L/S²), T = % top species, I =
 271 % intermediate species, B = % basal species, Omn = percentage of omnivorous, TL = mean
 272 trophic level, ChPath = characteristic path length, CC = clustering coefficient. NA: not available
 273 data.

Food web	<i>S</i>	<i>L/S</i>	<i>C</i>	<i>T</i>	<i>I</i>	<i>B</i>	<i>Omn</i>	<i>TL</i>	<i>ChPath</i>	<i>CC</i>	<i>Source</i>
<i>Marine non-polar webs</i>											
Car. reef (s)	50	11.1	0.22	0	94	6	86	2.9	1.6	0.36	Opitz (1996)
Benguela	29	7.0	0.24	0	93	7	76	3.2	1.6	0.30	Yodzis (1998)
NE US Shelf	79	17.8	0.22	4	94	3	62	3.1	1.6	0.31	Link (2002)
Carib. (l)	249	13.3	0.05	NA	NA	NA	NA	NA	1.9	0.16	Rezende et al. (2009)
Lough Hyne	350	14.7	0.04	NA	NA	NA	NA	NA	NA	NA	Riede et al. 2010
<i>Marine polar webs</i>											
Arctic I	140	6.8	0.05	40	56	14	80.7	2.3	NA	NA	Bodini et al. (2009)
Arctic II	159	8.6	0.05	NA	NA	NA	52	2.7	2.3	0.25	Kortsch et al. 2015
Antarctic	586	6.8	0.01	23	21	56	41.1	2.2	3.0	0.14	de Santana et al. (2013)
Weddell Sea	491	33.2	0.07	6.5	80	13.5	67	2.5	NA	NA	Jacob (2005)
Potter Cove	91	3.4	0.04	19	47	34	45	2.1	1.8	0.08	This study

274 **4. Discussion**

275 4.1. Food web complexity and structure

276 Potter Cove FW properties of complexity and structure showed several singularities that make
277 the web unique in terms of species-richness, link configuration and topological characteristics.
278 Network complexity was mainly assessed by linkage density (L/S) and connectance (C). Both of
279 these properties were found to be relatively low in the Potter Cove web: $L/S=3.4$ and $C=0.04$.
280 Nevertheless, direct comparisons of linkage density and connectance values suggest that marine
281 FWs tend to resemble each other, and that they are fundamentally different from other kinds of
282 FWs, based on their high values (Dunne et al. 2004). Opposite to this hypothesis of marine FW
283 similarity, de Santana et al. (2013) found that connectance in the Arctic marine FW was 5 times
284 larger than that of the Antarctic one (0.05 versus 0.01). Furthermore, within marine webs, polar
285 networks tend to display low values of linkage density (de Santana et al. 2013). In this sense,
286 complexity exhibited in the Potter Cove FW resembles closely to what is known so for FWs in
287 Polar regions.

288 Could low values of linkage density and connectance in Potter Cove network be a consequence
289 of methodological issues? Dunne et al. (2002b) suggested that both low- and high-connectance
290 FWs are unusual, and that extreme connectances may sometimes be artifacts of assembly
291 procedures. They exemplified this statement by showing that the lowest connectance webs they
292 studied ($C \approx 0.03$, Grassland and Scotch Broom), which is similar to Potter Cove FW
293 connectance value, are “source-webs”. These are constructed by linking food chains upward
294 starting from one or a few basal species. The Potter Cove FW is a species-rich ecological
295 network and not a source-web since it was not constructed upward from one or two basal species
296 but it is characterized by $> 30\%$ basal species. Thus there is no evidence we know of which

297 suggests that our low values of linkage density and connectance were a consequence of the
298 assembly procedure of the network. In turn this implies that the assembly-connectance
299 relationship in FWs is not as strong as previously thought (Dunne et al. 2002b).

300 Whether ecological networks display low or high L/S and C values is crucial to gain insight in
301 the ecosystem's synthetic properties like robustness. Empirical analyses of FWs support the
302 notion that the robustness of a FW increases with its linkage density and connectance (De
303 Angelis 1975, Dunne et al. 2002a, Montoya and Solé 2003). Low values of L/S and C found in
304 Potter Cove FW, combined with ongoing climate change effects on benthic communities in the
305 area (Pasotti et al. 2015b, Sahade et al. 2015), suggest potential ecosystem fragility which need
306 to be addressed.

307 Furthermore, direct comparison of common FW properties, like percentages of top, intermediate
308 and basal species, indicates that the Potter Cove network has strong structural differences and
309 shows unique features compared to other marine ecosystems. Important dissimilarities were
310 found in top and basal species values as Potter Cove FW shows a higher number of these trophic
311 species. After comparing 19 FW properties, Dunne et al. (2004) concluded that the excessively
312 low percentage of basal taxa in marine FWs compared to other systems is clearly an artifact of
313 poor resolution of primary producers and consumer links to them. One of the methodological
314 strengths of Potter Cove FW is the high taxonomic resolution of the basal nodes. A good
315 taxonomic resolution of the lower trophic levels, such as the macroalgal community, is essential
316 to understand Potter Cove ecosystem functioning, since there seems to be a species-specific
317 selective consumption (Barrera-Oro and Casaux 1990, Iken et al. 1997, Iken et al. 1998).

318 Furthermore, algal species show a marked pattern of depth distribution and tridimensional
319 structure (Quartino et al. 2005, Huang et al. 2007). Macroalgae are one of the main primary

320 producers in Potter Cove, and probably support a large fraction of secondary production of the
321 benthos community (Quartino et al. 2008). Implications in ecosystem functioning and stability
322 are only possible to elucidate in FWs where species involved in energy and matter transfer
323 processes are well represented.

324 Proportions of intermediate species (*I*) and omnivory (*Omn*) in Potter Cove FW are relatively
325 low when compared to other marine webs, but close to values for Antarctic FW as reported by de
326 Santana et al. (2013). Levels of *I* and omnivory are usually correlated in FW studies, as the
327 majority of species acting as predators and prey also feed on more than one trophic level
328 (omnivorous). The importance of omnivory for the structure and dynamics of FWs is a long-
329 standing controversy in ecology (Burns 1989, Polis 1991), and whether omnivory stabilizes or
330 destabilizes webs is not clear (Vandermeer 2006, Namba et al. 2008, Johnson et al. 2014). In
331 Antarctica a recent study suggests that omnivory is a beneficial trait as it allows for more
332 responsive and flexible utilization of food sources that may be temporally and spatially
333 constrained and unpredictable (Norkko et al. 2007). The omnivory reported here for Potter Cove
334 FW is the second lowest percentage among marine webs included in the present study, would
335 suggest a low stability for Potter Cove FW. Additionally, this result generates testable
336 hypotheses about the probable stabilizing role of omnivory in large communities, since it was
337 proven that the risk of secondary extinctions after primary loss of species depends on the trophic
338 position of the extinct species (Borrvall et al. 2000) and the diversity of that trophic level
339 (insurance hypothesis, Yachi and Loreau 1999).

340 The mean trophic level for this FW (2.1) is also relatively low, which is the result of several
341 singularities of the Potter Cove ecological network. Firstly, as already mentioned, the number of
342 basal trophic species is high, exceeding 30% of number of species (diversity). What's more, the

343 maximum trophic level was 4.27, lower than most other FWs studied (Dunne et al. 2002b, 2004),
344 which implies that top and basal species are separated by few intermediate taxa. It is worthy to
345 clarify here that Antarctic top predators, e.g. marine mammals, might increase maximum trophic
346 level of the web but were not included as they are rarely reported in the Cove. Therefore, the
347 transfers of energy or nutrients from the base to the top of Potter Cove FW is small, so that the
348 number of times chemical energy is transformed from a consumer's diet into a consumer's
349 biomass along the FW is also small. Another reason why the mean trophic level is low is the fact
350 that most predators at intermediate levels (e.g. amphipods, isopods, bivalves, *N. coriiceps*) feed
351 predominantly on algae species and/or detritus, being mainly the product of dead and
352 decomposed macroalgae in Potter Cove (Iken et al. 1998, Huang et al. 2006, Quartino et al.
353 2008). The macroalgal detritus decomposes and is eaten by detritivores and suspensivores (e.g.
354 sponges, ascidians, bryozoans, cnidarians), supporting an important amount of the secondary
355 production (Tatián et al. 2004). The obtained low mean trophic level for Potter Cove FW clearly
356 shows what species-specific and/or community studies have suggested. These characteristics of
357 ecological communities have a high impact on ecosystem functioning, such as nutrient and
358 carbon cycling, and trophic cascades (Post 2002).

359 Short characteristic path length for Potter Cove FW (\approx two degrees of separation) is similar to
360 lengths found in other marine FWs. The length between pairs of species within marine webs is
361 low (\approx 1.6 links) compared to other types of FWs, with values ranging from 1.3 to 3.7 (Dunne et
362 al. 2002b). This suggests that most species in Potter Cove FW are potentially very close
363 neighbours, and that negative effects could spread rapidly and widely throughout the web
364 (Dunne et al. 2002a).

365 Additionally, the clustering coefficient in this web (0.08) was an order of magnitude lower than
366 those reported for other marine FWs (Link 2002, Dunne et al. 2004). A low coefficient indicates
367 that most species are similarly connected to each other, i.e. there are no densely sub-groups of
368 species interacting with one other. Particularly, the clustering coefficient result of Potter Cove
369 FW might be the consequence of hubs (i.e. species with high degree, > 20 links) connected with
370 most of the species across the web and not with a specific group of species. The most connected
371 species, *N. coriiceps* (demersal fish) and *Ophionotus victoriae* (brittle star), have the widest
372 ecological niches in our study, being generalists and omnivores. By feeding across several
373 trophic levels and transversely in the FW, these species have a strong effect on clustering.
374 Specifically, *N. coriiceps probably* represents a keystone species in the benthopelagic coupling
375 process promoting the transfer of matter and energy between habitats (Barrera-Oro and Casaux
376 2008). At the same time, these hub species might be essential for understanding the spread of
377 perturbations (i.e. biodiversity loss) through the entire FW network.

378 4.2. Degree distribution and overlap graphs: implications for ecosystem 379 functioning

380 Webs with low connectance ($C \approx 0.03$), such as Potter Cove FW, are more likely to display
381 power law degree distributions (Dunnet et al. 2002a, Montoya and Solé 2002), consistent with
382 the small-world phenomenon. These are webs combining high clustering, like regular lattices and
383 short path length, like random graphs (Watts and Strogatz 1998). Therefore, the Potter Cove FW,
384 with a low estimated connectance ($C = 0.04$), should display a power law degree distribution.
385 However, it fits best to an exponential distribution according to the low clustering coefficient.
386 The existence of a universal functional form in the degree distribution of FWs is still under

387 debate, though Stouffer et al. (2005) have shown that approximately exponential degree
388 distributions can be derived from two different models: nested-hierarchy and generalized
389 cascade.

390 The influence of the degree distribution on the vulnerability of complex networks against
391 random failures and intentional attacks has become well known since the work of Albert et al.
392 (2000). Considering this relationship between degree distribution and vulnerability, Potter Cove
393 FW would be highly fragile to the removal of the most connected species, but not as much as in
394 power law networks (Albert et al. 2000, Dunne et al. 2002a, Estrada 2007). Furthermore, de
395 Santana et al. (2013) suggested that less connected communities should be more sensitive to the
396 loss of basal species than complex communities because the consumers in simple communities
397 are dependent on only a few species and cannot survive their loss. Nevertheless, we hypothesize
398 that although Potter Cove FW shows low connectance, it will be robust against basal node
399 extinctions due to the high percentage of these trophic species.

400 In addition, degree distribution of links in the competition graph showed that most species have
401 limited diets, feeding exclusively on few prey, whereas few species feed on a large amount of
402 food-sources, usually being generalists. The graph suggests that several predator species have
403 high prey overlap and thus the potential to strongly interact and compete for common prey; this
404 is the case for sponges, demersal fish and amphipods. We focused the analysis on fish and
405 amphipods as they are known to play an important role on the Antarctic marine ecosystem
406 (Barrera-Oro and Casaux 1998, Momo et al. 1998, Barrera-Oro 2002, Huang et al. 2006). Fish
407 data reflects that there is dietary overlap between *N. coriiceps* and *H. antarcticus* on the one hand
408 and between *Trematomus newnesi* and *N. rossii* on the other hand. Most of the dietary
409 comparisons for demersal Antarctic fish communities have dealt with food overlap between fish

410 species pairs (Barrera-Oro 2003). Dietary overlap index (“S” index of Linton et al. 1981)
411 between *N. coriiceps* and *N. rossii* in Potter Cove as estimated by Barrera-Oro (2003) was 55%,
412 meaning that these species could compete for more than half of their food-sources. The same
413 study estimated the index for *N. coriiceps* – *T. newnesi*, being 18%, and *N. coriiceps* – *H.*
414 *antarcticus*, being 19%. Barrera-Oro (2003) concludes that there is no evidence of food
415 competition among the shallow cold-water fish communities in Potter Cove. Nevertheless, our
416 results show that *N. coriiceps* and *H. antarcticus* have many prey in common, with a high degree
417 of overlapping. However, due to the differences in mobility, habitat use and adult size between
418 these two species (total length: 45 and 13 cm respectively), competition is probably low (Casaux
419 1998, Barrera-Oro 2003). Although the first one is a generalist and the latter a specialist, both
420 species can be grouped in the same feeding category given that they are benthos feeders, eating
421 amphipods (e.g. *Gondogeneia antarctica*, *Paradexamine* sp., *Prostebbingia* sp., *Eurymera*
422 *monticulosa*), gastropods (e.g. *Margarella antarctica*, *Nacella concinna*, *Eatoniella* sp.,
423 *Neobuccinum eatoni*), polychaetes (e.g. Nereidae), and krill in summer (*Euphausia superba*).
424 On the other hand, the competition graph for amphipods exhibited low dietary overlap among
425 species. It is worth mentioning that hyperiids and *Bovallia gigantea* are not connected, which
426 indicates that they do not share food sources with any other amphipods, nor between themselves.
427 Hyperiids and *B. gigantea* are both carnivores, though the latter mainly feeds on other species of
428 amphipods, such as *E. monticulosa*, *Prostebbingia* sp. and *G. antarctica* (Richard 1977). On the
429 contrary, hyperiids principally eat planktonic prey, such as copepods (Pakhomov and
430 Perissinotto 1996). The most important result of the overlap graph is that species are separated
431 according to their feeding strategies: herbivores (*P. gracilis*, *G. antarctica*, *O. bidentata* and
432 *Prostebbingia* sp. – left of the graph), detritivores (*C. femoratus* and *Paradexamine* sp. – middle

433 graph), and scavengers (*W. obesa*, *H. kergueleni*, *O. plebs* and *P. integricauda* – right of the
434 graph). This demonstrates the importance and utility of the analysis of competition graphs, in
435 order to better understand alternative energy pathways within apparent trophic guilds; analysis
436 that would be improved by adding information on each predator species (e.g. body size and
437 mass, niche specialization).

438 Common-enemy graph derived from Potter Cove FW showed a hyper-connected graph, which
439 implies that most prey species share at least one predator. The fact that the prey overlap graph of
440 this FW exhibited high connectivity and exponential distribution has implications for the
441 functioning of the ecosystem. High-connected prey in Potter Cove FW are: phytoplankton –
442 zooplankton, benthic diatoms – epiphytic diatoms, and fresh detritus – benthic diatoms. The
443 latter shows that several sources of food and alternative energy pathways exist in the Potter Cove
444 ecosystem: phytoplankton (Ahn et al. 1993), benthic microalgal production (Dayton et al. 1986,
445 Gilbert 1991), and horizontal advection of allochthonous food particles (Dunbar et al. 1989);
446 important sources of organic matter for marine organisms living in coastal Antarctic ecosystems.

447 In conclusion, comparison of FW properties revealed a particular combination of characteristics
448 for the Potter Cove ecological network: middle size ($S \approx 100$) compared to other marine FWs,
449 low linkage density and connectance (with no evidence of being an artifact of resolution or
450 assembly procedure), low %-omnivory, short path length and low clustering coefficient.

451 According to the overlap graphs and their degree distributions, and the consistency with field
452 observations and investigations, we suggest these analyses are useful tools to gain insight into
453 ecosystem functioning. What is more interesting, the common-enemy graph showed the
454 existence of alternative energy pathways consistent with field investigations in the Cove. As also

455 suggested for East Antarctica FW (Gillies et al. 2012), carbon flow among the benthic fauna in
456 Potter Cove is complex, with multiple sources of carbon being utilized, which can be asserted
457 given the good basal resolution of our network.
458 From a network perspective, Potter Cove FW properties suggest fragility and potential trophic
459 cascade effects although multiple energy pathways might add robustness to the web. Our results
460 suggest that species with a high number of links (e.g. *Notothenia corriceps*, *Ophionotus*
461 *victoriae*, *Gondogeneia antarctica*) could be considered as keystone species for the robustness of
462 Potter Cove ecosystem.

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684 **Appendices**

685 Supplementary material Appendix A and B are available at DOI [10.6084/m9.figshare.4498715](https://doi.org/10.6084/m9.figshare.4498715).