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.

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 m^3 s^{-1} in the Matias Creek and

104   from 0.08 to 3.8 m^3 s^{-1} in Potter Creek (Varela 1998). Suspended sediment discharges ranged

105   between 0.04 and 15 kg m^{-3} (average = 0.14 kg m^3), 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).

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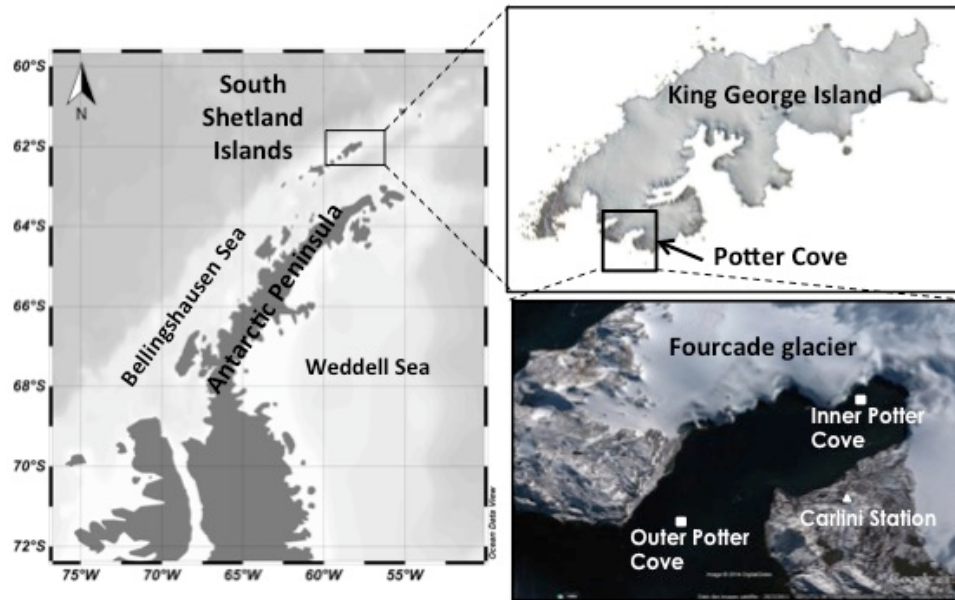
108   Fig. 1. Map of Potter Cove and its location on Isla 25 de Mayo/King George Island.

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

6

122   established by sampling few individuals (n ≈ 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 ocurrence (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

7

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

$$TLj = 1 + \sum_{i=1}^{S} lij \frac{TLi}{nj}$$

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).

9

3. Results

The Potter Cove FW (Fig. 2) includes 91 species, composed of 71 biological species, 17

trophospecies (i.e., merging two or more taxonomic species by trophic similarity) and 3 non-

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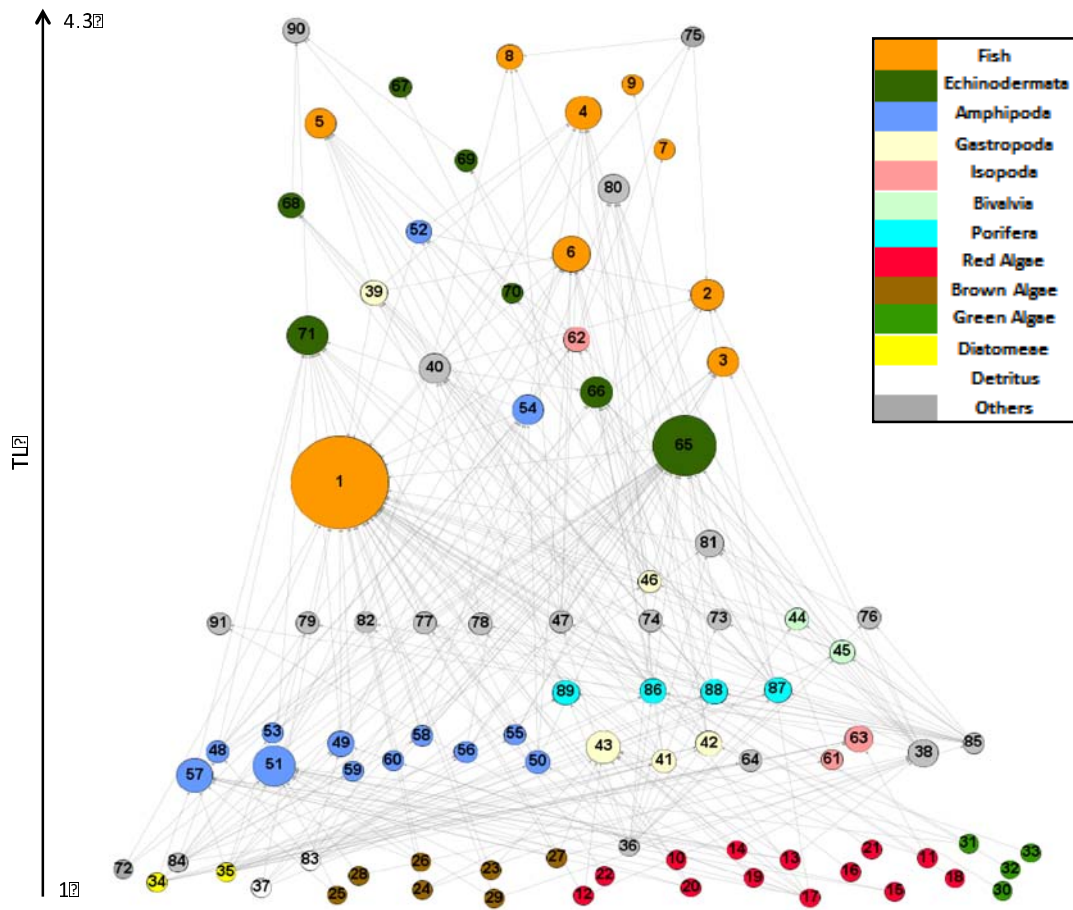
Fig. 2. Graphic representation of Potter Cove FW with the trophic level (TL) on the vertical scale and node width proportional to the total degree (in- and out-). Node colors are by functional group. Network was plotted with Visone (version 2.9.2). See electronic supplementary material (Appendix B) for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

Algae (24 species) comprise red (13 spp.), brown (7 spp.) and green algae (4 spp.). The next

trophic levels consist of 13 amphipod species, 3 isopod species, 4 sponge species (one

10

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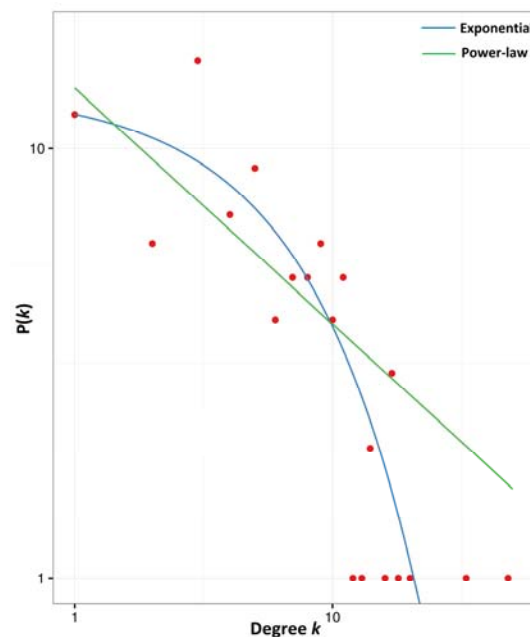
225   Fig. 3. Log-log degree distribution of links *P(k)* for Potter Cove FW. Two candidate models are
226   shown. Best fit is the exponential model.

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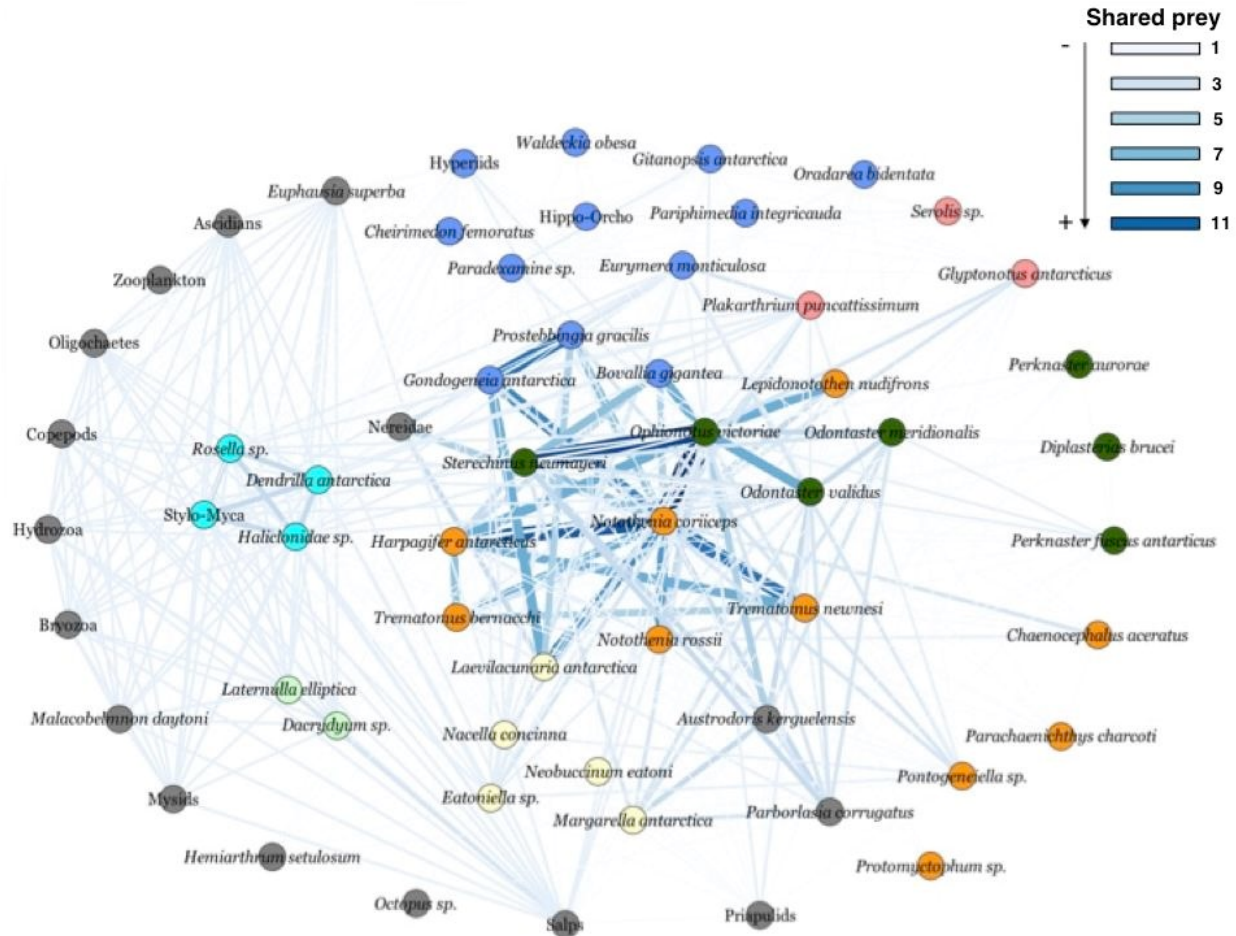
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Fig. 4. Competition graph for the Potter Cove FW. Node colors (as in Fig. 2): functional groups. Link width and colors: number of shared prey.

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

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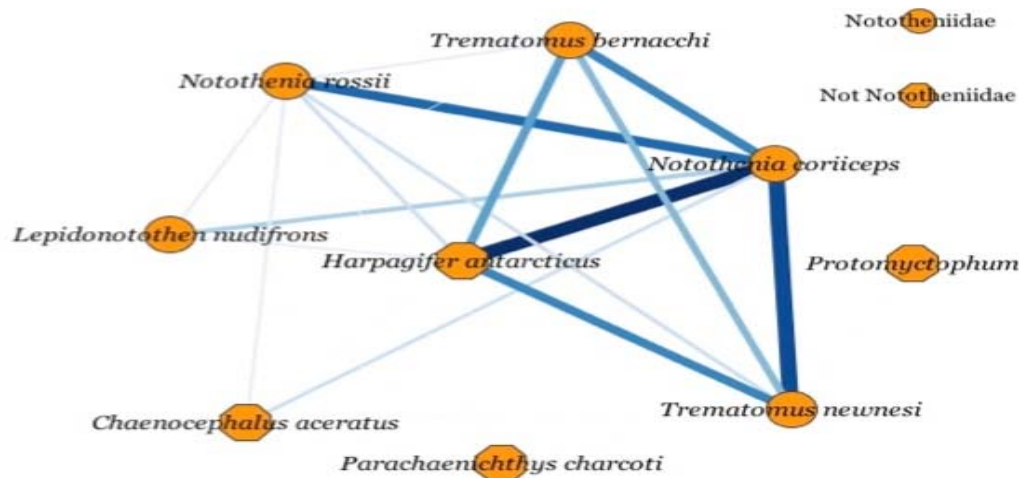
(b)
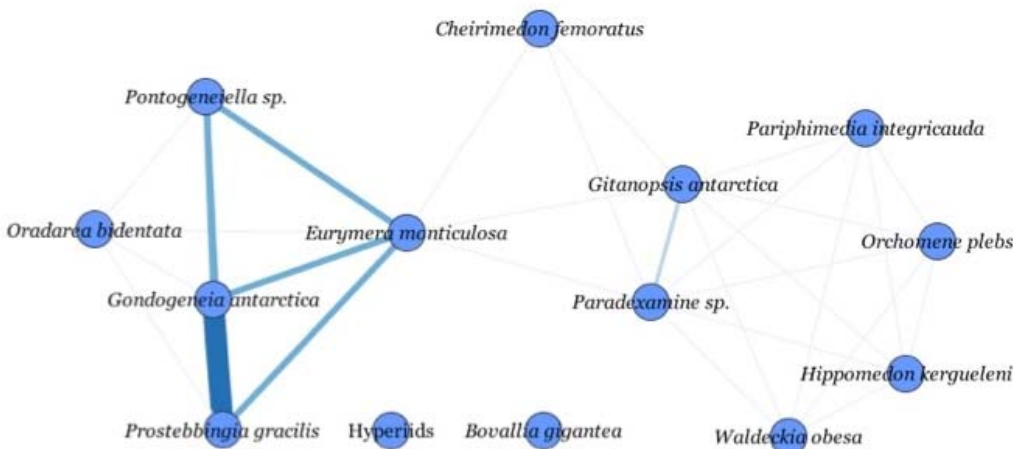
241   Fig. 5. Competition graphs for (a) demersal fish and (b) amphipod functional groups. Link width
242   and colors: number of shared prey (see Fig. 4).

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:

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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).

(a)   (b)

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

Comparison between the Potter Cove FW and other marine webs showed that linkage density

(L/S) and connectance (C) were lower in the Potter Cove web. The proportions of top and basal

species were relatively high, whereas the percentage of omnivory was the second lowest among

all webs that were compared. While the characteristic path length in Potter Cove FW was similar

to the rest of the FWs, the clustering coefficient was one order of magnitude lower (Table 3).

16

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$_\Delta$ are the Akaike corrected for small sample size and delta values for each
268 candidate model. * Indicates best-fit model.

	Model	**AICc**	**AIC$_\Delta$**
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/S^2), 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	*S*	*L/S*	*C*	*T*	*I*	*B*	*Omn*	*TL*	*ChPath*	*CC*	*Source*
Marine non-polar webs											
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
Marine polar webs											
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

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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

20

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 (≈ 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 (≈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).

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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 bentho-pelagic 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

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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 el 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

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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 allochtonous 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

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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.

463   **Acknowledgments**

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684 **Appendices**

685   Supplementary material Appendix A and B are available at DOI 10.6084/m9.figshare.4498715.