Are Antarctic and sub-Antarctic marine food webs different?

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ABSTRACT

Aim: Food web structure plays an important role in determining ecosystem stability to perturbations. High latitude marine ecosystems are being affected by environmental stressors and ecological shifts. In the West Antarctic Peninsula these transformations are driven by climate change, and in the sub-Antarctic region by anthropogenic activities. Understanding the differences between these areas is necessary to monitor the changes that are expected to occur in the upcoming decades. Here, we compared the structure and stability of Antarctic and sub-Antarctic marine food webs.
Location: Antarctic (Potter Cove, 25 de Mayo/King George Island, West Antarctic Peninsula) and sub-Antarctic (Beagle Channel, Tierra del Fuego, South America) regions.
Time period: 1965 - 2019
Major taxa studied: from phytoplankton to fish
Methods: We compiled species trophic (predator-prey) interactions and calculated complexity (number of species and interactions, connectance), structure (mean trophic level, omnivory, degree distribution, modularity, species roles and traits) and stability (QSS) metrics. To be able to make statistical comparisons, we used a randomization algorithm (Strona Curveball) maintaining the number of prey and predators for each species and calculated metrics for each simulation.
Results: The Beagle Channel food web presented higher values for complexity metrics (number of species and interactions), structure (mean trophic level, omnivory, modularity) but lower stability (QSS). Potter Cove fitted the exponential degree distribution, while Beagle Channel the power-law with exponential cutoff model. Both food webs presented the same connectance value (0.05), similar distribution of species in top, intermediate and top positions and topological roles, with only one network connector each.
Main conclusions: Our results showed that Beagle Channel food web is more complex, but less stable and sensitive to the loss of its most connected species. While the Potter Cove food web presented less complexity and greater stability to perturbations.

Key words: anthropogenic activities, climate change, food web, marine ecosystems, sub-Antarctic, West Antarctic Peninsula

1. INTRODUCTION

Food webs are a description of the trophic interactions (predator-prey) that occur in an ecosystem, representing the flows of energy and matter among organisms. Trophic interactions are key drivers of ecosystems structure, function and stability (Dunne, 2006). The occurrence, intensity and frequency of these interactions can and are being altered by climate change and anthropogenic stressors, by modifying the species patterns of distribution and abundance (Blois et al., 2013).

High-latitude marine ecosystems are being affected by drastic environmental and ecological transformations, driven by climate change and anthropogenic activities (Clarke & Harris, 2003; Hoegh-Guldberg & Bruno, 2010; Meredith et al., 2019). The West Antarctic Peninsula (WAP) had the highest heating rates recorded worldwide in the past half-century (Steig et al., 2009; Turner et al., 2014). It is considered that this area is undergoing a transition from a cold-dry polar-type to a warm-humid sub-Antarctic-type climate (Montes-Hugo et al., 2009), while human activities intensify (McCarthy et al., 2019; IAATO, 2019). As a consequence, physical and chemical changes (e.g., glacier retreat, increased sediment input, seasonal sea-ice reduction, surface salinity decrease) and biological responses are increasingly being reported (Cook et al., 2005; Ducklow et al., 2013; Fuentes et al., 2016; Schloss et al., 2012). Changes in communities' composition, species distribution and abundance (Lagger et al., 2017; Pasotti et al., 2015; Sahade et al., 2015) support the climate transition hypothesis.

At the southernmost tip of South America, is located the Beagle Channel, a sub-Antarctic drowned glacial valley. It is the closest continental area to the WAP and shares a relatively recent biogeographical history, from around 30 Ma, when the Antarctic Circumpolar Current was established (Barker & Thomas, 2004). As a result, these areas became two distinct biogeographical regions, with different environmental characteristics and biodiversity (Griffiths & Waller, 2016). Nowadays, the disturbances that affect such ecosystems have different origins. The Beagle Channel is mainly threatened by anthropogenic pressures: increasing levels of pollution (urban wastewaters, industrial activities, shipping traffic and tourism) (Amin et al., 1996; Gil et al., 2011), the introduction of exotic salmon species for aquaculture (Fernández et al., 2010; Nardi et al., 2019) and the fishing pressure of economically important species (Gustavo A. Lovrich, 1997). Although there is no clear evidence that this area is currently being affected by climate change, marine temperatures are projected to globally increase in the next 100 years (IPCC, 2013). Species distributions are expected to move poleward with warming, to maintain their preferred temperature range (Hickling et al., 2006). There are already reports of sub-Antarctic alien species in Potter Cove and the WAP (Cárdenas et al., 2020; Fraser et al., 2018) and many have been proposed to have the potential to invade Antarctica (Diez & Lovrich, 2010; Hughes et al., 2020). Understanding the differences (and similarities) between sub-Antarctic and Antarctic areas is necessary to monitor the changes that are occurring and are expected to magnify in the upcoming decades (Griffiths et al., 2017; Gutt et al., 2015) and to develop models that help us predict these ecosystems' responses.

In this study, we use a network approach to explore and compare the structure and stability of Antarctic (Potter Cove, South Shetland Islands, WAP) and sub-Antarctic (Beagle Channel, Tierra del Fuego) food webs. We expect that the particular environmental and biogeographic conditions of each ecosystem will translate into different network architecture (Song & Saavedra, 2020). We hypothesize that the warmer, more productive, with a more heterogeneous habitat Beagle Channel (Amin et al., 2011; Schloss et al., 2012) will present a more complex food web (Kortsch et al., 2018), measured as species richness (Duffy et al., 2017) and number of trophic interactions, hence, connectance, with more trophic levels (Young et al., 2013), higher omnivory (Thompson et al., 2007) and stronger modularity (Welti & Joern, 2015). It is expected for a more complex food web to present a lower stability against perturbations (May, 1973). While the strongly seasonal, ice-covered and less productive Potter Cove present a less complex and more stable food web.

2. MATERIALS AND METHODS

2.1. Study sites

Potter Cove is a fjord located at 25 de Mayo/King George Island (62° 14'S, 58° 38'W, South Shetland Islands) on the West Antarctic Peninsula (Figure 1b). It has an area of 7 km^2 (4 km long and 2.5 km wide). A shallow sill (<30 m) separates the cove into an inner, shallower (<50 m) part characterized by soft sediments inhabited by filter benthic species and an outer section, deeper (~100 m) with rocky bottom, colonized by a large biomass of macroalgae. Due to their high latitude location, marine antarctic ecosystems are extremely variable due to the strong seasonality in the photoperiod length. Winter reduction in irradiance and temperature controls the dynamics of environmental variables, such as sea-ice extent, mixing layer depth, water column particulate matter and nutrients concentration.

The Beagle Channel (Figure 1a) connects the Pacific and the Atlantic Oceans and is about 240 km long and 5 km wide, at its narrowest point. To facilitate the comparison, we selected a study area that comprises two distinguished coastal sites: Lapataia Bay (54° 51'S, 68° 34'W), located within the Tierra del Fuego National Park, with a maximum depth of 20 m and rocky bottoms with abundant macroalgae; and Ushuaia Bay (54° 49'S, 68° 19'W), where the city of Ushuaia is located, 140 m deep and with a soft substrate with small rocks and shells (Balestrini et al., 1998). Most coasts of the Beagle Channel are characterized by the presence of giant kelp (*Macrocystis pyrifera)* forests. Due to their complex morphology, kelps act as ecosystem engineers, providing refuge from predation and a habitat for prey, and altering water conditions (Adami & Gordillo, 1999; Bruno et al., 2018; Graham et al., 2007).

Water temperature, in Potter Cove, ranges from -2 to-1°C during winter and 0.3 to 2.1°C during summer (Schloss et al., 2012). While in the Beagle Channel temperature ranges from 4.2 - 4.3°C in winter, to 8.9 - 9.8°C in summer (Balestrini et al., 1998). Both sites have high availability of nutrients, meaning that the main limiting factor conditioning primary production is solar irradiation (Amin et al., 2011; Schloss et al., 2002). During summer, sediment runoff into the water column increases due to the input of glacier meltwater at both sites.

2.2. Food web assembly and topology

We collected and compiled trophic (prey-predator) interactions of species present in each site. For Potter Cove, we updated the food web published by Marina et al. (2018), maintaining the same criteria they used in their assembly: consider only trophic links confirmed by gut content studies and/or field observations; experimental and biomarkers (isotopes and fatty acids) studies were not taken into account; mammals, seabirds and pelagic fish were not considered since their contribution is not relevant in the matter and energy flows in the cove (Barrera Oro & Casaux, 2008). Most data were collected during austral summer months, when most research campaigns are carried out. More detailed information on Potter Cove food web assembly can be found in Marina et al. (2018)

We found scarcity and lack of species diet resolution for Beagle Channel compared to the availability for Potter Cove. This is why we decided to include information from biomarkers studies (Luciana Riccialdelli et al., 2017) despite Marina et al. (2018) did not. These authors considered that these studies do not identify prey, but rather assume species' diet and quantify it. Although, it is worth mentioning that diet information from stable isotopes studies can be corroborated bibliographically and incorporated into the food web. When there was insufficient species diet information, we included links reported in nearby sub-Antarctic ecosystems (Castilla, 1985; Díaz, 2016; Moreno & Jara, 1984). We also took into account diet information collected in other seasons than summer, since in Beagle Channel trophic interactions do not fluctuate significantly during the year, but rather species abundance (Adami & Gordillo, 1999; Aguirre et al., 2012; Almandoz et al., 2011). Mammals and seabirds were also not considered, although we included pelagic fishes given their abundance and importance as prey in Beagle Channel (Riccialdelli et al., 2020).

The trophic network was defined by an adjacency matrix (A) of pairwise interactions, in which each element a_{ij} = 1 when the j-species preyed on the i-species, and a_{ij} = 0 otherwise. From this matrix one can obtain a directed graph with L trophic links connecting S nodes or trophic species. Trophic species can correspond to: biological species groups, taxonomic groups above species level due to lack of diet resolution (genus, family), organisms that share the same sets of predators and prey, and non-living compartments of matter and energy (e.g., detritus, necromass). Henceforth, we will use the term "species" as synonymous with "trophic species" (Briand & Cohen, 1984).

We described the network structure and complexity with metrics that are widely used in food web studies (Delmas et al., 2018; Landi et al., 2018; Montoya et al., 2006), such us: link density, connectance, percentage of basal/intermediate/top species, mean trophic level and omnivory (Table 1).

In addition, as a summary of the network topology, we studied how trophic links were distributed among all species in the networks, the so-called cumulative degree distribution. For this purpose, node degree was calculated as the sum of all in- (number of prey) and out- (number of predators) trophic interactions. Then we fitted the cumulative degree distribution to the following models: exponential, log normal, Poisson, power-law, power-law with exponential cutoff and uniform. Model fit was done using maximum likelihood (Mccallum, 2008) and model selection was performed by the Akaike Information Criterion corrected for small sample size (Burnham & Anderson, 2002).

2.3. Modularity, species roles and traits

Food webs tend to naturally organize in non-random, modular patterns (Grilli et al., 2016). This means that groups of prey and predators interact more strongly with each other, than with species belonging to other groups. Modularity measures how strongly these subgroups of species, called modules, interact with each other compared to species from other modules (See Eq.3 in Supporting information). Modular organization is positively associated with stability and enhances the persistence of a food web, since perturbations can be retained within modules, constraining the spreading to the rest of the network (Stouffer & Bascompte, 2011).

Species can play different roles with respect to modularity, according to the pattern of trophic links they have within their own module and/or across modules. Nodes with the same role are expected to have similar topological properties (Guimera, 2005; Kortsch et al., 2015). To evaluate species' role similarity between Potter Cove and Beagle Channel, we computed the topological role for each species, classified as: *module hub*, species with a relatively high number of links, but most within its own module; *module specialist*, species with relatively few links and most within its own module; *module connector*, species with relatively few links mainly between modules and *network connector*, species with high connectivity between and within modules (See Eq.4 in Supporting Information). We combined topological roles with each species trophic level and module membership in one plot to provide an integrated visualization of these trophic networks' properties.

We also collected species' biology and feeding behavior information and classified them regarding habitat (pelagic, benthopelagic and benthic) and functional group (non-living, basal taxa, zooplankton, benthos and fish), in order to determine if module affiliation was associated with these traits, as observed in other marine trophic networks (Kortsch et al., 2015; Rezende et al., 2009). To determine if the proportions of species per traits changed across modules and among trait levels between food webs, we used Pearson's Chi-squared test and plotted the number of species habitat and functional group affiliation within each module and the percentage of species per trait level.

2.4. Quasi-Sign Stability (QSS)

Stability is a multidimensional concept (Donohue et al., 2013) and can be measured in different ways. Traditionally, it is conceived as the ability of an ecosystem to maintain its state over time, against external and internal forces that drive it away from that state (Saint-Béat et al., 2015). To evaluate network stability between Potter Cove and Beagle Channel food webs, we used a variation of the Quasi-Sign Stability metric (QSS) (Allesina & Pascual, 2008). It is calculated as the mean of the maximum eigenvalue for the simulated community matrices, where the magnitude of the element (a_{ij}) coefficients (interaction strength) is randomized, but the sign structure (type of interaction) is preserved. This metric is directly related with network local stability, which can reveal the amplification or not of small perturbations near the equilibrium point; values closer to zero indicate a more stable food web.

2.5. Food web structure and stability comparison using a randomization algorithm

In order to be able to perform a statistically robust comparison between food webs, we used the Strona Curveball algorithm (Strona et al., 2014) to generate an ecological meaningful distribution of the metrics (Cordone et al., 2020; Kéfi et al., 2016). It randomizes the network structure maintaining the number of prey and predators for each species, meaning that species have the same degree but can interact with different species that in the original network. We performed 1000 network randomizations for Potter Cove and Beagle Channel and calculated structure and stability metrics (mean trophic level, omnivory, modularity, QSS). Complexity metrics (number of species, link density, connectance) were not calculated since they do not vary due to the algorithm restrictions. If empirical values for each metric were within the distribution of the randomized simulated food webs, we considered that simulations fitted the empirical values enabling network comparison. Then, we calculated the 95% confidence interval and compared the distributions obtained for each metric using the two-sided Kolmogorov-Smirnov test (Massey, 1951).

2.6. Data analysis

All analyses, simulations and plots were performed in R version 4.0.3 (R Development Core Team, 2020), using the 'PoweRlaw' R package to fit distributions (Gillespie, 2015) and the 'multiweb' R package to calculate all network metrics and food web simulations (Saravia et al., 2019).

3. RESULTS

3.1. Food web topology

Potter Cove and Beagle Channel food webs differ with regard to structural and complexity properties. Potter Cove food web includes a total of 110 prey and predators, while the Beagle Channel food web consists of 145 species. Both networks have 3 non-living nodes (fresh detritus, aged detritus and necromass). Beagle Channel presents nearly twice the amount of total feeding interactions (1115) than Potter Cove (649), but the same connectance value (0.05). It should be noted that, despite having different number of species, both food webs present a very similar species distribution in basal (27% Potter, 25% Beagle) and top positions (6% Potter, 7% Beagle); being most of them intermediate species (67% for both ecosystems) (Table 2). Beagle Channel food web showed higher mean trophic level (2.3) and percentage of omnivory (55%) than Potter Cove (2.2 mean trophic level and 46% omnivory) (Figure 2a, b).

The cumulative degree distribution analysis showed strongly right-skewed degree distributions for both food webs, with most of the species with few links and few species with many links. The best fit for Potter Cove was the exponential model and the power-law with exponential cutoff for the Beagle Channel food web, according to the AICc analysis (Supporting Information Table S3). The power-law with exponential cutoff distribution is less steep than the exponential, which translates to Beagle Channel having more species with higher degree than Potter Cove food web.

3.2. Modularity, species roles and traits

Species topological role analysis showed that in both food webs most species are module connectors or specialists (species with few links, between modules or within its own module), with no module hub (species with many links within its own module) and only one network connector (species with many links between modules), but with different trophic position: the top predator (no species preying on it), black rockcod (*Notothenia coriiceps*) for Potter Cove, with a trophic level = 3.0; and the squat lobster (*Munida gregaria)* for Beagle Channel, with a trophic level = 2.4 (Figure 4).

Despite having significantly different modularity (how strongly the modules are tied together) (Figure 2f), the modularity analysis divided both food webs into four distinct modules (Figure 4).

We found that the proportion of species' traits (habitat and functional group) changed significantly across food webs' modules. Another interesting fact is that the Beagle Channel food web has significantly three times more fish species (31) than Potter Cove (9), but presented lower zooplankton ratio (0.23 Potter Cove, 0.06 Beagle Channel) (Figure 5g, h) due to lower taxonomical resolution for this last functional group.

Detailed list of all species, their module affiliation, role as network connector, module connector, module specialist and module hub, functional group, habitat use, degree and trophic level can be found in Supporting Information Table S1 for Potter Cove and Table S2 for Beagle Channel.

3.3. Food web structure and stability comparison with a randomization algorithm

All the analyzed metrics of structure and stability showed statistical differences ($p<0.01$, Supporting Information Table S4) between sites. An important remark is that all empirical values for the metrics fell within the distributions of the randomized simulated networks. Beagle Channel food web presented higher values for all of the analyzed metrics than Potter Cove (Figure 2).

4. DISCUSSION

The comparison presented here shows that Potter Cove and Beagle Channel food webs have different structure and link configuration, with important consequences for their robustness and stability. As we hypothesized, the sub-Antarctic food web is more complex, but less locally stable, and the Antarctic exhibits lower complexity, which appears to provide stability in the face of perturbations.

4.1. Food web differences

The Beagle Channel food web displayed higher number of trophic species (mainly due to higher fish richness), considerably more links, higher mean trophic level and omnivory, meaning a more complex structure, as we hypothesized. More productive, heterogenous and larger ecosystems, like Beagle Channel, in comparison with Potter Cove, are expected to promote food web complexity. They can sustain higher number of species and longer food chains, which correlates positively with omnivory, since species have a higher probability to encounter prey in different habitats and in a wider range of trophic positions (Kortsch et al., 2018; Thompson et al., 2007).

The different cumulative degree distributions show that Beagle Channel presents a higher number of generalist species than Potter Cove food web, supported by a greater proportion of omnivores, mainly fish. In contrast, the antarctic coastal marine food web is known to contain many specialized benthic fish species (Barrera-Oro, 2002).The distribution of species in the food web can also determine the vulnerability of the system to the loss of the most connected species. The power-law distribution presented by the Beagle Channel network suggests that this ecosystem is highly sensitive to perturbations affecting the species with highest degree, driving the system to collapse (Albert et al., 2000; Estrada, 2007). The emerging interest as a fishery resource over the squat lobster (*Munida gregaria*), the most connected prey and abundant species (Arntz & Gorny, 1994), might present a serious threat to the stability of this sub-Antarctic food web, if a proper management is not taken into account (Tapella et al., 2002).

In theory, exponential networks, as displayed by Potter Cove, are catastrophically fragmented by random removal of nodes (Albert et al., 2000). Cordone et al., (2018, 2020) simulated species extinction for Potter Cove and found no food web collapse, suggesting an apparent robustness to species loss. Our stability analysis supports their conclusion, as Potter Cove food web displayed lower significant value of QSS (more locally stable), meaning that it has higher probability to recover after a perturbation, such as a local loss of a species, than the Beagle Channel food web.

The lower stability of the Beagle Channel food web, in comparison with Potter Cove, can be attributed to its higher complexity. Ecological models show that complexity usually destabilizes food webs (May, 1973). This result empirically corroborates the hypothesis that QSS increases (stability decreases) with increasing number of trophic levels and omnivory (Borrelli & Ginzburg, 2014). Also, food webs with many generalist species, like Beagle Channel, are least resistant to disturbances because, when affected, they tend to cause secondary extinctions (Wootton, 2015). That is because generalists have many weak interactions which are known to be important for stability (McCann et al., 1998).

Although omnivory is not a direct measure of stability, it acts as a buffer of changes as the ecosystem presents alternative energy pathways in the face of perturbations. Omnivores are species able to adapt faster and at a wider range of environmental conditions by changing their foraging habits to feed on the most abundant prey (Fagan, 1997). In this sense, the highly significant omnivore proportion in Beagle Channel food web suggests that it could be more robust to variations in prey abundances than Potter Cove. Food web studies have found that the effect of omnivory on stability and measures of local stability (such as QSS) is influenced by species interaction's strengths (Gellner & McCann, 2012). Therefore, a thorough assessment of this effect would require knowledge on the distribution of interaction strength.

The strength modules are tied together was different between food webs, and even different compartmentalization mechanisms appear to be responsible in determine each food web structure. Compartmentalization has been proposed to arise as a result and combination of habitat heterogeneity within the environment, species functional group and the dependence of each node on energy derived from basal resources (Krause et al., 2003; Rezende et al., 2009;

Zhao et al., 2018). Potter Cove had each of the four modules associated to an independent type of basal resource (1- macroalgae, 2- aged detritus, 3- fresh detritus/necromass/diatoms and 4- phytoplankton) with different habitat. These results support the important role energy pathways and habitat type play in structuring Antarctic food webs. (Cordone et al., 2020). This pattern was not evident for Beagle Channel. Interestingly had one module with no primary productivity resource, meaning it depends on other modules for energy, and was conformed for all the top predators (fish). The higher modularity of the sub-Antarctic food web is probably associated to a more heterogeneous and complex habitat created by the kelp (Teagle et al., 2017). This macroalgae species have strong non-trophic interactions (mutualism, competition, etc.) with others species (invertebrates, fish, other macroalgae), since is not as important food resource as refugee and habitat (Miller et al., 2018; Riccialdelli et al., 2017), with indirect consequences in species predator-prey interactions (Kéfi et al., 2012). To fully understand the processes shaping the structure of this sub-Antarctic ecosystem we suggest the future incorporation of non-trophic interactions into the network.

4.2. Food web similarities

We would have expected the different biogeographical, climatic and evolutionary history between Potter Cove and the Beagle Channel to be reflected in a marked different trophic network structure, but we found several similarities. The two food webs showed the same connectance value (0.05) and similar proportions of basal, intermediate and top species. Marine food webs tend to resemble each other (Dunne et al., 2004), when compared to non-marine ecosystem; and in high latitudes, they usually exhibit low connectance values (between 0.01 and 0.05) (De Santana et al., 2013; Kortsch et al., 2015). In this sense, our results support previous studies of polar food webs complexity.

Connectance usually covaries with ecosystem primary productivity and the proportion of basal species (Vermaat et al., 2009). The surprisingly same connectance value for both food webs can be attributed to the fact that they present a very similar proportion of basal species and to the importance of macroalgae as an energy source in both ecosystems. Macroalgae provide a direct pathway of energy and matter into organisms that feed on them and indirectly through the detritus pathway (Momo et al., 2020; Luciana Riccialdelli et al., 2017).

We found that Potter Cove and Beagle Channel food webs are similarly compartmentalized in terms of number of modules. In both cases, the distribution of species topological roles showed that there is only one species responsible for linking modules and connecting the entire food web. However, such species have very different identity and trophic position in each ecosystem. In Potter Cove the connector is the black rockcod (*Notothenia coriiceps*), a demersal, generalist, omnivore and top predator fish (Barrera-Oro et al., 2019; Zamzow et al., 2011). For Beagle Channel it is the squat lobster (*Munida gregaria*), a generalist in terms of habitat and prey items

(Pérez-Barros et al., 2010; Romero et al., 2004; Vinuesa & Varisco, 2007). This species has been already proposed as a wasp-waist species (species with intermediate trophic level that has ecological importance by regulating the energy transfer between bottom and top trophic levels) for the Beagle Channel and adjacent areas (Riccialdelli et al., 2020). By feeding across many trophic levels and, in the squat lobster case, across pelagic and benthic habitats these species have a strong effect on food web connectivity, modularity and, therefore, stability. Any disturbance affecting these species could have catastrophic effects on the food web structure.

4.3. Climate change and anthropogenic activities impact on food web structure

The combination of climate change and the continuously growing human activities is proposed to have a homogenization effect between ecosystems (Blois et al., 2013; Clavel et al., 2011). In this scenario, it is expected that in the future the WAP will resemble today's sub-Antarctic region. One mechanism is by species shifting their distribution, pressured by changes in their environment, and invading new suitable habitats. Ecosystems with low connectance food webs (C~0.05), like Potter Cove and the Beagle Channel, are very vulnerable to invasions (Romanuk et al., 2009; Smith-Ramesh et al., 2017). The presence of exotic generalist species, many of which inhabit the Beagle Channel, was already reported for the WAP. One particularly worrying case is the recent discovery of sub-Antarctic king crabs (Lithodidae) on the continental slope of the Antarctic Peninsula (Thatje & Arntz, 2004). It is considered that the contemporary marine biota of Antarctica has been strongly shaped by the absence of durophagous (skeleton-crushing) predators for millions of years (Aronson et al., 2007). Viable populations of king crab generalist and durophagous predators (Gustavo Alejandro Lovrich & Vinuesa, 2016), would radically alter the structure of marine Antarctic food webs. It would increase connectance, since these species interact with multiple prey over space and time, while reducing food web compartmentalization (modularity) and, as a result, ecosystem resilience to perturbations (Stouffer & Bascompte, 2011). In the Beagle Channel, the invasion of the chinook salmon could change the entire ecosystem structure. This species by potentially preying on top predator fishes (Fernández et al., 2010) and the squat lobster (James & Unwin, 1996) could cause a rapid secondary extinction cascade (Donohue et al., 2017).

5. CONCLUSION

In a time of rapid anthropogenic and climate changes, that causes extensive ecosystem transformations, it is crucial to explore trophic interactions within food webs and understand their influence in ecosystem functioning. This study highlights the powerful tool network analysis applied to food webs are, since have allowed us to identify similarities and differences among two seemingly despair complex systems. Our results provide a baseline of information on the comparison food web structure and stability for Antarctic and sub-Antarctic ecosystems, that could be used as management tool to evaluate future modifications resulting from anthropogenic impacts and climate change.

The Beagle Channel food web can be summarized as more complex, but less locally stable and sensitive to the loss of its most connected and generalist species. However, the high degree of omnivores and its stronger modularity suggest plasticity to adapt to changes before collapsing. The results for Potter Cove suggest a less complex structure, while presenting higher probability to recover after a perturbation. Despite presenting different architecture, our result suggests that Antarctic and sub-Antarctic food web had evolved in a way that different structural characteristic can provide mechanisms to cope in the face of perturbations.

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7. Data Accessibility Statement

All source code and data supporting the results are publicly available on Github (https://github.com/123iamela/NetworkComplexity) and Zenodo.

8. TABLES

Table 1. List of network metrics analyzed, definitions, and relevant ecological implication related to food web structure and complexity.

Network metric	Definition and ecological meaning	Reference
Number of species	Number of trophic species (nodes) in a food web. Represent the species diversity and has implications for the persistence of the ecosystem.	May, 1973; Tilman, 1996
Number of interactions	Number of trophic interactions (links) in a food web. Represent the number of pathways along which matter and energy can flow.	Dunne et al., 2002
Connectance	Proportion of established interactions between species relative to the all possible ones. Estimator of food web robustness to perturbations and ecosystem stability. See Eq.1 in Supporting information.	Delmas et al., 2018; Dunne et al., 2002; May, 1973; Saint-Béat et al., 2015
Percentage of basal species	Proportion of nodes not feeding on any other species (e.g., primary producers, non-living nodes). Basal species impart the shape at the base of the food web.	Briand & Cohen, 1984
Percentage of top species	Proportion of species with no predators. Top predators can control ecosystem structure by top-down control through lower trophic levels.	Briand & Cohen, 1984; Frank et al., 2005

Percentage of intermediate species	Proportion of species with prey and predators. Intermediate species determine the connectivity between lower and upper trophic levels and positively correlate with omnivory.	Briand & Cohen, 1984
Mean trophic level	The trophic level (TL) of a species represents the number of links that separates it from the base of the food web and indicates the position the species occupies in the network. Mean TL of a food web shows how efficient the energy transfer from basal assemblage to top predators is and is related to stability. See Eq.2 in Supporting information.	Borrelli & Ginzburg, 2014; Thompson et al., 2007
Omnivory	Proportion of species that feed on resources on different trophic levels. It gives trophic flexibility to an ecosystem and has implications in the network stability depending on the interaction strength distribution.	Gellner & McCann, 2012; McCann & Hastings, 1997; Saint-Béat et al., 2015; Wootton, 2017

Table 2. Network metric values for Potter Cove and Beagle Channel food webs.

Network metric	**Potter Cove**	**Beagle Channel**
Number of species	110	145
Number of interactions	649	1115
Connectance	0.05	0.05
Basal species (%)	27	25
Top species (%)	6	8
Intermediate species (%)	67	67

9. FIGURES

9.1. Materials and methods

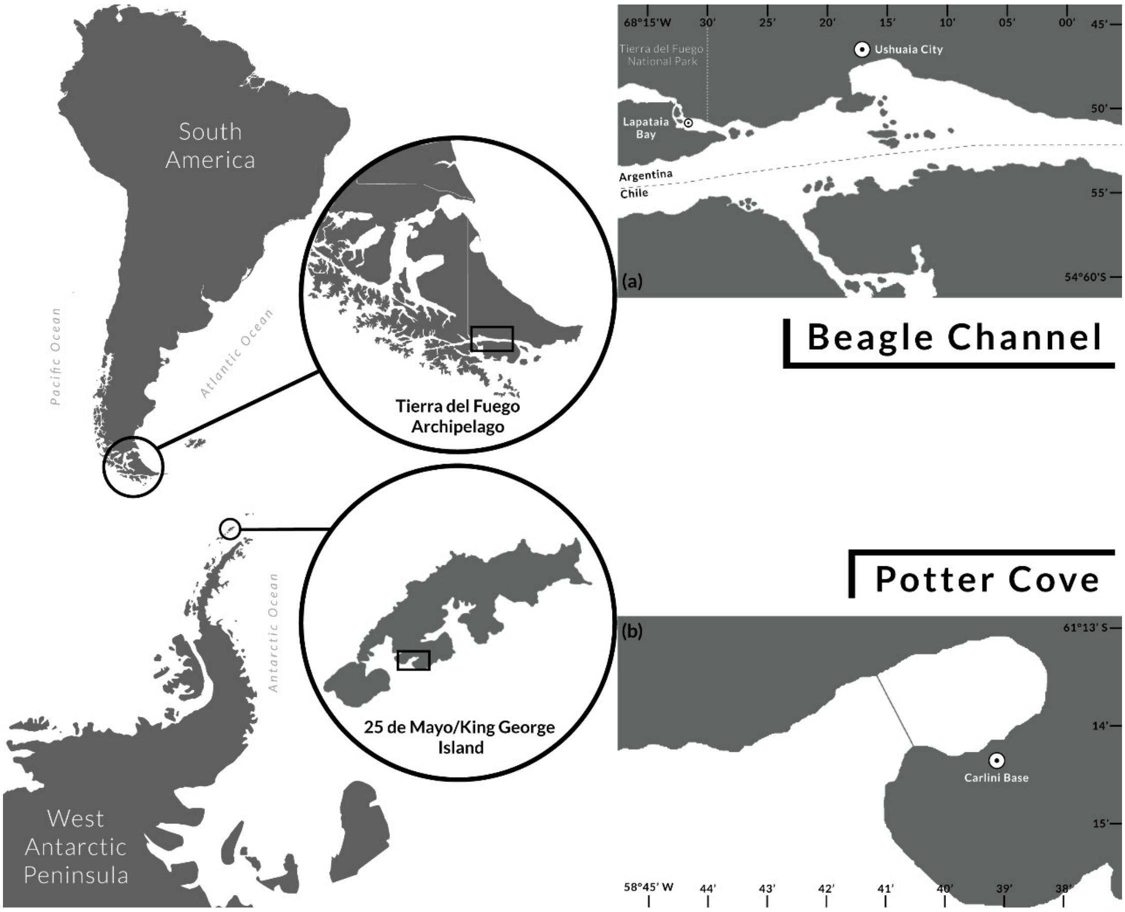

Figure 1. Map of **(a)** Beagle Channel at Tierra del Fuego Archipelago, South America and **(b)** Potter Cove at 25 de Mayo/King George Island, West Antarctic Peninsula.

9.2. Results

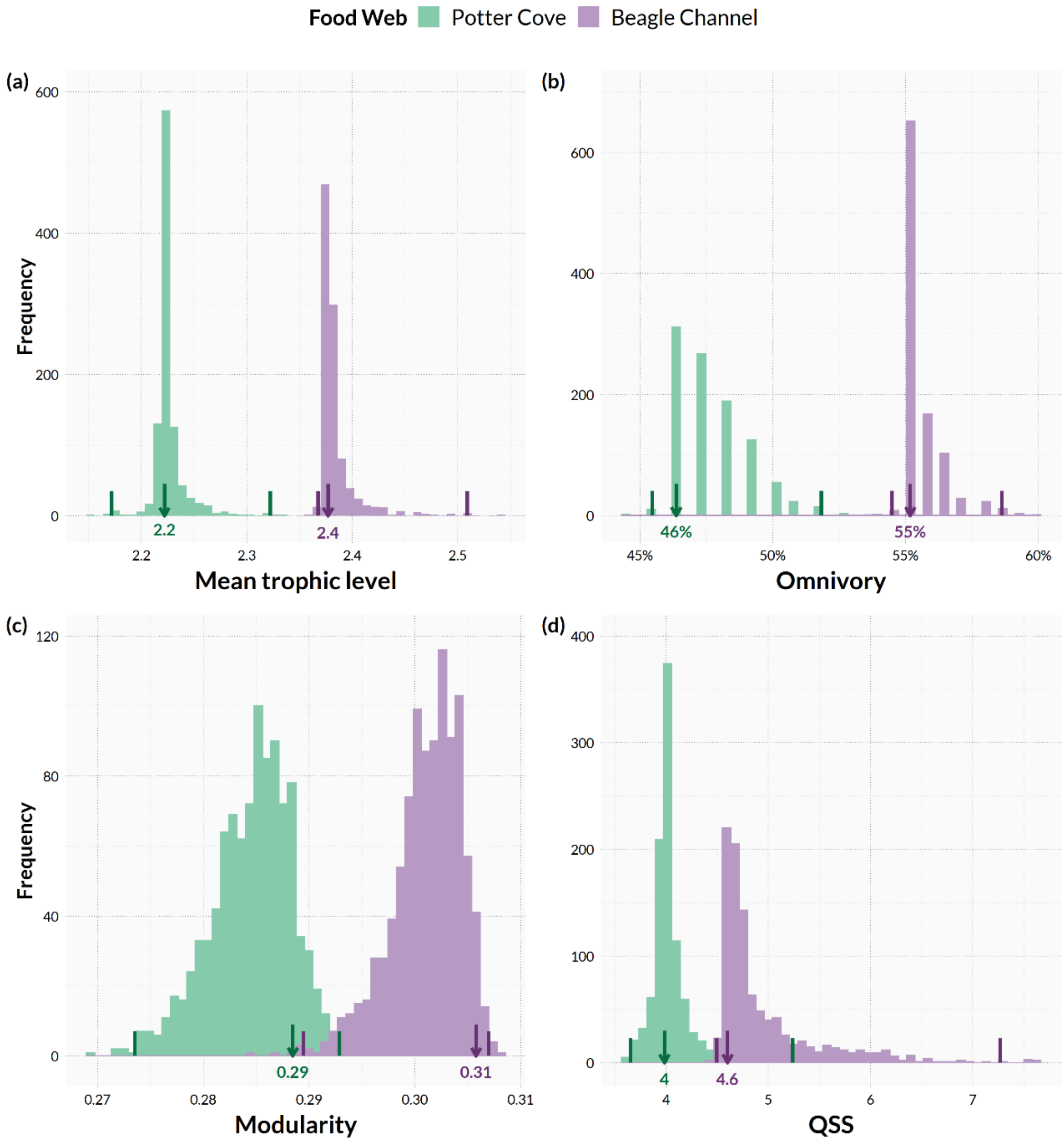

Figure 2. Null model of food web structure and stability. (a) Mean trophic level and **(b)** omnivory, **(c)** modularity and **(d)** QSS histograms of simulated networks performed for Potter Cove (green) and Beagle Channel (purple) food webs. Empirical metric values are represented by arrows and the value is shown below the arrow. Darker colored bars are randomizations' lower and upper 95% confidence intervals. We found statistical differences ($p<0.05$) between food webs in all the analyzed metrics.

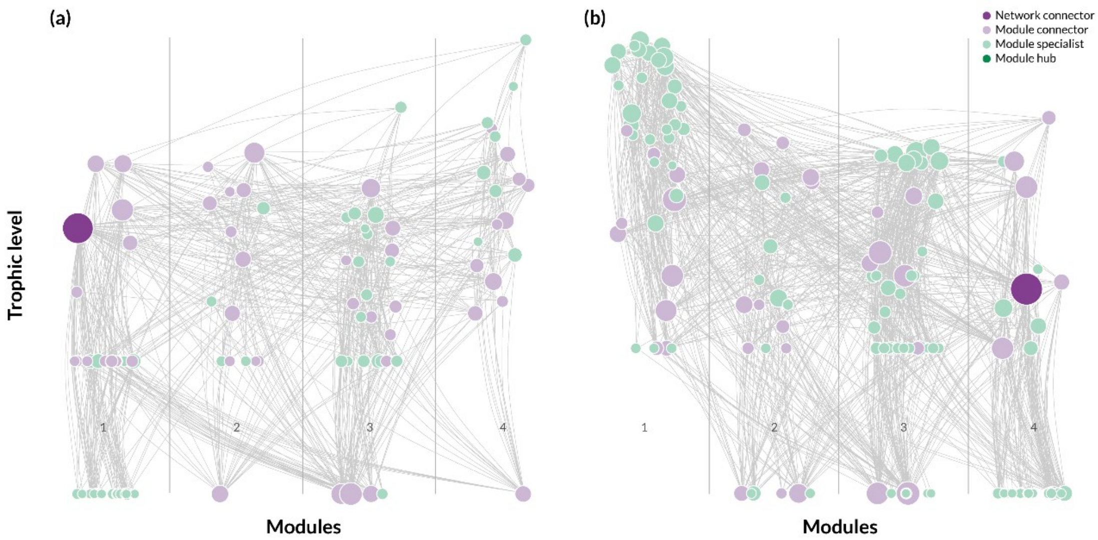

Figure 3. Food webs. Graphic representation of **(a)** Potter Cove and **(b)** Beagle Channel food webs. Each circle (node) represents a trophic species and the lines (links) represent feeding interactions between species. The vertical position of the nodes indicates the trophic position of a species and the horizontal position indicates the module affiliation of a species. The size of the nodes is proportional to the degree (number of links) of a species. The color of the node indicates species' topological role: dark purple=network connector (species with high connectivity between and within modules), light purple=module connector (species with few links mostly between modules), light green=module specialist (species with few links within its own module), dark green=module hub (species with high number of links mostly within its own module).

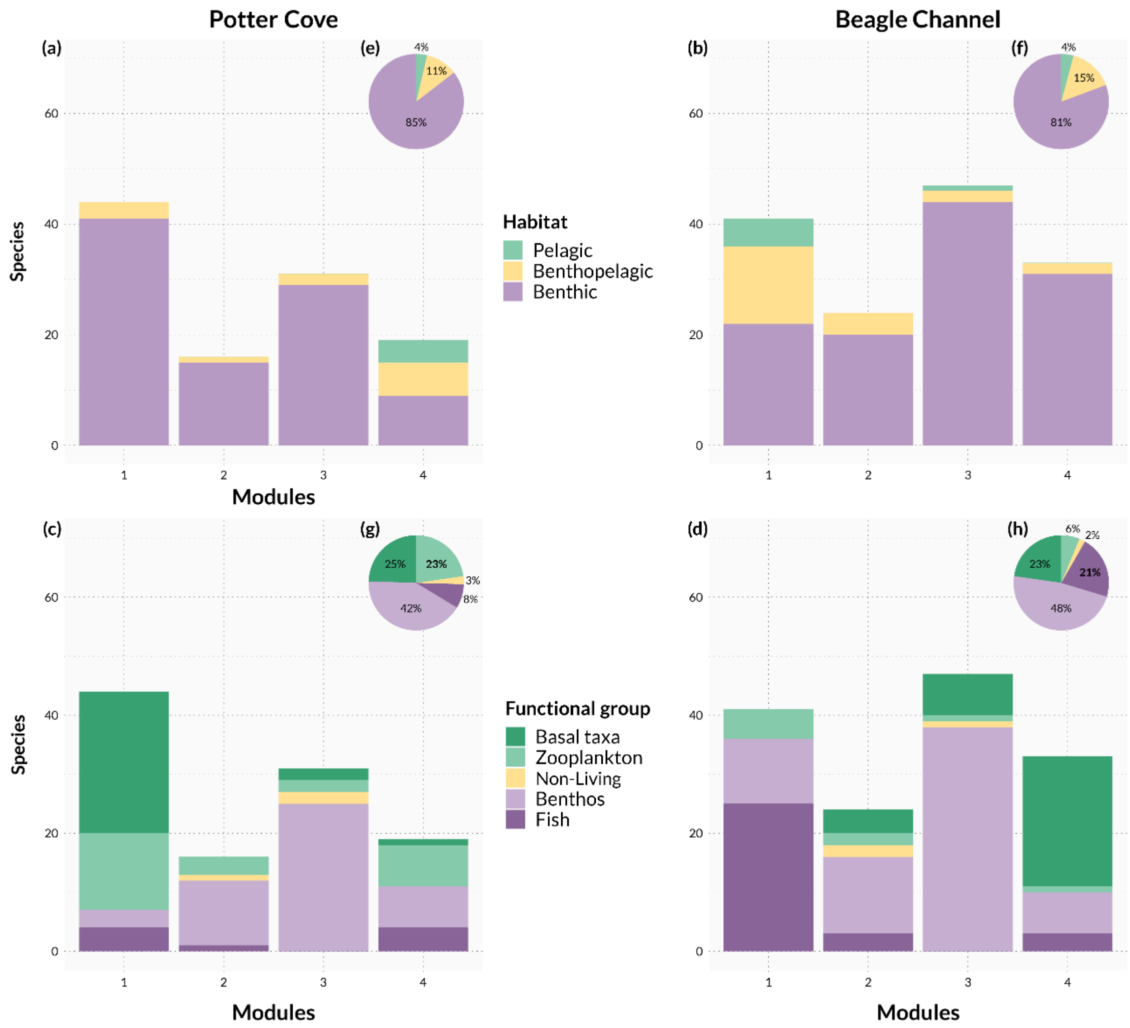

Figure 4. Food webs modules vs traits. Bar plot of the number of species within each module of **(a)** Potter Cove and **(b)** Beagle Channel colored by habitat: green=pelagic, yellow=benthopelagic, purple=benthic; significant differences were found between them (Potter Cove: Chi-squared = 34.43, p-value = <0.01. Beagle Channel: Chi-squared = 33.03, p-value = <0.01). Bar plots of **(c)** Potter Cove and **(d)** Beagle Channel food webs showing the frequency of species functional group affiliation: dark green=basal taxa, light green=zooplankton, yellow=non-living, light purple=benthos, dark purple=fish; significant differences were found between them (Potter Cove: Chi-squared = 76.53, p-value = <0.01. Beagle Channel: Chi-squared = 115.15, p-value = <0.01). Pie charts of species percentage within each type of habitat for **(e)** Potter Cove and **(f)** Beagle Channel; and functional groups for **(g)** Potter Cove and **(h)** Beagle Channel; significant differences were found only in the percentage of zooplankton and fish functional groups (Zooplankton: Chi-squared = 9.43, p-value = <0.01. Fish: Chi-squared = 5.89, p-value = 0.01).