Ecological networks of an Antarctic ecosystem: a full description of non-trophic interactions

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ABSTRACT

Interactions between organisms are very diverse and attend to multiple biological demands, hence understanding ecological communities requires considering different types of species interactions beyond predation. In this work, we assemble for the first time the non-trophic networks of an Antarctic ecosystem. We report mutualistic (+/+), competitive (-/-), commensalistic (+/0) and amensalistic (-/0) interactions between species of Potter Cove marine community (South Shetland Is., Antarctica). Based on network approach we present a full description of each type of interaction and analyze its distribution according to different species-level properties. Also, we construct a multiple interactions network including trophic and non-trophic interactions and study networks-level properties. We found more than double non-trophic interactions than trophic ones mostly corresponding to competitive interactions involving mid-trophic level species. Low-trophic level species were mainly involved in mutualistic and amensalistic interactions. We observed that interactions networks display differences of its structural properties. Finally, we study the importance of adding non-trophic interactions to gain insight into the function of the whole community. We show that including a description of species interactions in ecological networks analysis provides a better understanding of ecosystems as a whole which could be crucial to comprehend and predict ecosystems' responses to environmental disturbances.

Key words: non-trophic interactions, ecological networks, multiple interactions network, species-level properties, networks-level properties.

INTRODUCTION

Trophic interactions among species and topological analyses of food webs have lead multiple applications in ecological communities and many advances have been developed in this regard (Paine 1966, Cohen 1977, Post & Pimm 1983, Cohen & Briand 1984, McCann et al. 1998, Martinez et al. 1999, Williams & Martinez 2000, Dunne et al. 2002, Netuel et al. 2002, Pascual & Dunne 2006, Albouy et al. 2014, among many others). Nevertheless, it is widely known that interactions between co-occurring species of an ecological community involve much more than just trophic interactions (Kéfi et al. 2012, Pocock et al. 2012, Kéfi et al. 2015, 2016, Mougi 2016a). Indeed, many studies have reported different types of associations between species and consequently different types of non-trophic interactions in a given community (Bloom 1975, Kneib 1991, Amsler et al. 1999, McClintock et al. 2005, Bascompte & Jordano 2008). A particular example of this occurs in the West Antarctic Peninsula (WAP), one of the most affected places on earth by climate change, where a large number of species that are directly (or indirectly) related have been reported for mutual benefit - such as macroalgae species and amphipods through chemical mediation - and epibiotic interactions (Dayton et al. 1974, Gutt 1998, 2000, Aumack et al. 2010, Amsler & McClintock 2014).

On the other hand, non-trophic interactions have been studied in many communities considering different approaches, but their role on ecosystem structure and function was scarcely addressed. For example, Hacker & Gaines (1997) presented a qualitative theoretical model that considers how direct positive interactions (mutualism and commensalism) affect community species diversity. Mougi & Kondoh (2012) showed that multiple interaction types hold the key to understand community dynamics and suggested that antagonistic and mutualistic interactions can stabilize population dynamics. Also, Mougi (2016a, b) showed that non-trophic interactions such as amensalistic, commensalistic and mutualistic play a crucial role in communities' persistence. More recently, Guerrero-Ramírez & Eisenhauer (2017) assessed the influence of non-trophic interactions on biodiversity-ecosystem functioning relationships. Non-trophic interactions have also been studied from a network perspective, considering different types of interactions among species and different community traits. For instance, Bascompte & Jordano (2007, 2008, 2009) studied the structure and complexity of mutualistic networks suggesting that these networks can be regarded as the architecture of biodiversity. Furthermore, Bastolla et al. (2009) showed that the number of co-existing species in a community can be determined by both the structure of mutualistic networks and the structure of competition for common resources networks. Recently, some studies have analyzed trophic and non-trophic networks in order to understand the patterns and dynamics of diverse species interactions in nature (Kéfi et al. 2012, Pocock et al. 2012, Kéfi et al. 2015, 2018). Some works focused on ecosystems' stability or persistence by developing theoretical

(Thébault & Fontaine 2010) or analytical approaches (Allesina & Tang 2012) while others developed dynamical modeling (Kéfi et al. 2016). More recently, few studies have incorporated multiple interactions networks integrating more than two interactions types in the same network (Kéfi et al. 2016, Pilosof et al. 2017, García Callejas et al. 2018, Hervías-Parejo et al. 2020). So far, studies on species interactions in Antarctic ecosystems have focused on trophic interactions without considering non-trophic relationships and their importance in the structure and function of communities (Marina et al. 2018a, Cordone et al. 2020, McCormack et al. 2021).

Regarding Antarctic ecosystems, Potter Cove (25 de Mayo/King George Is., South Shetlands Is.) is one of the most biodiverse fjords of the WAP (Grange & Smith 2013). It is not only a biodiversity hotspot but also one of the ecosystems where drastic environmental and ecological changes are happening due to climate change (Schloss et al. 2012, Quartino et al. 2013, Sahade et al. 2015, Hernández et al. 2019). In this sense, an accurate assessment of the structure and function of Potter Cove is crucial to understand how WAP fjord ecosystems could respond to climate change (Vaughan et al. 2003, Turner et al. 2005, Meredith & King 2005, Bromwich et al. 2013, Nicolas & Bromwich, 2014). Potter Cove food web has been recently described and analyzed with a high-resolution level (Marina et al. 2018a, Cordone et al. 2020) and previous studies showed that this ecosystem is relatively robust to perturbations on macroalgae species (Cordone et al. 2018). However, little is known about the structure of non-trophic ecological networks in Potter Cove. Incorporating non-trophic interactions could add a new perspective and yield unexpected results about species role and ecosystem function (Kefi et al. 2012, Mougi 2016a, b).

In this work we present and characterize the networks describing the nontrophic interactions among species from Potter Cove marine ecosystem and describe the organization of the identified interactions in relation to species properties. We: 1) provide a detailed description of each type of interactions among species 2) analyze the distribution of the non-trophic interactions and 3) assemble trophic and non-trophic networks in a highly-resolved multiple interactions network. These aspects might help us to better understand the role of non-trophic interactions and community's function as a whole.

METHODS

Species Interactions

Non-trophic interactions

The identification of mutualistic (+/+), commensalistic (+/0) and amensalistic (-/0) interactions was done by compiling information through an extensive bibliographic search. More than 70 articles from Antarctic marine communities were reviewed in

order to identify non-trophic interactions between species in Potter Cove marine ecosystem (25 de Mayo/King George Is., South Shetland Is.) (Appendix I).

Competitive interactions (-/-) were established from the predator secondary graph, the so-called competition network. This network was obtained from the food web (or primary graph) of Potter Cove ecosystem described in Marina et al. 2018a. We considered a competitive interaction when two predators shared at least one prey.

Overall, we assembled four networks considering the following types of interactions: mutualistic, commensalistic, amensalistic and competitive. Species (networks nodes) were identified according to their taxonomic identity. Most of them were identified at species level (e.g. *Euphausia superba*) but some were identified as a group of biological species (e.g. Phytoplankton). Every network was plotted with the software Visone 2.18.

Trophic interactions

Information of co-occurring species and their feeding habits was obtained mostly from publications resulted from a cooperation program between Argentina and Germany that started in 1994 and continued for more than 20 years (Wiencke et al. 1998, 2008). Based on these data, Marina et al. 2018a described the Potter Cove food web including 91 species and 307 interactions. Here, we incorporated such trophic relationships (+/-) for constructing the multiple interactions network described below.

Network assemblage

Non-trophic networks

We considered the same set of species interacting with each other at multiple levels when we developed the non-trophic networks. Mutualistic (+/+), commensalistic (+/0) and amensalistic (-/0) networks were first described as binary matrices representing presence (1) or absence (0) of an interaction. As mentioned above, competitive network was based on the definition of secondary graph (Box I).

Box I

We described non-trophic networks webs as complex networks defined by *n×m* binary matrices with the form

$$A = \left[\alpha_{ij}\right]^{n \times m} \quad (1)$$

The matrix A describes the interactions between the sets of species n and m and its elements, α , represent the presence or absence of an interaction in the web F as following:

$$\alpha_{i,j} = \begin{cases} 1, \ k_{ij} \in (F) \\ 0, \ k_{ij} \notin (F) \end{cases}$$
(2)

Where k_i , k_j are two any nodes of the n and m set respectively, and $k_{ij} \in F$ indicates the interaction between i and j. Note that if n=m, A would be an adjacency matrix that could represent, for example, a food web.

The construction of the competitive network was developed based on the definition of secondary graph and can be explained as follow:

Given the food web *F*, the vertices of the competition graph called G(F) are the same as those of *F*, i.e., one vertex for each species in the community. The edges of G(F) between distinct vertices *i* and *j* are undirected and represent an overlap between diets of species *i* and *j*, i.e. these edges exist if and only if there exists some third vertex *k* in *F* such that *i* eats *k* and *j* eats *k*. Thus, in G(F) two vertices are linked by an edge if there are arrows in *F* from *k* to *i* and from *k* to *j*, for at least one *k*; or if one row *k* of the adjacency matrix has elements equal to 1 in both column *i* and column *j* (Cohen 1978).

Multiple interactions network

We constructed the multiple interactions network based on the 91 trophic species reported by Marina et al. (2018a) for Potter Cove marine ecosystem. We included five types of interactions among species: predator-prey or trophic (+/-), mutualistic (+/+), commensalistic (+/0), amensalistic (-/0) and competitive (-/-).

Network construction was developed considering a square matrix, M, where each interaction was represented by a pair of integers in the interval [-1, 1]. The sign of the non-zero elements indicates if that species benefits (+) or not (-) from the interaction. For example, a competitive interaction between nodes A and C is represented by the pair (-1; -1) in the M_{AC} and M_{CA} positions (Figure 1). A commensalistic interaction is represented by the pair (1; 0) or (0; 1) depending on which species benefits from that interaction. Analogously, an amensalistic interaction is represented by the pair (0; -1) or (-1; 0). Trophic interactions were represented considering which species is the prey and which is the predator in the feeding relationship, i.e. (1; -1) or (-1; 1), where -1 is the prey and 1 is the predator. Finally, mutualism has a single representation pair in the matrix (1; 1) since both species benefit from that interaction.

	Α	в	С	D	Ε
Α	0	1	-1	0	1
в	0	0	0	0	-1
С	-1	0	0	0	0
D	0	0	0	0	0
Ε	1	1	0	-1	0

Figure 1. Representation of the different types of interactions in the multiple interactions network. Each interaction was identified by a combination of integers between -1 and 1.

Network Analysis

We quantified a set of network-level properties to describe each studied network; properties that have been suggested to have implications for the functioning and stability of ecological communities (Pascual & Dunne 2006, Fortuna et al. 2010). Such properties are: 1) number of species (S); 2) total number of interactions or links (L), 3) density (L/S) and 4) percentage of basal (B), intermediate (I) and top (T) species.

We considered connectance (C) as the ratio between observed (L) and possible (S²) interactions:

$$C = L/S^2 \tag{3}$$

where L is the total number of interactions or links, S is the number of species in the interaction matrix. This property is considered as an estimator of community sensitivity to perturbations and it covaries with other network properties (Dunne et al. 2002, Poisot & Gravel 2014).

We also explored species-level properties with the aim of identifying those species that are more important considering the total number and the distribution of its (trophic and non-trophic) interactions. For this, we analyzed: 1) species degree as the sum of incoming and outcoming interactions for each species (all prey and predators of a species in the trophic network, for instance); 2) basal, intermediate and top categories and 3) trophic level for each species. Basal species are those with predators but without prey, intermediate species have prey and predators, and top species have prey but no predators. Trophic level for each species was calculated as one plus the mean trophic level of all of the species resources, where the trophic level of a resource is the chain

length from the resource to a basal species (Williams & Martinez 2004). Properties 2) and 3) were included here based on the trophic network data provided by Marina et al. 2018a.

RESULTS

Non-trophic networks

In Potter Cove marine ecosystem, there were more than twice non-trophic interactions than trophic ones. Within non-trophic interactions, the majority were among predators competing for the same prey (competitive = 76%), followed by mutualistic (15%), commensalistic (5%) and amensalistic (4 %) (Table 1, Appendix II).

More than 60% of the mutualistic interactions identified corresponded to the relationship between some species of amphipods herbivorous (mesograzers) and some macroalgae. About relationships involving commensalistic and amensalistic interactions, most of them (> 90%) corresponded to epibiotic relationships, i.e. relationships between two different organisms in which one of them serves as a substrate for the other, for example ascidians and/or epiphytic diatoms using macroalgae as substrate (Appendix II). We considered this last interaction as an amensalistic interaction (0/-) because epiphytes represent a potentially harmful organism for macrophytes as they compete with them for light and nutrients (Amsler & McClintock 2014) and epiphytes do not specially need the algae to survive since they can grow on different substrate such as rocky or sediments.

Network-level properties

Regarding networks-level properties, non-trophic networks displayed relatively low number of species (S) and interactions (L). However, linkage density (L/S) and connectance (C) were higher in non-trophic networks than in the food web, where competitive (-/-) and mutualistic (+/+) networks presented the highest values for L/S (Table 1). The multiple interactions network presented the highest value for linkage density and the second lowest value of connectance (Table 1). Furthermore, non-trophic networks displayed distinctive characteristics if we consider basal/intermediate/top species categories: 1) in mutualistic and amensalistic networks no top species were involved and 2) in competitive network, interactions occurred among intermediate and top species, where intermediates dominated (Table 1).

	S	L	L/S	С	B	Ι	Т
Mutualistic (+/+)	36	88	2.4	0.36	69	31	0
Commensalistic (0/+)	23	29	1.2	0.16	57	26	17
Amensalistic (0/-)	25	24	0.96	1	49	0	0
Competitive (-/-)	59	478	8.1	0.13	0	74	26
Trophic (+/-)	91	307	3.37	0.04	34	47	19
Multiple interactions network	91	926	10.17	0.11	34	47	19

Table 1. Complexity and structural properties of the non-trophic networks. S = number of species, L= number of links, L/S= density, C= connectance. B, I and T = percentage of basal, intermediate and top species respectively.

Topology of the non-trophic networks was very different depending on the type of interaction: the networks of mutualistic and commensalistic interactions displayed a fragmented topology (Figure 2A,2B) while the network of amensalistic interactions displayed a unique component where one species is connected with the rest (Figure 2C) and competitive interactions network showed a high-connected graph (Figure 2D). The configuration of the multiple interactions network displayed a hyper-connected web (Figure 3).

Species-level properties

When we explored species-level properties, we observed that species of Potter marine ecosystem with the highest number of non-trophic interactions were also those at mid-trophic levels (intermediate species) (Figures 4, 5). Only one species with the most (upper 10%) non-trophic interactions was not in an intermediate species due to its generalist feeding strategy (*Notothenia coriiceps*, trophic level = 2.80). This upper 10% percent is distributed between species of a variety of functional groups, all of them closely related to the benthos (Echinodermata, Amphipoda, Porifera, Gastropoda, demersal fish). For most of these species, the dominant type of non-trophic interaction was competition followed by mutualism (Figures 4, 2A-2D). On the other hand, the species with the least (bottom 10%) non-trophic interactions were mainly macroalgae, with low-trophic levels (basal species). Here mutualism ruled the relationships. Top species, without predators, exhibited a wide range in the number of non-trophic

interactions (min = 8, max = 34). However, the great majority of these interactions were for competing for the same prey (Figures 5, 2D).

It is important to note that species from all trophic levels presented commensalistic interactions, although in low numbers. On the contrary, amensalistic interactions are represented by species from lowest-trophic levels (basal species) (Figure 5). Some of the species with the highest number of this type of interaction (epiphytic diatoms) were also one of the most (upper 10%) connected species regarding non-trophic interactions (Figure 4). Considering all interactions types (multiple interactions network), the species with the highest degree were also those with the highest number of non-trophic interactions, and at mid-trophic levels as mentioned above (Figure 3).



Figure 2. Representation of non-trophic networks: A) mutualistic; B) commensalistic; C) amensalistic and D) competitive network. Species (nodes) ID is represented by a number (Appendix III) and color represents functional groups.



Figure 3. Multiple interactions network of Potter Cove marine ecosystem. Vertical position indicates the trophic level of each species (node) identified by a number (Appendix III) and the size is proportional to its degree (total number of interactions). Link colors indicates the type of interaction.



Figure 4. Number of non-trophic interactions per species. Bar colors indicates the type of interaction and grey circles represent species trophic level (decreasing order).



Figure 5. Distribution of non-trophic interactions among basal, intermediate and top species.

DISCUSSION

This work presents the first description of non-trophic interactions for an Antarctic ecosystem including also trophic interactions in a highly-resolved network. The network-level properties of the multiple interactions network are different from those of the single-interaction networks. This provides an overview of the species interactions in the community according with different properties and feeding strategies.

Distribution of interactions

The distribution of the non-trophic interactions identified in Potter Cove community were mostly represented between intermediate trophic level species, i.e. with values in a range of [2, 3.2]. This result is related to the fact that the percentage of intermediate species in Potter Cove food web is close to 50%. However, it is not as high as other marine food webs (Dunne et al. 2004, Vermaat et al. 2009, Marina et al. 2018b). A large number of trophic interactions at this trophic level is related to a large number of competitive interactions; a large number of competitive interactions is, ultimately, related to the criterion used here to define competition (sharing at least one prey). In this sense, amphipods and demersal fish were the trophic guilds that dominated competitive interactions. Clearly, these interactions are not species-specific but comprise a large hyper-connected network dominated by intermediate species. On the other hand, the non-trophic/non-competitive interactions were mainly associated with sessile and basal species that provide habitat, shelter or facilitate feeding for other species. Mutualistic interactions involve mesograzers that are often found in close association with macroalgae. Mesograzers benefit macroalgae by removing smaller epiphytic algae that often compete with macrophytes for light and nutrients. Simultaneously, these algae present a chemical defense that makes them non-palatable and prevents them from being consumed by the mesograzers. As a benefit of this association, amphipods gain refuge and avoid predation by omnivorous fish (Aumack et al. 2010, Amsler & McClintock 2014). Furthermore, commensalistic and amensalistic interactions involve filtering organisms that take advantage of the elevated position (in relation to the sea floor) that the substrate gives. Through this elevated position they gain better access to food due to the speed of marine currents that is usually higher in elevated areas than close to the sediment (Gutt 2000).

Species properties and networks importance

As we mentioned above, in Potter Cove ecosystem the classification of species in basal, intermediate and top species, their diet, their trophic level and mobility (mobile or sessile) allowed us to describe the type of non-trophic interactions in which species participate. In this sense, it is possible to extrapolate these patterns to other marine ecosystems, for example, to polar benthic communities that are rich in basal and sessile species (Pineda-Metz et al. 2019, Bae et al. 2021). These analyses are, indeed, necessary to build realistic and reliable ecological models and gain insights into characteristics related to interaction types (Kéfi et al. 2015, 2016, Mougi 2016a, 2016b) showing, for instance, that the addition of different interaction types could expose new interacting groups of species that vary in the way they (non-trophically) interact with the whole community, leading to important functional implications related to the species roles in the community (Sanders et al 2015).

Some studies argue that studying both trophic and non-trophic networks allow us to better understand the whole community function and that the combination of different structural patterns of interactions networks is essential to comprehend, for example, the mechanisms behind communities' stability (Mougi & Kondoh 2012, Kéfi et al. 2016, García-Callejas et al. 2017, Freilich 2018). Previous analyses of Potter Cove food web showed that there is an important energetic subsidy from detritus and basal species to the entire community and suggested that topological features such as the proportion of basal, intermediate and top species are key to understand the ecosystem response against diversity loss (Marina et al. 2018a, Cordone et al. 2018, Cordone et al. 2020). Hence, the importance of incorporating and studying different types of species interactions (trophic and non-trophic) at different trophic levels from a network perspective. More specifically, adding non-trophic interactions and its distribution among species might be fundamental to understand particular topological properties exhibited by Potter Cove marine ecosystem (Marina et al. 2018a, 2018b).

Non-trophic interactions role

It is known that non-trophic interactions play a role on ecosystem function that may be ambiguous and might probably depend on many factors related with the type of community being studied, the level of resolution of the networks analyzed, the researches perspectives/objectives and the type of analyses that the studies involve (analytical, descriptive, structural, dynamical, etc.). Nonetheless, non-trophic interactions are key elements that should be considered, for example, when studying ecological communities' dynamics and stability (Kéfi et al. 2012, 2015, 2016, 2018, Mougi 2016b, García-Callejas et al. 2017, Hervías-Parejo et al. 2020). There were some attempts to address this question and the findings were very different. Allesina & Tang (2012) suggested that trophic interactions increase stability while mutualistic and competitive interactions are destabilizing. However, many real ecosystems such as Chilean rocky shores - that exhibit numerous positive and negative interactions - showed a persistent and resilient response to perturbations (Kéfi et al 2015, 2016). In this sense, the following question should be addressed: if mutualistic and competitive interactions destabilize ecosystems, why are they so commonly found in ecological communities as empirical data suggest? One possible answer could be that analytical models might not be sufficient when analyzing structural and functional aspects of real ecosystems. This is, partly, because mathematical reduction assumes an abstraction with the consequent loss of a lot of attributes and characteristics of the biological system. However, mathematical modeling of ecosystems is still useful and allows us to tackle life's complex phenomena. In this sense, increasing the realism of such models, as in this study by incorporating non-trophic interactions, will help us to better understand the structure and dynamics of ecosystems.

To resume, in this work we have collected several demands that remain unanswered about the importance of adding non-trophic interactions when studying structure and function of real ecosystems. So far, very little is known about how nontrophic interactions are distributed among species or if the amount of these interactions is related with some topological and structural features of the community, even the association between species-level properties and interaction types remains unclear. Including a full description of the species and its relationships in ecological network analyses - like presented here - is of matter importance (Kéfi et al. 2012, 2015, 2016, Moughi 2016a, 2016b, Lurgi et. al 2020) and provides an insight into the analysis of ecosystems as a whole and not as a group of individual species. Therefore, addressing species properties analysis according to the type of interaction identified is necessary because it may help us to assess and predict ecosystems' responses to environmental disturbances that cause direct consequences on biodiversity especially when it comes to ecosystems seriously affected by climate change.

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APPENDIX I

References of the academic articles used for the construction of the non-trophic networks of Potter Cove.

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APPENDIX II

Description of the interactions identified for the Potter Cove marine ecosystem: mutualistic (+/+), competitive (-/-), commensalistic (0/+) and amensalistic (0/-). Each species in the column interact with each species in the row.

Types of Non-trophic Interactions		
+	+	
Amphipods: Gondogeneia	Macroalgae: Callophyllis atrosanguinea, Curdiea racovitzae,	
antárctica. Prostebbingia gracilis	Georgiella confluens, Gigartina skottsbergii, Iridaea cordata,	
	Myriogramme manginii, Neuroglossum delesseriae,	
Gastropod: Nacella concinna	Pantoneura plocamioides, Picconiella plumosa, Plocamium	
	cartilagineum, Pyropia plocamiestris, Trematocarpus	
	antarcticus, Adenocystis utricularis, Ascoseira mirabilis,	
	Desmarestia anceps, Desmarestia antárctica, Desmarestia	
	menziesii, Geminocarpus geminatus, Phaeurus antarcticus, Lambia antárctica, Monostroma hariotii, Urospora	
	penicilliformis, Ulothrix sp.	
Amphipods: Gitanopsis	Macroalgae: Iridaea cordata, Desmarestia menziesii,	
antárctica. Oradarea bidentata	Desmarestia anceps, Plocamium cartilagineum	
Briozoos	Porifera: Haliclonidae sp., Stylo-Myca, Rosella sp., Dendrilla	
Benthic diatoms	antarctica	
Amphipod: Paradexamine sp.	Macroalgae: Plocamium cartilagineum	
Echinoderm: Sterechinus	Macroalgae: Iridaea cordata	
neumayeri	Pyropia plocamiestris	
0	+	
Macroalgae: Callophyllis	Ascidiae	
atrosanguinea, Curdiea		
racovitzae, Georgiella confluens, Gigartina skottsbergii, Iridaea		
cordata, Myriogramme		
manginii, Neuroglossum		
delesseriae, Palmaria decipiens,		
Pantoneura plocamioides,		
Picconiella plumosa, Plocamium		
cartilagineum, Pyropia		
plocamiestris, Trematocarpus		
antarcticus,		
Bryozoa		
Porifera: Rosella sp., Dendrilla	Fish: Trematomus bernacchi,	
antárctica, Haliclonidae sp.,	Pennatulacea: Malacobelmnon daytoni	
Stylo-Myca Echinoderm: Sterechinus	Deriferes Decelle en Dendrille entération Unidencides en	
neumayeri, Ophionotus victoriae	Porifera: <i>Rosella sp., Dendrilla antárctica, Haliclonidae sp.,</i> Stylo-Myca	
neumayen, opmonotas victoride		
Epiphytic Diatoms	Macroalgae: Callophyllis atrosanquinea, Curdiea racovitzae,	
•••	Georgiella confluens, Gigartina skottsbergii, Iridaea cordata,	
	Myriogramme manginii, Neuroglossum delesseriae, Palmaria	
	decipiens, Pantoneura plocamioides, Picconiella plumosa,	
	Plocamium cartilagineum, Pyropia plocamiestris,	

	Trematocarpus antarcticus, Adenocystis utricularis, Ascoseira mirabilis, Desmarestia anceps, Desmarestia antárctica, Desmarestia menziesii, Geminocarpus geminatus, Phaeurus antarcticus, Lambia antárctica, Monostroma hariotii,
	Urospora penicilliformis, Ulothrix sp.
-	-
Notothenia coriiceps	Notothenia rossii Lepidonotothen nudifrons Trematomus newnesi
	Trematomus bernacchi
	Harpagifer antarcticus
	Parachaenichthys charcoti
	Chaenocephalus aceratus
	Protomyctophum
	Nereidae
	Austrodoris kerguelensis
	Nacella concinna
	Laevilacunaria antarctica
	Laternulla elliptica
	Neobuccinum eatoni
	Eurymera monticulosa
	Pontogeneiella sp.
	Gondogeneia antarctica
	Hyperiidea
	Bovallia gigantea
	Prostebbingia gracilis
	Oradarea bidentata
	Glyptonotus antarcticus
	Plakarthrium puncattissimum
	Ophionotus victoriae
	Odontaster validus
	Diplasterias brucei
	Odontaster meridionalis
	Perknaster fuscus antarticus Storachinus noumenori
	Sterechinus neumayeri Ostopus sp
	<i>Octopus sp.</i> Priapúlida
	Parborlasia corrugatus
	Salpidae
Notothenia rossii	Lepidonotothen nudifrons
	Trematomus newnesi
	Trematomus bernacchi
	Harpagifer antarcticus
	Parachaenichthys charcoti
	Chaenocephalus ceratus
	Austrodoris kerguelensis
	Laevilacunaria antarctica
	Laternulla elliptica
	Eurymera monticulosa
	Pontogeneiella sp.
	Gondogeneia antarctica

	Hyperiidea
	Prostebbingia gracilis
	Oradarea bidentata
	Glyptonotus antarcticus
	Ophionotus victoriae
	Odontaster validus
	Priapúlida
	Salpidae
Lepidonotothen nudifrons	Trematomus newnesi
	Trematomus bernacchi
	Harpagifer antarcticus
	Parachaenichthys charcoti
	Chaenocephalus aceratus
	Austrodoris kerguelensis
	Hyperiidea
	Bovallia gigantea
	Glyptonotus antarcticus
	Ophionotus victoriae
	Odontaster validus
	Sterechinus neumayeri
	Priapúlida
	Salpidae
Trematomus newnesi	Trematomus bernacchi
	Harpagifer antarcticus
	Parachaenichthys charcoti
	Chaenocephalus aceratus
	Protomyctophum
	Hyperiidea
	Bovallia gigantea
	Glyptonotus antarcticus
	Ophionotus victoriae
	Odontaster validus
	Diplasterias brucei
	Odontaster meridionalis
	Perknaster fuscus antarticus
	Sterechinus neumayeri
	Parborlasia corrugatus
Trematomus bernacchi	Harpagifer antarcticus
	Austrodoris kerguelensis
	Glyptonotus antarcticus
	Ophionotus victoriae
	Odontaster validus
	Diplasterias brucei
	Odontaster meridionalis
	Perknaster fuscus antarticus
	Octopus sp.
	Priapúlida
	Parborlasia corrugatus
	Salpidae

Harpagifer antarcticus	Parachaenichthys charcoti
	Chaenocephalus aceratus
	Austrodoris kerguelensis
	Hyperiidea
	Bovallia gigantea
	Glyptonotus antarcticus
	Ophionotus victoriae
	Odontaster validus
	Diplasterias brucei Odontaster meridionalis
	Perknaster fuscus antarticus
	Sterechinus neumayeri
	Priapúlida
	Parborlasia corrugatus
D	Salpidae
Parachaenichthys charcoti	Chaenocephalus aceratus
	Hyperiidea
	Ophionotus victoriae
Chaenocephalus aceratus	Hyperiidea
	Ophionotus victoriae
Nereidae	Laevilacunaria antarctica
	Gondogeneia antarctica
	Prostebbingia gracilis
Margarella antarctica	Austrodoris kerguelensis
	Ophionotus victoriae
	Odontaster validus
	Odontaster meridionalis
	Perknaster fuscus antarticus Perknaster aurorae
	Sterechinus neumayeri
	Parborlasia corrugatus
Austrodoris kerguelensis	Laevilacunaria antarctica
	Eurymera monticulosa
	Pontogeneiella sp.
	Gondogeneia antarctica
	Prostebbingia gracilis
	Oradarea bidentata
	Glyptonotus antarcticus
	Ophionotus victoriae
	Odontaster validus
	Odontaster meridionalis
	Perknaster fuscus antarticus
	Perknaster aurorae
	Sterechinus neumayeri
	Priapúlida
	Parborlasia corrugatus
	Salpidae
Eatoniella sp.	Nacella concinna
	Paradexamine sp.
	Eurymera monticulosa

Pontogeneiella sp.
Gondogeneia antarctica
Cheirimedon femoratus
Gitanopsis antarctica
Prostebbingia gracilis
Plakarthrium puncattissimum
Hemiarthrum setulosum
Ophionotus victoriae
Odontaster validus
Priapúlida
Haliclonidae sp.
Stylo-Myca
Rosella sp.
Dendrilla antarctica
Eurymera monticulosa
Pontogeneiella sp.
Gondogeneia antarctica
Prostebbingia gracilis
Plakarthrium puncattissimum
Hemiarthrum setulosum
Ophionotus victoriae
Odontaster validus
Priapúlida
Haliclonidae sp.
Stylo-Myca
Rosella sp.
Dendrilla antarctica
Eurymera monticulosa
Pontogeneiella sp.
Gondogeneia antarctica
Prostebbingia gracilis
Oradarea bidentata
Plakarthrium puncattissimum
Laternulla elliptica
Euphausia superba
Hyperiidea
Copépoda
Ascidiae
Oligochaeta
Hydrozoa
Bryozoa
Salpidae
Misidáceos
Zooplankton
Haliclonidae sp.
Stylo-Myca
Rosella sp.
Dendrilla antarctica
Malacobelmnon daytoni
Funhausia sunerha
<i>Euphausia superba</i> Hyperidea

	Copepoda
	Ascidiae
	Oligochaeta
	Hydrozoa
	Bryozoa
	Salpidae
	Mysidacea
	Zooplankton
	Haliclonidae sp.
	Stylo-Myca
	Rosella sp.
	Dendrilla antarctica
	Malacobelmnon daytoni
Neobuccinum eatoni	Paradexamine sp.
	Pariphimedia integricauda
	Gitanopsis antarctica
	Waldeckia obesa
	Hippo-Orcho
	Serolis sp.
	Glyptonotus antarcticus
	Ophionotus victoriae
Euphausia superba	Hyperiidea
	Copepoda
	Ascidiae
	Oligochaeta
	Hydrozoa
	Bryozoa
	Salpidae
	Mysidacea
	Zooplankton
	Haliclonidae sp.
	Stylo-Myca
	Rosella sp.
	Dendrilla antarctica
	Malacobelmnon daytoni
Paradexamine sp.	Eurymera monticulosa
r araacxamme sp.	Pariphimedia integricauda
	Cheirimedon femoratus
	Gitanopsis antarctica
	Waldeckia obesa
	Hippo-Orcho
	Serolis sp.
	Glyptonotus antarcticus
	Plakarthrium puncattissimum
	Ophionotus victoriae
	Odontaster validus
	Haliclonidae sp.
	Stylo-Myca
	Rosella sp.
Furning and in articulars	Dendrilla antarctica
Eurymera monticulosa	Pontogeneiella sp.

	1
	Gondogeneia antarctica
	Cheirimedon femoratus
	Gitanopsis antarctica
	Prostebbingia gracilis
	Oradarea bidentata
	Plakarthrium puncattissimum
	Hemiarthrum setulosum
	Ophionotus victoriae
	Odontaster validus
	Priapúlida
	Haliclonidae sp.
	Stylo-Myca
	Rosella sp.
	Dendrilla antarctica
Pontogeneiella sp.	Gondogeneia antarctica
	Prostebbingia gracilis
	Oradarea bidentata
	Plakarthrium puncattissimum
	Hemiarthrum setulosum
	Ophionotus victoriae
	Odontaster validus
	Priapúlida
	Haliclonidae sp.
	Stylo-Myca
	Rosella sp.
	Dendrilla antarctica
Gondogeneia antarctica	Prostebbingia gracilis
	Oradarea bidentata
	Plakarthrium puncattissimum
	Hemiarthrum setulosum
	Ophionotus victoriae
	Odontaster validus
	Priapúlida
	Haliclonidae sp.
	Stylo-Myca
	Rosella sp.
	Dendrilla antarctica
Hyperiidea	Ophionotus victoriae
Typernaea	Copépoda
	Ascidiae
	Oligochaeta
	Hydrozoa
	Bryozoa
	Salpidae
	Misidáceos
	Haliclonidae sp.
	Stylo-Myca
	Rosella sp.
	Dendrilla antarctica
	Malacobelmnon daytoni
Pariphimedia integricauda	Gitanopsis antarctica
	Waldeckia obesa

	Hippo-Orcho
	Serolis sp.
	Glyptonotus antarcticus
	Ophionotus victoriae
Bovallia gigantea	Ophionotus victoriae
bovania giganica	Sterechinus neumayeri
Cheirimedon femoratus	Gitanopsis antarctica
enenmeden jemeratus	Plakarthrium puncattissimum
	Ophionotus victoriae
	Odontaster validus
	Haliclonidae sp.
	Stylo-Myca
	Rosella sp.
	Dendrilla antarctica
Gitanopsis antarctica	Waldeckia obesa
	Hippo-Orcho
	Serolis sp.
	Glyptonotus antarcticus
	Plakarthrium puncattissimum
	Ophionotus victoriae
	Odontaster validus
	Haliclonidae sp.
	Stylo-Myca
	Rosella sp.
	Dendrilla antarctica
Prostebbingia gracilis	Oradarea bidentata
	Plakarthrium puncattissimum
	Hemiarthrum setulosum
	Ophionotus victoriae
	Odontaster validus
	Priapúlida
	Haliclonidae sp.
	Stylo-Myca
	Rosella sp.
	Dendrilla antarctica
Waldeckia obesa	Hippo-Orcho
	Serolis sp.
	Glyptonotus antarcticus
	Ophionotus victoriae
Hippo-Orcho	Serolis sp.
	Glyptonotus antarcticus
	Ophionotus victoriae
Serolis sp.	Glyptonotus antarcticus
,	Ophionotus victoriae
Glyptonotus antarcticus	Ophionotus victoriae
	Odontaster validus
	Sterechinus neumayeri
	Priapúlida
	Parborlasia corrugatus
	Salpidae
Plakarthrium puncattissimum	Hemiarthrum setulosum
· ····································	Ophionotus victoriae
	Odontaster validus
	Priapúlida
	Haliclonidae sp.
	Stylo-Myca
	Julyio-iviyua

	Rosella sp.
	Dendrilla antarctica
Ophionotus victoriae	Odontaster validus
	Diplasterias brucei
	Odontaster meridionalis
	Perknaster fuscus antarticus
	Perknaster aurorae
	Sterechinus neumayeri
	Priapúlida
	Parborlasia corrugatus
	Salpidae
	Haliclonidae sp.
	Stylo-Myca
	Rosella sp.
	Dendrilla antarctica
Odontaster validus	Diplasterias brucei
	Odontaster meridionalis
	Perknaster fuscus antarticus
	Perknaster aurorae
	Sterechinus neumayeri
	Priapúlida
	Parborlasia corrugatus
	Salpidae
	Haliclonidae sp.
	Stylo-Myca
	Rosella sp.
	Dendrilla antarctica
Diplasterias brucei	Odontaster meridionalis
Diplusterius brucer	Perknaster fuscus antarticus
Odontaster meridionalis	Perknaster fuscus antarticus
	Perknaster aurorae
	Sterechinus neumayeri
	Parborlasia corrugatus
Perknaster fuscus antarticus	Perknaster aurorae
r chinaster juseus unturneus	Sterechinus neumayeri
	Parborlasia corrugatus
Perknaster aurorae	Sterechinus neumayeri
Terkhaster darorde	Parborlasia corrugatus
Sterechinus neumayeri	Parborlasia corrugatus
Copepoda	Ascidiae
Сорерона	Oligochaeta
	Hydrozoa
	Bryozoa
	Salpidae
	Mysidacea
	Zooplankton
	Haliclonidae sp.
	Stylo-Myca Rosella sp.
	Dendrilla antarctica
	Malacobelmnon daytoni
Assidias	
Ascidiae	Oligochaeta
	Hydrozoa
	Bryozoa
	Salpidae
	Mysidacea
	Zooplankton

	ttelle e idea en
	Haliclonidae sp.
	Stylo-Myca
	Rosella sp.
	Dendrilla antarctica
<u></u>	Malacobelmnon daytoni
Octopus	Parborlasia corrugatus
Oligochaeta	Hydrozoa
	Bryozoa
	Salpidae
	Mysidacea
	Zooplankton
	Haliclonidae sp.
	Stylo-Myca
	Rosella sp.
	Dendrilla antarctica
	Malacobelmnon daytoni
Hydrozoa	Bryozoa
	Salpidae
	Mysidacea
	Zooplankton
	Haliclonidae sp.
	Stylo-Myca
	Rosella sp.
	Dendrilla antarctica
	Malacobelmnon daytoni
Bryozoa	Salpidae
	Mysidacea
	Zooplankton
	Haliclonidae sp.
	Stylo-Myca
	Rosella sp.
	Dendrilla antarctica
	Malacobelmnon daytoni
Priapulida	Salpidae
	Haliclonidae sp.
	Stylo-Myca
	Rosella sp.
	Dendrilla antarctica
Salpidae	Mysidacea
	Zooplankton
	Haliclonidae sp.
	Stylo-Myca
	Rosella sp.
	Dendrilla antarctica
	Malacobelmnon daytoni
Mysidacea	Zooplankton
	Haliclonidae sp.
	Stylo-Myca
	Rosella sp.
	Dendrilla antarctica
	Malacobelmnon daytoni
Zooplankton	Haliclonidae sp.
	Stylo-Myca
	Rosella sp.
	Dendrilla antarctica
	Malacobelmnon daytoni
Haliclonidae sp.	Stylo-Myca

	Rosella sp.		
	Dendrilla antarctica		
	Malacobelmnon daytoni		
Stylo-Myca	Rosella sp.		
	Dendrilla antarctica		
	Malacobelmnon daytoni		
Rosella sp.	Dendrilla antarctica		
	Malacobelmnon daytoni		
Dendrilla antarctica	Malacobelmnon daytoni		

ΤL 2,50 2,00 2,00 2,00 2,00 3,33 2,00 3,00 2,00 2,00 2,00 2,00 2,00 2,00 2,00 3,13 2,00 2,00 2,97 3,06 3,67 3,35 3,46 3,25 3,21 1,00 2,50 2,50 4,13 2,50 2,50 2,50 2,50 3,41 2,70 2,50 1,00 1,00 2,00 2,25 2,25 2,25 2,25 4,27 2,50

ID	Species	TL]	ID	Species
1	Notothenia coriiceps	2,80		47	Euphausia superba
2	Nothotenia rossii	3,25		48	Paradexamine sp.
3	Lepidonotothen nudifrons	3,07		49	Eurymera monticulosa
4	Trematomus newnesi	3,65		50	Pontogeneiella sp.
5	Trematomus bernacchi	3,59		51	Gondogeneia antarctica
6	Harpagifer antarcticus	3,32		52	Hyperiidea
7	Parachaenichthys charcoti	3,50		53	Pariphimedia integricauda
8	Chaenocephalus aceratus	4,02		54	Bovallia gigantea
9	Protomyctophum sp.	3,70		55	Cheirimedon femoratus
10	Callophyllis atrosanguinea	1,00		56	Gitanopsis squamosa
11	Curdiea racovitzae	1,00		57	Prostebbingia gracilis
12	Georgiella confluens	1,00		58	Waldeckia obesa
13	Gigartina skottsbergii	1,00		59	Hippo-Orcho
14	Iridaea cordata	1,00		60	Oradarea bidentata
15	Myriogramme manginii	1,00		61	Serolis sp.
16	Neuroglossum delesseriae	1,00		62	Glyptonotus antarcticus
17	Palmaria dicipiens	1,00		63	Plakarthrium punctatissimum
18	Pantoneura plocamioides	1,00		64	Hemiarthrum setulosum
19	Picconiella plumosa	1,00		65	Ophionotus victoriae
20	Plocamium cartilagineum	1,00		66	Odontaster validus
21	Pyropia plocamiestris	1,00		67	Diplasterias brucei
22	Trematocarpus antarcticus	1,00		68	Odontaster meridionalis
23	Adenocystis utricularis	1,00		69	Perknaster fuscus antarcticus
24	Ascoseira mirabilis	1,00		70	Perknaster aurorae
25	Desmarestia anceps	1,00		71	Sterechinus neumayeri
26	Desmarestia antarctica	1,00		72	Squid
27	Desmarestia menziesii	1,00		73	Copepoda
28	Geminocarpus geminatus	1,00		74	Ascidiae
29	Phaeurus antarcticus	1,00		75	Octopus sp.
30	Lambia antarctica	1,00		76	Oligochaeta
31	Monostroma hariotii	1,00		77	Hydrozoa
32	Urospora penicilliformis	1,00		78 70	Bryozoa Brian úlida
33	Ulothrix sp.	1,00		79 80	Priapúlida Parborlacia corrugatus
34	Epiphytic diatoms Benthic diatoms	1,00		80 01	Parborlasia corrugatus
35		1,00 1,00		81 82	Salpidae
36 37	Phytoplankton Aged Detritus	1,00		83	Mysidacea Fresh Detritus
37	Nereidae	2,00		83 84	Necromass
39	Margarella antarctica	3,25		85	Zooplankton
40	Austrodoris kerguelenensis	3,23		86	Haliclonidae sp.
40	Eatoniella sp.	2,00		80 87	Stylo-Myca
41	Nacella concinna	2,00		88	Rossella sp.
42	Laevilacunaria antarctica	2,00		89	Dendrilla antarctica
43 44	Dacrydium sp.	2,00		90	Urticinopsis antarctica
44	Laternula elliptica	2,30		90 91	Malacobelemnon daytoni
45	Neobuccinum eatoni	2,55		71	manacoberenmon daytom
40		2,07	l		

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